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A SYSTEMATIC MONOGRAPH OF THE NEOTROPICAL JUNCACEAE

City University of New York

Ph.D. 1982

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A SYSTEMATIC MONOGRAPH OF THE
NEOTROPICAL JUNCACEAE

by

HENRIK BALSLEV

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York

1982

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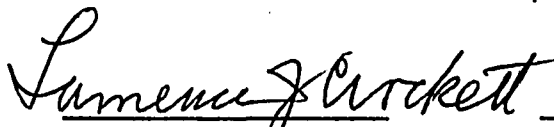
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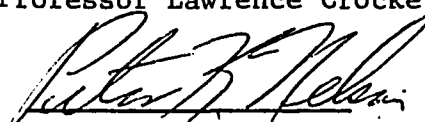
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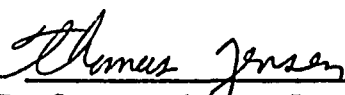

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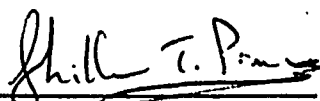
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ABSTRACT

A SYSTEMATIC MONOGRAPH OF THE NEOTROPICAL JUNCACEAE by HENRIK BALSLEV.

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York. 1982. Advisor: Dr. Tetsuo M. Koyama, The City University of New York and The New York Botanical Garden.

'A systematic monograph of the Neotropical Juncaceae' is a taxonomic treatment of the species of Juncaceae occurring in the neotropical region, which is the region of the Americas delimited by the tropics of Capricorn and Cancer. Juncaceae is a family of some 300 species of glumiflorous Monocotyledons, similar in general habit to grasses (Poaceae) and sedges (Cyperaceae), from which it is most easily distinguished by its floral morphology. The flowers are complete, trimerous and pentacyclic, i.e. with two whorls each of three $\pm$ equal tepals, two whorls each of three stamens, and one whorl of three carpels. The fruit is a dry capsule with 3-many seeds. The plants form densely compacted cushions, dense tussocks, or they are solitary, from a few centimeters to 2 meters high. Inflorescence characters are important for distinction of genera. Oxychloe, Distichia, Patosia and Rostkovia have 1-flowered inflorescences, but differ in number and structure of bracteoles and bracts. Juncus and Luzula have many-flowered inflorescences, but differ in ovule-number, leaf sheath and blade margin structure. Three subgenera of Luzula are based on inflorescence structure, and eleven subgenera of Juncus are based on leaf

blade anatomy and inflorescence structure. In the Neotropics six of the eight genera, and 49 of the ca. 300 species of the family occur. Rostkovia is subantarctic with two species, one of which occurs in Ecuador. Distichia is Andean with two species, both in the Neotropics. Patosia is monotypic in the southern Andes, and barely reaches the Neotropics in Bolivia. Oxychloe has six species in the southern Andes, one of which reaches southern Peru. Luzula is mainly temperate with ca. 75 species, eight of which reach the Neotropics. Juncus is likewise temperate, and includes ca. 225 species of which 36 reach the Neotropics. Ecologically neotropical Juncaceae are restricted to the highlands, and usually occur above 1000 meters altitude.

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Doctor Tetsuo M. Koyama of The New York Botanical Garden has functioned as my advisor during this study. I highly appreciate the help and advice he has given me. His open and unimposing way has given a freedom essential to independent thinking and pleasure in the work. His high standards and hard work have been a never-failing inspiration. Though carried out at The New York Botanical Garden (NYBG) and the Lehman College of the City University of New York (CUNY), the present work is a continuation of my studies at the Botanical Institute of the University of Aarhus, Denmark. My interest in botany was initiated there, and I wish to thank the staff of that institution for the stimulating working conditions they offered me. Dr. Kai Larsen's enlightening lectures on plant taxonomy turned my interest to botany. Mag. Scient. Lauritz Holm-Nielsen and Mag. Scient. Benjamin Øllgaard were my advisors and provided never-failing support and encouragement. My debt to them is beyond estimation. While in New York I have enjoyed the stimulating contact with a dynamic and ambitious staff at the NYBG and the Lehman College of CUNY. Dr. Ghilleen T. Prance, Vice President for Science at NYBG, has provided constant inspiration and encouragement in my work, and in addition he and his family, Anne, Rachel, and Sarah, have opened their home for me in the nicest thinkable way, providing a relaxing and refreshing refugium whenever I needed to escape the unpleasant climatic oscillations of the Bronx. Dr. Patricia Holmgren, Director of the Herbarium, has never failed in providing the best possible working conditions in the herbarium. Drs. James L. Luteyn, Scott Mori, Noel Holmgren and María Lebrón-Luteyn have given freely of

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TABLE OF CONTENTS

	page
Title page	o
Copyright page	i
Approval page	ii
Abstract	iii
Acknowledgements	v
Table of contents	ix
List of tables	x
List of illustrations	xi
 INTRODUCTION	 1
TAXONOMIC HISTORY OF NEOTROPICAL JUNCACEAE	6
MORPHOLOGY AND ANATOMY	9
1. Habit	9
2. Roots	10
3. Stem Rhizome	12
Culm	17
4. Leaves Rhizome scales	21
Cataphylls	21
Blade bearing leaves	22
Inflorescence bracts	30
Bracteoles	32
5. Inflorescence	34
6. Flowers Tepals	46
Stamens	46
Pistil	49
7. Pollen	50
8. Fruit	53
9. Seeds	55
 CYTOLOGY	 90
CHEMISTRY	99
POLLINATION	100
ECOLOGY	102
GEOGRAPHIC DISTRIBUTION	106
USES	111
SYSTEMATIC TREATMENT	112
NUMERICAL LIST OF TAXA	434
LIST OF EXSICCATAE	437
LITERATURE CITED	476
AUTOBIOGRAPHICAL STATEMENT	496

LIST OF TABLES

- TABLE I. Size of Pollen Grains and Tetrads in Juncaceae
- TABLE II. Diploid chromosome numbers in Juncus.
- TABLE III. Diploid chromosome numbers in Luzula.
- TABLE IV. The characters and features used by Lourteig (1968)
to distinguish Juncus stipulatus, J. chilensis and
J. scheuchzerioides.

LIST OF ILLUSTRATIONS

- FIGURE 1. Rhizome types in Juncus.
2. Leaf blade cross section in the subgenera of Juncus.
 3. The inflorescence of Distichia muscoides.
 4. Inflorescence types in Luzula, and a suggested phylogeny.
 5. Floral morphology of Juncaceae.
 6. SEM images of Juncus seeds (J. planifolius, J. tenuis)
 7. SEM images of Juncaceae seeds (Rostkovia magellanica, Oxychloe andina, and Distichia muscoides).
 8. SEM images of Luzula seeds (L. gigantea, L. denticulata, L. ecuadoriensis, L. excelsa, L. vulcanica, L. racemosa).
 9. SEM images of Juncus subg. Juncus seeds (J. roemerianus, J. maritimus , and J. acutus)
 10. SEM images of Juncus subg. Poiophylli seeds (J. tenuis var. dichotomus, J. uruguensis, and J. bufonius).
 11. SEM images of Juncus subg. Genuini seeds (J. procerus, J. effusus, and J. arcticus).
 12. SEM images of Juncus subg. Graminifolii seeds (J. planifolius, J. marginatus, and J. cyperoides).
 13. SEM images of Juncus subg. Septati seeds (J. microcephalus, J. pallescens, and J. ecuadoriensis).
 14. SEM images of Juncus subg. Septati seed (J. stipulatus).
 15. SEM images of Juncus subg. Septati and subg. Ensifolii seeds (J. liebmannii, J. ebracteatus, and J. ensifolius).

- FIGURE 16. Histogram of diploid chromosome numbers in Juncus.
17. Histogram of diploid chromosome numbers in Luzula.
 18. The altitudinal distribution of Juncaceae in Ecuador.
 19. Examples of north temperate and south temperate elements of Neotropical Juncaceae.
 20. Habit and detail of Distichia muscoides and Rostkovia magellanica.
 21. The distribution of Distichia.
 22. The distribution of Rostkovia magellanica and Patosia clandestina.
 23. Habit and details of Patosia clandestina.
 24. Habit and details of Oxychloe andina.
 25. The neotropical distribution of Oxychloe andina.
 26. The neotropical distribution of Luzula and L. denticulata.
 27. Habit of Luzula gigantea.
 28. The neotropical distribution of Luzula campestris.
 29. The neotropical distribution of Luzula gigantea and L. caricina.
 30. Habit of Luzula ecuadoriensis.
 31. The neotropical distribution of Luzula ecuadoriensis and L. excelsa.
 32. Habit and details of Luzula vulcanica.
 33. The neotropical distribution of Luzula racemosa and L. vulcanica.

FIGURE 34. Habit and detail of Luzula racemosa.

35. The neotropical distribution of Juncus and J. acutus.
36. The neotropical distribution of Juncus roemerianus and J. maritimus.
37. Habit of Juncus imbricatus, J. tenuis, J. capillaceus and J. bufonius, all of subg. Poiophylli.
38. The neotropical distribution of Juncus bufonius and J. tenuis var. tenuis.
39. The neotropical distribution of Juncus tenuis var. platycaulos and var. dichotomus.
40. The neotropical distribution of Juncus imbricatus and J. arequipensis.
41. The neotropical distribution of Juncus capillaceus and J. uruguensis.
42. Habit of Juncus effusus, J. procerus, and J. arcticus, all from subg. Genuini.
43. The neotropical distribution of Juncus effusus and J. aemulans.
44. The neotropical distribution of Juncus conglomeratus and J. procerus.
45. The neotropical distribution of Juncus arcticus var. mexicanus and var. montanus.
46. The neotropical distribution of Juncus arcticus var. andicola and J. ramboi subsp. colombianus.

- FIGURE 47. Habit and details of Juncus ramboi subsp. colombianus.
48. The neotropical distribution of Juncus marginatus and J. repens.
49. Habit of Juncus cyperoides.
50. The neotropical distribution of Juncus cyperoides and J. microcephalus.
51. Habit and details of Juncus pallescens and J. microcephalus.
52. The neotropical distribution of Juncus pallescens and J. acuminatus.
53. Habit and details of Juncus ecuadoriensis.
54. The neotropical distribution of Juncus ecuadoriensis and J. breviculmis.
55. The neotropical distribution of Juncus guadeloupensis and J. achalensis.
56. The neotropical distribution of Juncus debilis and J. stipulatus.
57. Habit and details of Juncus stipulatus.
58. The neotropical distribution of Juncus liebmannii.
59. Habit of Juncus liebmannii var. quitensis.
60. Habit and details of Juncus ebracteatus.
61. The neotropical distribution of Juncus ebracteatus and J. micranthus.
62. The neotropical distribution of Juncus nodosus and J. densiflorus.

FIGURE 63. Habit of Juncus densiflorus.

64. Habit and details of Juncus echinocephalus.

65. The neotropical distribution of Juncus echinocephalus
and J. ustulatus.

66. The neotropical distribution of Juncus xiphioides.

INTRODUCTION

The present work has been prepared as a contribution on Juncaceae for the FLORA NEOTROPICA monograph series. My interest in the neotropical flora arose while an assistant on the Third Danish Botanical Expedition to Ecuador in 1976. That expedition was led by Benjamin Øllgaard of the Botanical Institute of the University of Aarhus, and directed towards the study of the genus Lycopodium. For four and a half months we travelled in the Ecuadorean mountains collecting Lyco-podium, but also making many general collections (Øllgaard & Balslev, 1979). Upon returning to Denmark I became involved in the treatment of the collections, and after a few months I decided to abandon my work on East African plants then in progress. Thus involved in the Institute's program on the Ecuadorean flora it was natural for me to select a topic within that program as a thesis topic for my Cand. Scient. degree. The decision to make a treatment of Juncaceae for the FLORA OF ECUADOR, edited by the Swedish Drs. Harling and Sparre, was a natural one, but governed as much by practical considerations as by an interest in the problems involved in the study of this particular family. As a thesis topic, I had to select a relatively small group of plants to be able to finish the treatment within a limited time, and I had to select a group which needed treatment and would not conflict with other work for the Flora. Now that I have spent much of the last four years studying this plant family, I know that I could equally well have selected it for its own sake and for the problems it possesses.

My work on the Ecuadorean Juncaceae started in 1977, but I only finished my coursework at the Botanical Institute in January 1978. From then until August 1978 I worked full time on this work and finished it on the 21st of August. In the meantime Drs. Tetsuo M. Koyama and G. T. Prance of the New York Botanical Garden had been visiting professors at the Botanical Institute, and the possibilities of continuing my studies at NYBG had been discussed, an application for a Fellowship had been submitted, and granted. From the 2nd of September 1978 I thus continued my work on the Juncaceae at NYBG under guidance of Dr. Koyama, as a Graduate Fellow of the NYBG, and fulfilled other requirements towards a Ph. D. degree at the City University of New York.

The work on monographing the neotropical Juncaceae has had some problems which I believe are peculiar to this group, and others which are of a more general nature. One problem takes its origin in the fact that Juncaceae is a mainly temperate family which, for a large part, has migrated into the neotropical region. Many of the taxonomical problems involved in the study of neotropical Juncaceae thus lie outside the region under study. It has been a constant part of study deciding how far to penetrate into problems outside the neotropical region to solve the taxonomy of populations within the region. As an example I can mention Juncus marginatus. This is a common species in most of United States, penetrating with a few populations into Central America, to Venezuela with one known population, and again becoming common in temperate South America, south of the tropical region. There is considerable confusion as to whether it really is one species, three species, or two species one of which has two

varieties. To solve this problem 21 names of specific and varietal rank are involved. Of these, 14 are based on different types, and seven are nomenclatural synonyms. Only one of the types is from the neotropical region, one is from temperate South America, and the remaining are from the United States. The North American Juncaceae have not been monographed or revised since Engelmann (1866/1868), except for regional and floristic works. That means that a considerable amount of work is necessary to consult the older literature on North American Juncaceae, and to localize the types, many of which are not cited in the protologue, etc. The next problem would be to decide which of the contrasting hypotheses about the taxonomy of the North American populations is the best, but the herbaria contain literally thousands of specimens of this common species or group. It turns out that it would be a thesis topic of its own to solve the problems of Juncus marginatus in North America, and to be able to properly classify the neotropical populations. This type of problem has been constant during the entire study, and it has been necessary to decide where to stop in many such cases.

Another problem in the study of the neotropical Juncaceae has been the lack of recent work on the group. This is of course a pleasing type of problem since it forces the researcher to penetrate to very profound levels in the history of research on the group under study. All work on neotropical Juncaceae antedates modern nomenclature. Buchenau, the great monographer of Juncaceae, applied names of his taste rather than the oldest name of a given taxon. He discarded the name Juncus ebracteatus because the species it belongs

to does have bracts. Instead he called it Juncus trinervis which is a later name that nicely describes the three nerved tepals of the species. If there was any confusion about a name he would discard it rather than solve the problem. Juncus effusus and J. conglomeratus were mixed in Linnaeus' herbarium, even if described by himself. To avoid this problem Buchenau applied the later name J. leersii to J. conglomeratus. Only recently has the name J. conglomeratus been reinstated properly through the selection of a lectotype. I do not say this to blame Buchenau. He did not have the modern rules of botanical nomenclature, and did not use such techniques as selecting a lectotype to conserve a commonly used name. Buchenau's work on tropical American Juncaceae was published in 1879 and 1886, and appeared basically unchanged in his later monographs (1890, 1906). All later floristic and regional work on neotropical Juncaceae has by and large copied Buchenau's work, and no one has studied types and original descriptions. A large part of the present work has therefore gone into the study of the old literature with the original descriptions, and to locate type specimens of many of these old names. Still much work remains to be done on the typification of the old Juncaceae names. This is especially true for the North American and European Juncaceae, which are so important for the understanding of the neotropical ones.

Much of the present work is based on the examination of herbarium specimens, and it is fortunate that Juncaceae lend themselves so well to this method of study. Practically all specimens are complete with roots, rhizome, culms, leaves, and inflorescences, and the specimens do not become distorted by pressing and drying procedures. To study

the morphology of the species one has a perfect sample in a herbarium specimen. The herbarium method has its obvious limitations for extraction of such information as the ecology of the species etc. In addition to examination of herbarium material I have had the opportunity to study the species in the field on three occasions. My first encounter was during the above mentioned expedition to Ecuador in 1976, when I spent four and a half months in the field collecting mostly Lycopodium, but often with the chance of getting acquainted with other plants. In the spring of 1980 I spent one month in Ecuador and Colombia, when I had the opportunity to make many collections of Juncaceae and study the species in their natural habitats. From November 1980 to February 1981 I travelled in Ecuador, Peru and Bolivia studying and collecting Juncaceae. During that time I encountered Juncaceae on 200 different occasions. In total I have been able to collect all six genera of Juncaceae occurring in the neotropical region, and 25 of the 49 species treated in this work. On these travels I have also collected material for anatomical and cytological work, but this part of the study has not been completed at this point. Some observations on the leaf blade cross section of Juncus are included. Quite some time has been spent studying the sculpturing of the outer seed coat of most of the species of neotropical Juncaceae by SEM.

TAXONOMIC HISTORY OF NEOTROPICAL JUNCACEAE

Juncaceae is a mainly temperate family of which the neotropical species do not constitute one or a few taxonomically circumscribed groups within the family. Instead most have their closest relatives in the temperate regions. Our knowledge of neotropical Juncaceae has therefore developed mainly as a sideline to our knowledge of temperate members of the family, and much of the taxonomic history of neotropical Juncaceae is extracted from the history of temperate Juncaceae. Many of the species occurring in the tropical regions were first described from temperate areas. Some of these were described as new when discovered in the tropics, and only later put into synonymy with the appropriate temperate species.

Linnaeus (1753) did not have any neotropical material of Juncaceae at his disposal for Species Plantarum, but nevertheless six of the 15 species treated therein are now known to occur in the neotropical region. The first South American collection of Juncaceae to be mentioned in the literature is a plant collected by Forster at the Magellan Strait during Captain Cook's circumnavigation (1770). This collection was described by Linnaeus filius (1781) as Juncus grandiflorus but is now known as Marsippospermum grandiflorum (Linnaeus f.) J. D. Hooker. It does not, however, reach the neotropical region. The next collections to be reported from South America were those of Dombey from Peru (1777-1788) and Commerson from Monte Video, Buenos Aires and the Magellan Strait (1766-1769). These were described by Lamarck (1789). After that an increasing number of species were described, reported on,

synonymized, etc. in monographs and other treatments of Juncaceae. The detailed history of the description and classification of South American Juncaceae up until 1879 was given by Buchenau (1879), who cited Rostkovius (1801), Desvaux (1808, 1809), Humboldt, Bonpland & Kunth (1816), Meyer (1822, 1823, 1827, 1828, 1849), Gaudichaud (1824), Laharpe (1825, 1827), d'Urville (1826), Bentham (1839), Hooker & Walker Arnott (1841), Kunth (1841), Nees & Meyen (1843), Hooker (1844-1847), Seubert (1847), Hooker (1848), Gay (1854), Steudel (1855), Philippi (1857, 1860, 1864), Buchenau (1874), and Grisebach (1874, 1879).

Buchenau's critical treatment (1879) summarized all the knowledge available on South American Juncaceae at the time. It was, however, based on few collections from the tropical parts of South America, whereas he had much richer material from temperate South America. The Méxican and Central American Juncaceae were treated by Buchenau (1886), and in a historical survey he included mostly references already mentioned above for South America. Two important additional works are Liebmann's account on the Méxican Juncaceae (1850), in which many new names were proposed, and Buchenau's critical comments on Liebmann's work (Buchenau, 1873). The next important contribution to our knowledge of neotropical Juncaceae is Buchenau's worldwide monograph of Juncaceae (Buchenau, 1890). Only one new species of neotropical Juncaceae was described in that work, but many names were synonymized, or 'species' were assigned varietal rank. Important was the establishment of the genus Patosia. The Antillean Juncaceae were summarized by Buchenau in Urban (1900), who described the new species Juncus guadeloupensis, endemic to the island Guadeloupe. In 1906

Buchenau published his final monograph on Juncaceae in Engler's Pflanzenreich series. This is a finely polished summary of his more than 40 years of work on the family. The neotropical Juncaceae were treated with one new variety and a few realignments relative to his 1890 monograph. Since Buchenau's monograph (1906), the neotropical Juncaceae have been treated only in local checklists and floras, such as Consatti (1940) for México, Standley & Steyermark (1952) for Guatemala, Standley (1937) for Costa Rica, Woodson & Schery (1945) for Panamá, Howard (1979) for the Lesser Antilles, Fournet (1978) for Guadeloupe and Martinique, Balslev (1979) for Ecuador, and Macbride (1931) for Peru. Most of these works are extracts from Buchenau's work, some of them uncritical. The subtropical and temperate South American Juncaceae were treated by Barros (1953, 1962). Many new species, varieties and forms were suggested in those works. Since many species are shared between temperate and tropical South America it has been necessary to consult Barros' treatments quite carefully. Unfortunately, his studies did not include the examination of type material, and I am unable to accept most of his circumscriptions of taxa.

In summary, most neotropical Juncaceae described before 1879 appeared in scattered publications. The South American species of Juncaceae were summarized by Buchenau (1879), the Mexican and Central American ones by Buchenau (1886), and the Antillean ones by Buchenau in Urban (1900). The entire family was monographed twice by Buchenau (1890, 1906). Since then several treatments have appeared in local floras. The temperate South American species were treated by Barros in 1953 and 1962.

MORPHOLOGY AND ANATOMY

1. Habit

Neotropical Juncaceae are all herbs. Distichia, Patosia and Oxychloe are cushion forming. Distichia muscoides has forking shoots with densely inserted, distichously arranged leaves. The shoots are arranged in a dense manner so the entire colony attains a flat or bulging appearance. The cushion may be as little as 15 cm or as much as several meters across, depending on its age. The surface of the cushion is very hard due to the sclerified leaves and dense arrangement of the shoots. Usually few or no other plants gain foothold in the cushion. Distichia filamentosa forms much looser cushions and is often intermixed with other plants. Patosia clandestina forms very dense cushions that may occupy areas even larger than those of Distichia and form gently undulating mats. Oxychloe andina forms loose cushions, and is often intermixed with other plants. The sharply pointed, prickly leaf apices make it an unpleasant acquaintance to the collector. Juncus, Luzula and Rostkovia are usually erect caespitose or solitary herbs ranging from a few centimeters to about two meters high. Some, such as Juncus stipulatus, may form mats on newly deposited sand layers, and others may occasionally be procumbent, such as J. bufonius. The strongly developed rhizome of some Juncus species is characteristic.

2. Roots

The roots of Juncaceae emerge as adventitious roots along the rhizome, or, in the cushion forming genera Oxychloe, Patosia and Distichia, along the ascending stems, penetrating the dense cover of leaf sheaths. They are 0.2-3 mm in diameter and equally thick along their lengths. When fresh they are white, but turn yellow to brown with age because of damage and suberization of the outer cell layers. Immediately behind the root cap there is a root hair zone. In some species, and according to Buchenau (1906) under certain ecological conditions such as sandy soil, the root hairs will persist as a wooly cover, a condition sometimes remarked upon in species descriptions as 'radices velutinae.' The cross section of the root shows the typical division into a central core surrounded by an endodermis, and around this a cortex enclosed by an epidermis.

The central core may have one or several vessels depending on its thickness. In thick roots with many vessels the phloem is arranged in a somewhat orderly fashion in groups corresponding to the vessels. The central vessel may be surrounded by cells with thickened walls, and as the root grows older more and more of the cells in the central core become sclerified.

The endodermis is a one-cell-layer thick cylinder enclosing the central core. The cells are densely and very regularly arranged. In cross section the cells of the endodermis are easily recognized by their U-shaped wall thickenings; that is, the inner and the anticlinal walls are secondarily thickened, but the outer wall remains thin.

The cortex may have a few layers of sclerified cells adjacent to

the endodermis but is otherwise composed of several layers of parenchyma cells. The cells of the middle part of the cortex are radially arranged. In some species, e.g. many Juncus, radial and longitudinal clefs develop, so the cortex changes into a system of radially arranged lamellae. These lamellae are first several cell layers thick. By continued division they finally become one layered. The cytoplasm of the lamella cells then dies, and the lamellae turn into papery cellulose sheets. Ultimately they disintegrate, and the central core then lies as a thread inside a tube consisting of the outer cortex cylinder and the epidermis.

The epidermis consists of one layer of cells which are slightly longer radially than tangentially, as seen in cross section. The epidermal cells are arranged in longitudinal rows. From the normal epidermal cells smaller ones are cut off in such a fashion that alternate longitudinal rows of large and small cells result. The small cells give rise to root hairs, which may become as long as the diameter of the root.

The development of the cortex into lamellae in some species and not in others led Buchenau (1890) to suggest two types of roots in Juncaceae, the 'Luzula-type' without lamellae, and the 'Juncus-type' with lamellae. The ecological significance of the lamellae is obvious. The air spaces between them permit transportation of air into the root system. This is important for such plants as Juncus which usually grows in swampy habitats, whereas Luzula without lamellae is usually found in drier habitats.

3. Stem

The stem of Juncaceae exhibits various degrees of specialization as adaptation to different ecological conditions. In the cushion forming genera Distichia, Oxychloe, and Patosia the stems branch regularly. The sidebranches are about as thick as the main branch and ascend. The shoot attains the appearance of a bifurcating system, dying back at the base, and continuing growth at the top. The internodes are shortened to one or a few millimeters, and the leaves are therefore densely inserted. The leaf sheaths overlap and surround one another, so the stem is not visible. In Rostkovia there is a differentiation of the stem into an underground ascending part and an above-ground erect part. The underground part is not as specialized as in Juncus (see below), but the above-ground part is similar to the culm in that genus. In Luzula the basal part of the stem is usually found in the loose layer of litter on the ground and is not truly subterranean. It is usually ascending, terminates in a leaf rosette, and continues into an erect part terminated by the inflorescence. The part below the leaf rosette is here called the 'rhizome' even if not always subterranean. The inflorescence bearing part is called the 'culm'. In Juncus there usually is a clear differentiation between a part of the stem adapted to grow below the ground and another part of the stem to grow above the ground. The part below the ground (the rhizome) is long-lived, and the part above the ground (the culm) is ephemeral.

Rhizome.

The part of the stem which is adapted to grow below the ground is

the rhizome. Its stem nature is revealed by the presence of foliar structures. These are the rhizome scales, which are described in more detail under 'leaves'. The rhizome is long-lived, dies back basally, and perpetuates itself, in principle indefinitely, apically. Several different types are encountered, and the appearance of the rhizome is usually quite characteristic for a given species. The types are not sharply distinct, but different enough to be separated into five categories:

1. Branching-ascending rhizomes (Fig. 1 A,B) have loose branching and the internodes are conspicuous. At each node there is a scale, and some adventitious roots usually emerge. At most nodes, but not all, side branches emerge, and the side shoot ascends to the surface of the ground, where it produces a leaf rosette. This type of rhizome is found in Juncus stipulatus and J. cyperoides, and seems to represent an adaptation to unstable soil conditions. At lake shores and riverbanks I have seen series of leaf rosettes of J. stipulatus corresponding to consecutive layers of sand deposits. The branching-ascending type is often combined with stoloniferous rhizomes.

2. Stoloniferous rhizomes (Fig. 1F) are horizontally creeping with long internodes, usually without conspicuous scales. At each node a vertical branch is produced which gives rise to a leaf rosette and a culm. Sometimes a branching-ascending rhizome is produced from the stolon. Among the neotropical species stoloniferous rhizomes are found in Juncus ebracteatus and J. nodosus. In combination with branching-ascending rhizomes it is also found in J. stipulatus and J. cyperoides, though rarely preserved in herbarium specimens. In

FIGURE 1

Rhizome types in Juncus.

- 1A. Branching-ascending rhizome of J. stipulatus.
- 1B. Stoloniferous combined with branching-ascending rhizome of same.
- 1C. Densely branching rhizome of J. microcephalus.
- 1D. Short creeping rhizome of J. effusus.
- 1E. Long creeping rhizome of J. arcticus.
- 1F. Stoloniferous rhizome of J. ebracteatus.

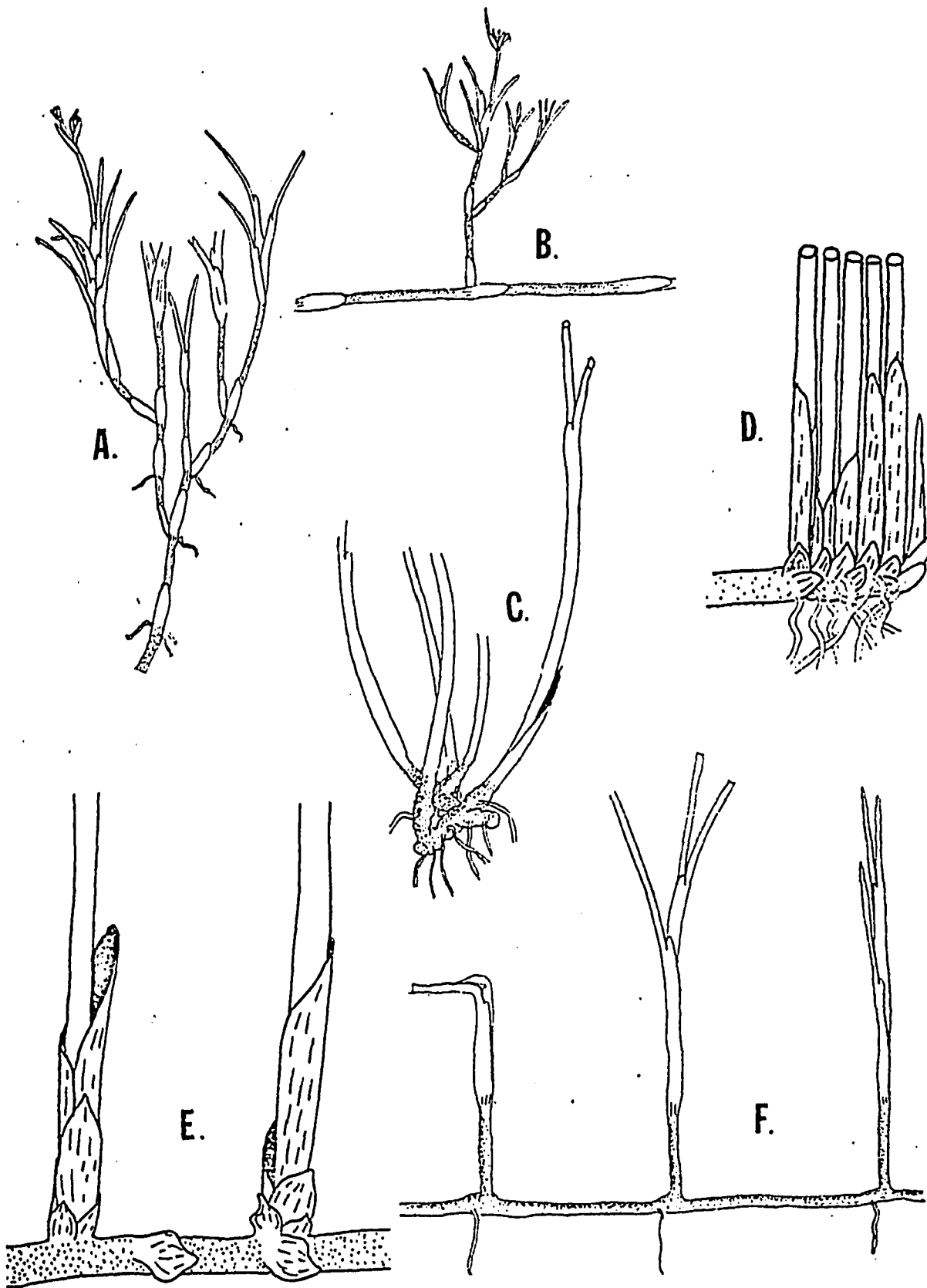


FIGURE 1

J. nodosus the nodes from which the vertical branches originate are thickened to form little bulbs. The only difference between stoloniferous and long-creeping rhizomes (see below) is the relative internode length. Stoloniferous rhizomes usually have internodes which are more than 6-7 times as long as the rhizome diameter.

3. Densely branching rhizomes (Fig. 1 C) show an irregular branching with short internodes. Scales are usually inconspicuous. There seems to be no pattern of the branching. Parts of the rhizome may creep horizontally and give rise to a row of culms, but this is not a regular feature. The culms arise in more or less dense tufts. This type of rhizome is common and occurs in most subgenera of Juncus.

4. Short creeping rhizomes (Fig. 1 D) creep horizontally and the culms arise in dense rows from the upper side of the rhizome. The internodes are so short as to be indistinguishable. Short-creeping rhizomes branch in the horizontal plane. Densely inserted scales cover the surface and sometimes split to form a filamentous layer. Due to the branching of the rhizome in the horizontal plane, the entire plant appears densely caespitose. The linear arrangement of the culms does not appear until the plant is broken up. This type of rhizome is characteristic of many species in Juncus subg. Genuini, e.g. Juncus effusus, but is also found in subg. Poiophylli, e.g. in J. imbricatus.

5. Long-creeping rhizomes (Fig. 1 E) are different from short-creeping ones only in having distinct internodes, which may be as much as five times as long as the diameter of the rhizome. There is no sharp boundary between the two types, and employing different terms serves only to describe different relative internode lengths. Species with

long-creeping rhizomes tend to form loose stands which may occupy considerable areas, instead of growing in dense tufts. The long-creeping rhizomes branch in the horizontal plane. Scales are always obvious and may be hard and thickened or thin and membranaceous.

The cross section of the rhizome is strikingly similar to that of the root. There is a central core with vascular bundles scattered in a parenchyma tissue. Surrounding the central core is a one-cell layer thick cylinder of cells with thickened inner and anticlinal walls. This is called the 'endodermoid layer' (Cutler, 1969), and is similar to the endodermis of the root. Surrounding the endodermoid layer is the cortex, which has three more or less well defined zones. The inner zone consists of 1-3 layers of narrow, rounded parenchyma cells. The middle zone consists of radial cell plates, which separate longitudinal air channels. The cell plates are 1-5 cell layers thick, and have on their sides the remains of cells which disintegrated to create the air channels. In some species from drier habitats the air channels are lacking, and are replaced by a continuous parenchyma tissue. The outer zone of the cortex is parenchymatous and 1-10 cell layers thick. Surrounding the cortex is a one-cell layer thick epidermis.

Culm.

The above-ground part of the stem is the culm. The culm is short lived and functions to expose the leaves to the light and the inflorescence for pollination and seed dispersal. Leaves may be inserted in basal rosettes, along the culm, or both. The inflorescence is terminal on the culm. The culms are usually erect or ascending, but sometimes procumbent. They may be a few centimeters high or they may reach two

meters, varying in diameter from less than a millimeter to about a centimeter. The diameter is usually slightly smaller apically, but some species have culms that are evenly thick from base to top. They are terete, or in Juncus xiphioides, laterally compressed. The surface is smooth, longitudinally striate or with longitudinal ridges. The external appearance depends on the presence or absence of sclerenchyma strands below the epidermis and the size of these strands. In cross section four zones can be recognized. In the center is the pith (1), which is surrounded by the vascular cylinder (2). The vascular cylinder is surrounded by the cortex (3), and externally is the epidermis (4). Each of these four zones show variation, some of which are taxonomically significant, and some of which are ecologically dependent.

The pith may be parenchymatous with scattered vascular bundles, as seen in Juncus maritimus and J. acutus, or it may be parenchymatous without vascular bundles as seen in J. ramboi. In Luzula, Oxychloe, and Rostkovia there is a breakdown of the central pith parenchyma to form an open space. In Juncus the pith is aerenchymatous with star-shaped cells in many species. The star-shaped cells vary from rather thick ones with short arms, as seen in J. arcticus, to thinner ones with long arms, as seen in J. effusus. In some species there is a further specialization, and only spindle-like threads remain, and the culm is tube-like. In this latter case the hollow pith may be interrupted by septa, in the same way as in the leaf blades of subg. Septati.

The vascular cylinder is only an actual cylinder in its specialized stage. In some species, such as Juncus acutus, the vascular bundles are scattered throughout the cross section. In J. arcticus

the vascular bundles are arranged in several concentric rings. Within one ring the bundles are of the same size, but the inner rings generally have larger bundles than the outer ones. The vascular bundles are usually associated with considerable amounts of sclerenchyma. The sclerenchyma of adjacent bundles may connect laterally, and the bundles are then embedded in a sclerenchyma cylinder surrounding the pith. In Distichia sclerenchyma may fill up the central part of the stem, so there is a vascular core rather than a vascular cylinder (see Cutler, 1969, Fig. 1. D).

The cortex is occupied by chlorenchyma, parenchyma, air channels and sclerenchyma in varying proportions. The chlorenchyma is usually present as a 1-10-cell-layer thick palisade tissue below the epidermis. In Rostkovia the cells are irregularly lobed in cross section and longer than wide in longitudinal section (Cutler, 1969). The chlorenchyma may have areas of wide, thin-walled cells, which degrade to air channels. Parenchyma is usually found towards the vascular cylinder, and fills up the spaces between the vascular bundles. The boundary between chlorenchyma and parenchyma may be quite sharp. Air channels are found in the chlorenchyma of many species, e.g., Distichia muscoides, Juncus arcticus and Rostkovia magellanica. Sclerenchyma is found as longitudinal strands in the cortex, especially in the subgenera Juncus, Genuini and Poiophylli of Juncus. In subg. Juncus the sclerenchyma strands are almost triangular in cross section and are found just below the epidermis. They almost cover the inner surface of the epidermis, and their prominence contributes to the very stiff and hard appearance of the species of that subgenus. In subg. Poiophylli sclerenchyma strands may or may not

be present. Species with sclerenchyma strands, such as Juncus imbricatus and J. capillaceus have externally ridged culms, whereas species without strands have smooth culms. In Juncus subg. Genuini the presence or absence of sclerenchyma strands divides the species into the two informal groups 'Junci genuini valleculati' and 'Junci genuini laeves' (Buchenau, 1906). Among the neotropical species of subg. Genuini only J. arcticus has no subepidermal sclerenchyma strands. The remaining species have various numbers of strands. The two closely related species J. effusus and J. conglomeratus are distinguished by this character, as discussed in the systematic treatment.

The epidermis cells are 4-6 sided and 4-5(-10) times as long as wide in surface view. The stomata are paracytic with the long axis parallel to that of the culm, sometimes confined to longitudinal rows, which may be somewhat sunken in grooves. In cross section the epidermis is one cell layer thick. The cells vary from slightly wider than high (1+ x 1) to conspicuously higher than wide (1 x 3). The outer and anticlinal walls are usually thickened.

4. Leaves

The leaves of Juncaceae vary depending on their position on the plant, and also from one taxon to another. Five leaf types may be recognized: Rhizome scales, Cataphylls, Blade bearing leaves, Inflorescence bracts, and Bracteoles. Taxonomically important variation is discussed under these five types.

Rhizome scales.

The rhizomes of Juncus have small scale-like leaves. These are a few millimeters long, or up to about a centimeter. Their texture varies from thin and membranaceous to thickened and sclerified. Their outline may simply be a half circle, they may widen a bit from the base and then taper abruptly to a point as in J. arcticus, or they may be elongate and completely sheath the rhizome as in J. stipulatus. Many species, especially those with densely branching rhizomes, have inconspicuous scales that wear off.

Cataphylls.

Leaves inserted basally on the culms often have the blade reduced to a minute, needle-like appendage, inserted apically on an otherwise normally developed sheath. Such leaves are called 'cataphylls' (Buchenaу, 1875, 1890, 1906). Cataphylls may be small (to 1 cm long), membranaceous, and then inconspicuous; or larger (to 25 cm long), somewhat sclerified, strongly pigmented, and very conspicuous. They may be absent, or they may be the only leaves present apart from the rhizome scales. Cataphylls are found in Rostkovia magellanica and in several species of Juncus. In the latter genus they are characteristic

of subg. Genuini, which has no blade-bearing leaves. They are common in subg. Poiophylli in combination with blade bearing leaves. In subg. Septati they sometimes occur and are characteristic of the J. densiflorus group. In German cataphylls are known as 'niederblätter', and in English they have often been called 'basal sheaths'.

Blade bearing leaves.

In the small cushion-forming genera Oxychloe, Patosia and Distichia blade bearing leaves are densely inserted along the entire stem. The sheaths are often longer than the blades, and clasp one another so the stem is completely covered. The margins of the sheaths terminate in two rounded auricles. The blade is linear with an adaxial groove in Oxychloe and Patosia, conical and round in cross section in Distichia. The blade-bearing leaves of Rostkovia magellanica have well distinguished sheaths that terminate in two rounded auricles. The blade is linear, with a wide adaxial groove and a narrow abaxial groove along the midrib. A unique feature of this genus is the arrangement of the stomata, which are concentrated in two bands, one on each side of the abaxial groove. These bands, barely visible to the naked eye but easily visible with a hand lens, often reveal themselves by a different coloration. In Luzula the blade-bearing leaves are peculiar in having closed sheaths and hairy margins. These features are not found in the other genera of Juncaceae and distinguish Luzula very sharply. The sheaths are short (less than 1 cm) on the rosette leaves, but up to 7 cm long on the cauline leaves. There are no auricles at the junction of the sheath and the blade. The blades are linear, but in some cases so short that they are almost lanceolate. The cross section of the blade is flat, usually without bifacial differentiation.

High altitude forms of Luzula racemosa sometimes have somewhat thickened and adaxially grooved blades. The apex is acute, or, in Luzula campestris and L. caricina, terminated by a somewhat obtuse callosity.

In Juncus, the sheaths are tightly adpressed to the culm, the two margins overlap but never fuse. The margins are gradually membranaceous, that is, their thickness is reduced gradually towards the edge, or they are distinctly membranaceous, that is, with a thin rim clearly set off from the chlorophyllous main part of the sheath. In either case they terminate in two auricles where the sheath joins the blade. The shape and texture of the auricles characterize some species, especially in subg. Poiophylli. The blade is linear in all species, but the cross section varies. Subgeneric divisions of Juncus are based mostly on the leaf blade cross section (Fig. 2).

Subg. Juncus has round or oval blade cross sections with slight ridges. The interior is filled with parenchyma of rounded cells. Sclerenchyma strands are found just below the epidermis and scattered in the interior. The subepidermal sclerenchyma strands are triangular in cross section and separated from one another only by the width of the stomata. Interior sclerenchyma strands are surrounded by parenchyma sheaths. Vascular bundles are scattered through the cross section or arranged in concentric circles, but there is no central aerenchyma.

In subg. Poiophylli there is a variation (or phylogenetic trend) ranging from bifacial blades, over gradual reduction of the adaxial side, to terete unifacial blades. The adaxial side, when present, has an epidermis of large hyaline, transparent cells called 'bulliform cells' (Duval-Jouve, 1871). The abaxial side, in contrast, has small-celled epi-

dermis that appears green. The blades of Poiophylli therefore have obvious externally visible bifacial differentiation. (This distinguishes it from subg. Graminifolii, which also has flat leaves, but without externally visible bifacial differentiation). Juncus bufonius and J. tenuis var. tenuis have flat or slightly concave leaves, the thickness of which is approximately the same over the whole cross section. Bulliform cells constitute one layer only, and occupy most of the adaxially visible surface of the blade. Juncus bufonius lacks or has only small sclerenchyma strands along the margins (which is defined as the transition line between the small celled epidermis and the bulliform cells). In J. tenuis such sclerenchyma strands are always present and more strongly developed. The vascular bundles lie in one row midway between the abaxial and adaxial epidermis, associated with some sclerenchyma, but without girders connecting them to the epidermis. Chlorenchyma occupies the space between the two surfaces and may be traversed by longitudinal air channels in J. tenuis. In J. imbricatus and J. capillaceus the cross section is irregularly oval with an adaxial channel. Bulliform cells constitute several layers, but occupy only a small part of the adaxially visible surface of the blade. Both J. imbricatus and J. capillaceus have well developed sclerenchyma strands below the epidermis at the transition line from small cells to bulliform cells (the area homologous to the margin of flat leaves). Chlorenchyma lies in a U-shaped arch in cross section. The vascular bundles lie in an arch centrally in the chlorenchyma. The bundles are associated with considerable amounts of sclerenchyma, which may form girders connecting them to the epidermis. When such girders are present the blade attains

an external ridged appearance. In cross section the epidermal cells adjacent to the sclerenchyma girders are enlarged. There may be additional sclerenchyma strands below the epidermis which are not attached to vascular bundles. In Juncus uruguensis the blade has no externally visible row of bulliform cells, and a small-celled epidermis covers the entire blade. The cross section is round or ovate, and the entire surface is homologous to the abaxial surface of the flat blades of e.g. J. bufonius.

Juncus subg. Genuini is generally characterized as having bladeless cataphylls only, and no blade bearing leaves. A few species, however, have blades on the basal one or two sheaths. Among the neotropical species this is the case in J. arcticus, in which var. mexicanus is characterized by the presence of blades on one or two of the basal sheaths. When present, the blades are round to oval in cross section. There is no distinction between an abaxial and an adaxial side. The entire blade surface has a small-celled epidermis and is homologous to the abaxial side of the flat blade in subg. Poiophylli. The blades of subg. Genuini, therefore, when present, are similar to those of J. uruguensis, which is the most advanced species in subg. Poiophylli in this respect. It should be mentioned here that the blade of the lower inflorescence bract in subg. Genuini always is round in cross section (see under 'Inflorescence Bracts'). Furthermore a controversy exists as to whether the 'Sterile Culms' in subg. Genuini really are culm-like leaves. Since they are indistinguishable from culms, externally and in their internal anatomy, and since no definite proof exists that they are leaves, I prefer to consider them culms.

FIGURE 2. - Leaf-blade cross-section of the subgenera of Juncus.

The left column indicates the inflorescence type of the subgenera.

The cross section of Juncus acutus is redrawn from Peisl (1957), that of J. xiphioides from Cutler (1969). The remaining drawings are made from actual specimens: Juncus tenuis from Holm-Nielsen & Jeppesen 260 (AAU); J. capillaceus from Asplund 16151 (S); J. imbricatus from Harling 6603 (AAU); J. marginatus from Petersen 1340 (NY); J. repens from Ekman 10808 (NY); J. cyperoides from Holm-Nielsen et al. 4697 (AAU); J. pallescens from Davidse 8036 (AAU); J. stipulatus from Holm-Nielsen et al. 5812 (AAU); and J. liebmannii from Holm-Nielsen 5317 (AAU). The external two lines delineates the epidermis; chlorenchyma and parenchyma is indicated with a dotted signature; vascular bundles as rings with smaller rings inside, sclerenchyma with black, and air spaces without signature.

Infl. Subg.

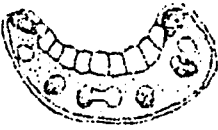
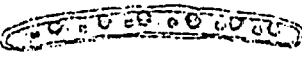
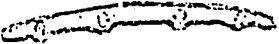
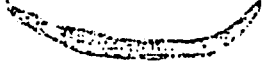
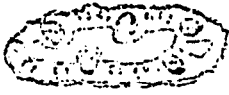
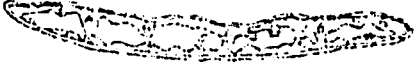
Pacemose	Juncus	 <i>J. acutus</i>		
	Poiophylli	 <i>J. tenuis</i>	 <i>J. capillaceus</i>	 <i>J. imbricatus</i>
	Genuini	 <i>J. arcticus</i>		
Facemose-Anthelate	Graminifolii	 <i>J. marginatus</i>	 <i>J. repens</i>	 <i>J. cyperoides</i>
	Septati	 <i>J. pallescens</i>	 <i>J. stipulatus</i>	 <i>J. liebrannii</i>
	Ensifolii	 <i>J. xiphioides</i>		

FIGURE 2.

Juncus subg. Graminifolii has flat leaves. The thickness is even over the entire cross section, and no macroscopic differentiation between the two sides of the blade is visible. Under the microscope the adaxial cells are slightly larger, and the stomates are restricted to the abaxial side. The leaf margin is rounded in Juncus marginatus and J. repens, but acute in J. cyperoides. The marginal epidermal cells are curious in J. repens in that they hook into one another in cross section. The chlorenchyma is without dorsiventral differentiation and generally consists of isodiametric cells, but sometimes the cells are quite irregularly shaped. Juncus repens and J. cyperoides have longitudinal air channels in the chlorenchyma. The vascular bundles occur in numbers from six to twenty in each cross section. They are mostly found midway between the two surfaces, but may be closer to either one. They may be well developed with an outer and an inner bundle sheath and plenty of sclerenchyma, or small with only a single one-layered parenchymatous bundle sheath. All intermediates are found, sometimes in the same section. Juncus marginatus usually has at least some of the bundles heavily sclerified, whereas J. repens and J. cyperoides have no or very little sclerification.

In Juncus subg. Septati the leaf blades are round or oval in cross section. They are hollow or have very loose aerenchyma in the pith. At regular intervals the hollow pith is interrupted by transverse septa, which in dried specimens appears as nodules. In fresh plants the septa are not always visible, but may be detected if the blade is pulled between two fingers held tightly together. There is no differentiation in adaxial and abaxial sides, and the entire surface of the blade is considered homologous to the abaxial side of the blade in subg.

Graminifolii. The epidermis is uniform around the entire cross section, but the cells may be somewhat irregularly shaped in longitudinal grooves. Stomates are superficial or sunken. Below the epidermis is a 2-6-layered chlorenchyma of radially elongated cells. Below the chlorenchyma is parenchyma with vascular bundles embedded. The parenchyma cells are isodiametric and not very densely arranged. The innermost parenchyma cells are usually crushed or compressed. The parenchyma is continuous around the central lacuna, or sometimes developed only around the vascular bundles. The vascular bundles occur in one or two rings within the parenchyma, but occasionally a little bundle may be seen in the chlorenchyma. They are surrounded by parenchyma sheaths and inside these a sclerenchyma sheath. The number of bundles in a cross section varies from 20 to 40 in my material, but higher and lower numbers occur in other species (Cutler, 1969). Small bundles may lack sclerenchyma sheaths. The vascular bundles enter the septa and form a network embedded in parenchyma.

In Juncus subg. Ensifolii the cross section of the blade shows it to be hollow, but laterally compressed with sharp edges. The two sides reach together and are united by tissue bridges at several points. Several longitudinal lacunae are found rather than one as in subg. Septati. The epidermis has sunken stomates in J. xiphioides (Cutler, 1969), but otherwise the wall of the leafblade has the same structure as in subg. Septati. The airchannels are septate like those of Septati but the septa of the different channels are not at the same level, so the blades do not appear nodulated. The laterally compressed cross section gives the blades of subg. Ensifolii an Iris-like appearance.

Inflorescence bracts.

Inflorescence bracts are foliar structures supporting flower bearing branches in their axils, that is, they constitute all the foliar structures in the inflorescence except the bracteoles.

In the small genera Oxychloe, Patosia and Distichia the single flower originates in the axil of a normal leaf on the stem (Fig. 3). The inflorescence bracts therefore show no specialization. In Rostkovia the single flower is subtended by one lower bract which is 3-5 times as long as the tepals, and an upper bract which is about as long as the tepals. Because of their insertion immediately below the flower, and because they never support branches in their axils they fit the definition of 'bracteoles' (see below). That is so, however, only because of the very simple one-flowered condition of the inflorescence. The lower bract is similar to the blade of the basal leaves except for its length. It has a wide adaxial and a narrow abaxial groove, and two bands of stomata along the abaxial groove.

In Luzula the inflorescence bracts change gradually from the basal part of the inflorescence to the terminal part. The bracts that support the basal branches in the inflorescence of L. gigantea look just like the linear, green leaves of the basal rosette, except that they have longer sheaths. Upwards along the rachis the bracts are similar but smaller. Further up in the inflorescence the bracts become progressively shorter and narrower, and they change from green to red-brown or membranaceous. The margins of the more terminal bracts are split into hair-like lobes. In species with spike-like inflorescences the lowest bract is considerably shorter than the basal leaves and intermediates are lacking. However, from the lowest bract and

upwards, there is the same gradual reduction in size and the same trend towards membranaceous bracts with the margins splitting into hair-like lobes. In Luzula vulcanica the bracts are all membranaceous, and the ones supporting the flower clusters are usually broadly lanceolate instead of linear.

In Juncus there is quite a variation in the inflorescence bracts, some of it taxonomically important. The primitive condition is lower inflorescence bracts similar to the basal and cauline leaves, with a gradual modification upwards in the inflorescence. Often, however, there is a distinction between the lower bract, which is modified in various ways, and the upper ones. The species descriptions therefore often give special mention to the 'lower inflorescence bract'. In subg. Juncus the lower inflorescence bract looks just like a short basal leaf. It has a sheath and a round, slightly ridged blade that terminates in a hard (sclerified) pointed tip. The lower bract tends to stand upright and push the inflorescence to one side, but it has the obvious appearance of a leaf (cf. subg. Genuini). The upper inflorescence bracts are much shorter. In subg. Poiophylli, Juncus bufonius and J. tenuis have inflorescence bracts similar to basal leaves. There is a gradual transition upwards to progressively shorter bracts. Juncus imbricatus has the lower bract somewhat set off from the upper ones. In J. capillaceus the lower bract is sometimes much longer than the following ones. It attains an upright position, and appears somewhat like a continuation of the culm. In subg. Genuini the trend described above is completed, and the culm like lower bract of the inflorescence is characteristic of the subgenus. The sheath of the lower bract is short, the blade is

round in cross section and stands upright in continuation of the culm axis. Anatomically the round blade is indistinguishable from the culm. The inflorescence therefore appears to be inserted laterally on a culm, and is said to be 'pseudolateral'. The culm-like lower bract is sometimes called the 'spathe'. It varies in length, both absolute and relative to the culm proper. Its relative length is important in distinguishing for example Juncus effusus from J. procerus. The upper bracts in subg. Genuini are always much smaller, flat, and generally membranaceous. In subg. Graminifolii there is not much differentiation between the lower inflorescence bract and the upper ones, but only a gradual reduction in size. In subg. Septati the lower inflorescence bract usually has the appearance of the basal leaves. The upper bracts show progressive reduction in size, or may all be conspicuously shorter. In this subgenus there is a trend of reduction of the blade of the lower inflorescence bract. In J. echinocephalus the main part of the lower inflorescence bract is the sheath, and the blade is rudimentary. This is in contrast to the subgenera Poiophylli and Genuini, in which the trend is towards more prominent blades and smaller sheaths. Subg. Ensifolii has a prominent lower bract similar to the basal leaves, and smaller upper bracts.

Bracteoles.

Bracteoles are foliar structures inserted on the pedicel just below the flower, which never give rise to branches in their axils. They are membranaceous and shorter than the tepals, apically obtuse or acute. Bracteoles are found in all genera except Rostkovia but may not be homologous.

In Distichia there are 3-4 to each flower. They are small, about

1/10 as long as the tepals, obtuse, very thin, hyaline and inconspicuous. In Patosia there is one bracteole per flower. It is membranaceous and more than half as long as the tepals. In Oxychloe there are two bracteoles to each flower. They are similar to those of Patosia. In Luzula each flower is clasped by 2-3 bracteoles which look like small inflorescence bracts. They are membranaceous, acute, and their margins are dissolved into ciliate lobes. In Juncus bracteoles are present in the subgenera Poiophylli and Genuini (and in the not neotropical subg. Subulati), and absent in the remaining subgenera. There are always two of them. They are inserted in the median plane and densely clasp the flower. They are subtriangular, usually obtuse, and look quite different from the bracts. The presence of bracteoles in Juncus is strictly correlated with cymose inflorescence. Even if difficult to observe at first, the presence of bracteoles is the best characteristic by which the subgenera Poiophylli and Genuini are distinguished from the remaining subgenera. In these the flowers are merely subtended by the floral bract at the base of the pedicel.

5. Inflorescence

The inflorescence is one flowered in all the small genera.

Rostkovia magellanica has a single flower terminating the 15-30 cm high culm. A basal erect bract which is 4-5 times as long as the tepals appears almost as a continuation of the culm. An upper thinner bract is about as long as the tepals. Distichia has unisexual flowers inserted laterally on the stem 5-10 nodes below the shoot apex (Fig. 3). They appear in the axil of a leaf which is indistinguishable from the remaining leaves. A two-keeled bifid prophyll is inserted basally and adaxially on the pedicel. Two to four minute rounded membranaceous bracteoles are inserted just below the tepals. The female flowers of Distichia are born on short pedicels, and they do not reach above the shoot apex. Only the receptive stigmas project above the shoot apex and the dense cushion of crowded shoots. To compensate for the short pedicel the mature capsule is lifted above the cushion by a gynophore so the seeds may be dispersed. The male flowers of Distichia in contrast are borne on long pedicels lifting them above the cushions of densely crowded shoots, where the anthers and the pollen are exposed to dispersing agents. Oxychloe andina and Patosia clandestina are similar to Distichia in most ways but neither have gynophores. and in Oxychloe andina the difference in length between the female and the male pedicel is not pronounced.

The two larger genera, Juncus and Luzula, both have manyflowered inflorescences. In very rare cases depauperate specimens may be one-flowered.

The inflorescence of Luzula shows great diversity of eminent taxo-

FIGURE 3

The inflorescence of Distichia muscoides. The leaves of the basal part of the stem have been removed. The inflorescence is one-flowered, and the flower is inserted in the axil of a normal leaf seven nodes below the apex. The flower is unisexual and female. The capsule, which is just maturing, is being lifted out of the perianth by the growing gynophore.

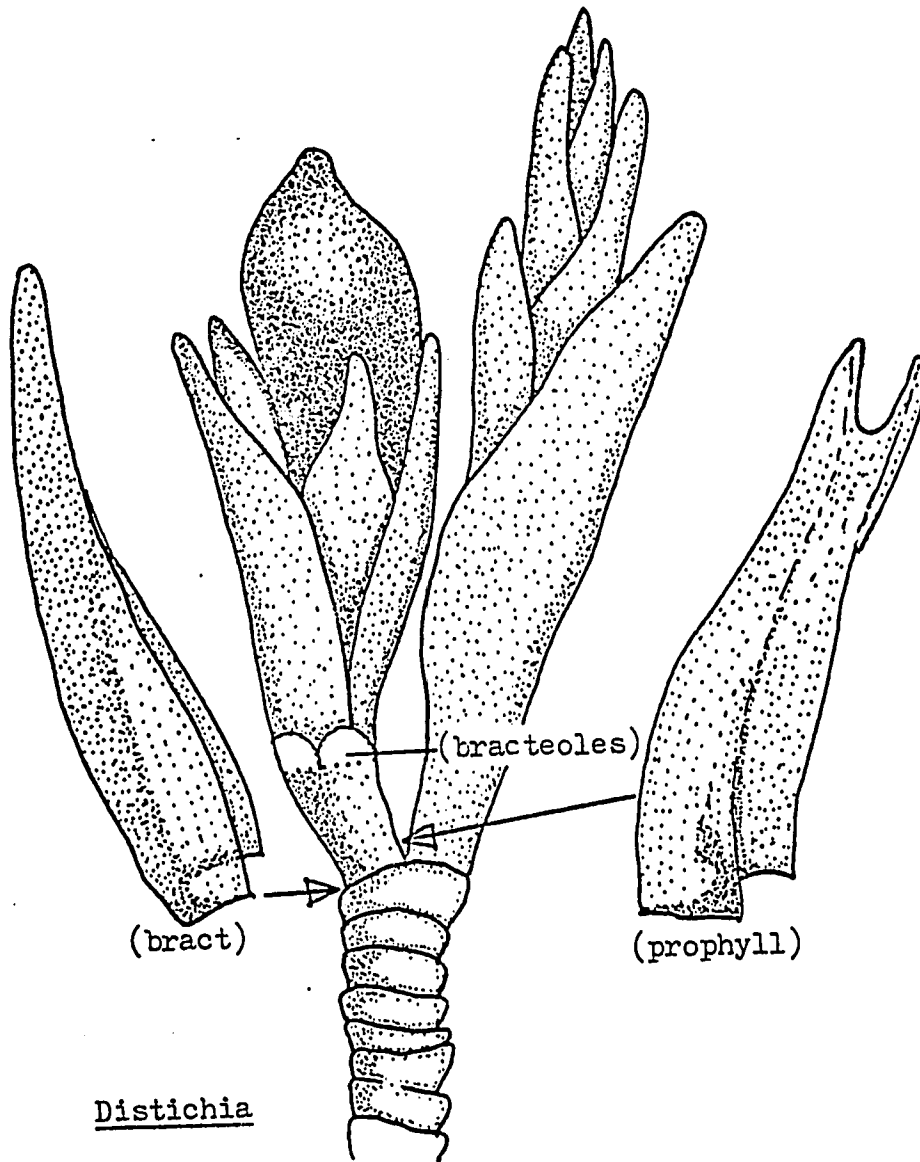


FIGURE 3 .

nomic significance (Fig. 4). Subg. Anthelaea has loose many-flowered panicles, i.e., the individual flowers are not congested into heads or clusters. The most profusely branched panicles occur in L. gigantea. In this species an erect culm emerges from the leaf rosette. The culm changes into a rachis, which is also erect but apically nodding. The entire inflorescence occupies the major part of the plant height. The rachis segments are 5-15 cm long. From 4-5 nodes originate lateral, many-flowered nodding panicles. Because of the long rachis segments separating these partial inflorescences the entire inflorescence appears storied. The bracts inserted on the rachis are large and similar to the leaves of the basal rosette. Higher up in the inflorescence the bracts are shorter, narrower, and membranaceous; those supporting the ultimate branches are only 2-3 mm long. The margins of the upper bracts are divided into ciliate lobes, more so the higher up in the inflorescence. A bifid membranaceous prophyll is inserted basally on each sidebranch. Immediately below each flower are 1-2 bracteoles, likewise of membranaceous texture. The inflorescence of the remaining neotropical Luzulae may (in an Aristotelean sense) be derived from the above described much branched inflorescence types of Luzula gigantea (Fig. 4). The inflorescence of L. denticulata may be derived simply by eliminating the basal (lateral) partial inflorescences so that only the terminal part remains. The inflorescence of L. denticulata thus consists of one loose terminal panicle, the structure of which is similar to a partial inflorescence of L. gigantea. These two species are the only two neotropical representatives of subg. Anthelaea, which is characterized by loose panicles. The remaining neotropical Luzulae all belong to subg. Luzula in which

FIGURE 4

Inflorescence types in Luzula, and a suggested phylogeny.

From the primitive type in L. gigantea there is a reduction of the lower loose panicles to form one loose terminal panicle in L. denticulata. Another trend involving congestion of the flowers into clusters and contraction of the peduncles, leads over L. excelsa to L. racemosa and L. vulcanica. The inflorescences of L. campestris and L. caricina are abnormal in this phylogenetic series.

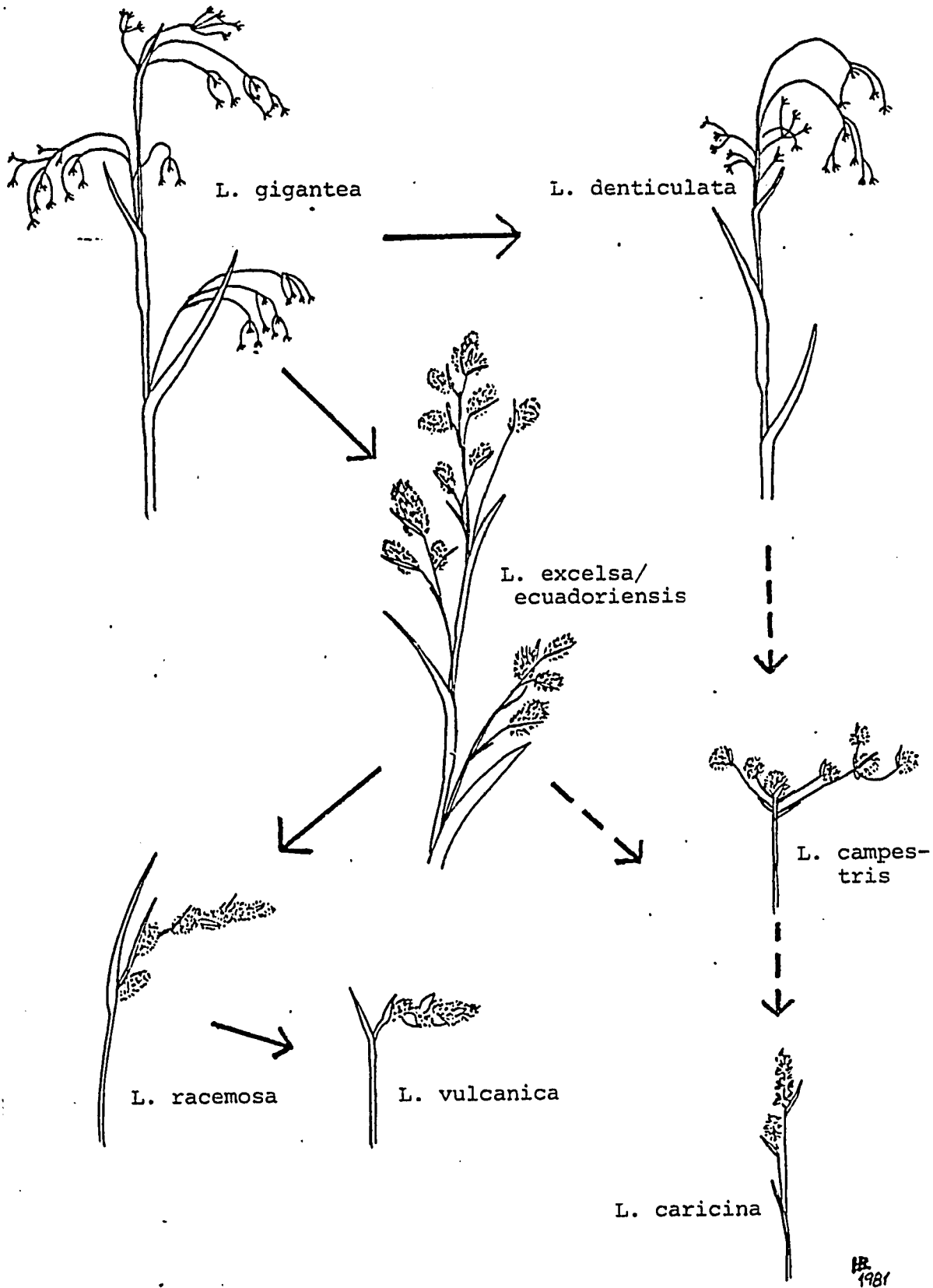


FIGURE 4

the flowers are congested into elongate or rounded clusters. These clusters may then be arranged in a variety of ways from loose panicles to dense spikes or anthelae. The inflorescences of L. ecuadoriensis and L. excelsa thus have the flowers congested into clusters. The clusters are arranged in loose panicles, and the entire inflorescence is subdivided by long rachis segments in the same way as that of L. gigantea. The overall appearance of the two species is also similar to that of L. gigantea, and the only diagnostic differences are those of the inflorescences mentioned above. The derivation of L. ecuadoriensis and L. excelsa from L. gigantea may therefore be accomplished simply by the congestion of the ultimate inflorescence parts, leaving the parts close to the rachis open. The inflorescence of L. racemosa and L. vulcanica also have the flowers congested into clusters. In these two species, however, the clusters are arranged in spike-like structures. Each cluster is borne on a very short peduncle and appears sessile. The basal flower cluster of L. racemosa may have a slightly enlarged peduncle, or sometimes the entire inflorescence is slightly opened up to form intermediates towards L. excelsa. The inflorescences of L. racemosa and L. vulcanica can thus be derived from the L. ecuadoriensis/excelsa type by further contraction, i.e. the disappearance of the open parts next to the rachis. Luzula campestris has an inflorescence of rounded (rather than elongate) flower clusters. These are arranged in an unbranched or once branched anthela. That is, they are borne on peduncles that originate crowded at the top of the culm, and those originating basally in the crowd are longer than those originating apically. The basal inflorescence branches thus overtop the apical ones. The inflorescence of

L. caricina is a terminal erect elongate spike-like cluster which is slightly stretched so small segments of the rachis are visible. In addition to the terminal cluster there usually is a lateral cluster inserted as much as eight centimeters below the terminal one. This lateral flower cluster is borne on an erect peduncle lifting it up to just below the terminal one so that the inflorescence does not appear subdivided. The inflorescences of L. campestris and L. caricina do not fit easily into the above described series of modifications of the L. gigantea inflorescence. Several 'steps', which are not represented in our material, are necessary to link these two species with the remaining ones. Luzula campestris and L. caricina differ also in having obtuse callose tipped leaf blades. Consequently they may be phylogenetically more isolated than indicated in the below applied classification where they, following the tradition, are included in subg. Luzula because of their flowers being borne in clusters.

In Juncus two basic types of inflorescences are found. One is cymose and occurs in the subgenera Poiophylli and Genuini. The other is racemose and occurs in the subgenera Juncus, Graminifolii, Septati, and Ensifolii. This latter racemose type was subdivided by Novara (1976) into those with short-shoots ('braquiblastos') at the extreme of all ramifications (subgenera Graminifolii, Septati, and Ensifolii), and those with short-shoots at all internodes constituting ramifications of unequal order (subg. Juncus).

The inflorescence of Juncus subg. Juncus is terminal on the culm. It is supported by a rigid lower inflorescence bract with a conspicuous sheath and a short erect apically hard pointed blade which

is round in cross section. This lower inflorescence bract may in some cases appear as a continuation of the culm, but the conspicuous sheath reveals it as a foliaceous structure. The main axis of the inflorescence is a somewhat condensed shoot with short but recognizable internodes. At each node originates lateral shortshoots of 1st order with extremely short internodes. At each node of the 1st order lateral shortshoots originates longshoots of 2nd order. These have an obvious basal naked part and terminal branching giving rise to lateral shortshoots of 3rd order. This may be repeated to 5th or 6th order branching. Characteristic is that neither principal shortshoots or longshoots are terminated by a flower, and the branching is therefore racemose. It is also characteristic that there is an alternation between shortshoots and longshoots. The flowers originate on pedicels in the axils of floral bracts, but there are no additional bracteoles on the pedicel.

The subgenera Graminifolii, Septati and Ensifolii have basically similar inflorescences. The culm terminates in a flowerhead. The flowerhead is a racemose system of condensed short-shoots, and the entire inflorescence is thus racemose. Below the terminal flowerhead originates usually several sidebranches, separated by very short nodes, and therefore crowded. The basal branches are the longest ones, and overtop the ones inserted closer to the head. The term 'anthela' or 'anthelate' (as adjective) corresponds to this inflorescence type in which the basal branches overtop the more apical ones. The lowest sidebranch originates in the axil of the 'lower inflorescence bract' which differs from the remaining bracts of the inflorescence and exhibits diagnostic features. The sidebranches are terminated by flowerheads, and sidebranches of 2nd order may or may not originate just below these heads. In the most profusely

branched inflorescences sidebranches of 5th and 6th order occur. The total number of flowerheads in one inflorescence varies from two to over a hundred. The thickness of the branches and the degree of congestion of the entire inflorescence vary, and the number of flowers in an individual head varies from five to over fifty. Variation within these characters may be found even within the same species, but nevertheless the inflorescence often presents taxonomically highly useful characteristics. The inflorescence of J. echinocephalus is thus congested into one large head or rarely two. The ultimate inflorescence branches of J. pallescens are thicker than 0.45 mm in diameter, whereas those of the closely related J. microcephalus are less than 0.30 mm in diameter. The inflorescence of the subgenera Septati, Graminifolii and Ensifolii is thus characterised by being racemose, by having the flowers congested into heads (= shortshoots terminating the main branches), and by the entire inflorescence being anthelately arranged. In addition it is characteristic that each flower is borne in the axil of a bract (the floral bract), but there are no additional bracteoles on the pedicel.

The inflorescence of subg. Poiophylli is cymose. The culm is terminated by a flower, and below this terminal flower originates one to several sidebranches, each terminated by a flower. The sidebranches may again give rise to sidebranches of 2nd order etc.. The branching is also anthelate, i.e. the lower branches overtop the ones originating higher up. In addition to the floral bract (in the axil of which the pedicel originates), each flower is clasped by two bracteoles which are inserted on the pedicel just below the flower. The inflorescences in subg. Poiophylli varies as to number of flowers and degree of congestion. The degree to which the lower inflorescence bract differs

from the following ones also varies. Thus Juncus bufonius has gradual transition from the lower bract to the upper ones, whereas J. capillaceus has the lower bract much enlarged and almost culm-like, clearly set off from the remaining ones. The regularity of the branching and the number of sidebranches originating below a flower also varies. The extreme case with only one sidebranch below the flower, repeated several times is called a 'drepanium'. Since the bracts are inserted in the plane defined by the main axis and the sidebranch, the entire branching of a drepanium will also be in one plane. Since the bract is always inserted on the abaxial side of the branch, the branching will likewise always go to the abaxial side. Because of the constant branching to one side the drepanium may attain a curved appearance and is called a 'sickle'.

The inflorescence of subg. Genuini is cymose like that of Poiohylli. It differs mainly in the extreme development of the lower inflorescence bract, which in this subgenus has attained a culm like appearance, and is erect continuing the axis of the culm. The sheath of the lower inflorescence bract is much reduced and the blade is round in cross section with an internal anatomy that is indistinguishable from that of the culm. The length of the lower inflorescence bract,

sometimes called the 'spathe', varies. It may occupy as much as one third of the entire plant height or it may be much shorter and occupy as little as one tenth of the entire plant height. Because of the erect culm-like nature of the lower bract the inflorescence is pushed to one side and appears lateral, even if truly terminal. The term 'pseudolateral' is often used to describe this condition. The branching

of the inflorescence is in principle similar to that of subg. Poio-
phylli, and every pedicel originates in the axil of a floral bract and
has two bracteoles. Parts of the inflorescence may consist of drepania
as in Poio-phylli. In addition an other further specialized branching
type may occur. This type is called a 'rhiphidium' and occurs when
the prophyll gives rise to a sidebranch in its axil. Since the pro-
phyll is adaxial and inserted in the plane defined by the axis and the
sidebranch the rhiphidium is branching in one plane and exhibits a zigzag
arrangement.

6. Flowers

The flowers of Juncaceae are actinomorphic, trimerous and pentacyclic with regular alternation of the whorls (Fig. 5). Occasionally there is a reduction in the inner whorl of stamens to make the flower tetracyclic.

Tepals.

The six tepals in two whorls of three are free from one another. They are 2-7 mm long, lanceolate, obtuse, acute or acuminate, green stramineous, reddish brown, castaneous or almost black. The margins are often membranaceous, either gradually thinner towards the edge, or with a distinct papery rim. The membranaceous margin may widen towards the tip of the tepal to form two auricles, which are inflexed and not visible unless unfolded as seen in Rostkovia magellanica. The outer tepals are often slightly longer, thicker and more rigid than the inner ones. They may be concave (U-shaped in cross section with the opening towards the center of the flower), and the inner ones flat. The texture of the tepals is characteristic in a given species. Juncus effusus has soft, flexuose tepals, whereas J. arcticus and J. ramboi have rigid ones. Juncus pallescens differs from its near relative J. microcephalus by its more rigid tepals. This character is, however, difficult to quantify when observed macroscopically.

Stamens.

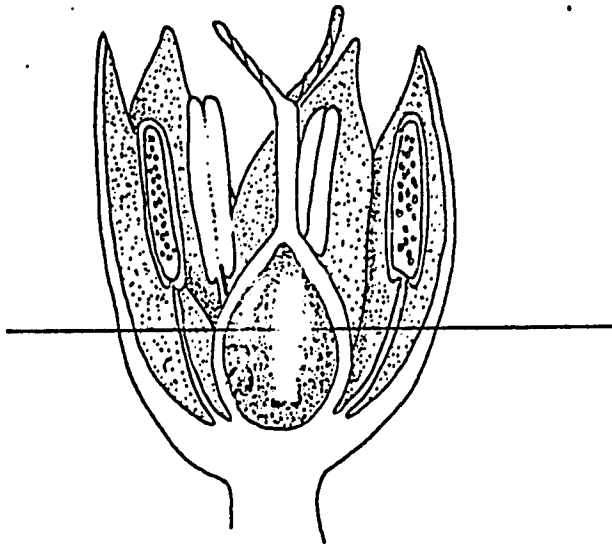
There are six stamens in two whorls of three in regular alternation with the tepals. The inner whorl may be reduced or absent. The filaments are free, filiform or widened at the base, white or hyaline. The

FIGURE 5

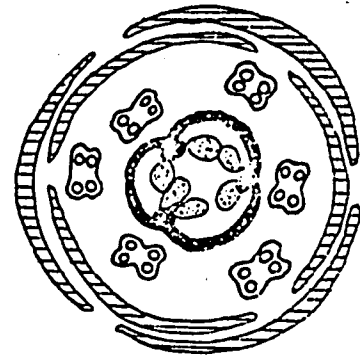
Floral morphology in Juncaceae.

5A. Semidiagrammatic longitudinal section of a flower of Juncus.

5B. Floral diagram showing the five whorls of 2 x 3 tepals,
2 x 3 stamens, and 3 carpels in regular alternation.



A.



B.

FIGURE 5

anthers are 4-locular or, by breakdown of the inner wall, secondarily 2-locular, oblong to linear, basifixed, yellow to whitish, introrse, and open by longitudinal slits. At pollen shedding they twist around their own axis to the right. In Distichia, Patosia, Oxychloe and Rostkovia the connectives are prolonged into a mucronate apical appendage. Such an appendage is never present in Juncus and Luzula. The relative anther filament length varies, but is usually constant in a given species, and therefore of taxonomic significance. Variation during development, both in absolute and relative length, complicates the usage of this character. It is, however, significant that all the small genera have anthers which are about ten times as long as the filaments. Juncus and Luzula have relatively shorter anthers. Reduction in number of stamens is of taxonomic significance, but is not always constant, sometimes not even in a single population or individual.

Pistil.

The pistil consists of three united carpels opposite the outer tepals. The ovary is globular to oblong. The style is round and from 0.5 mm to 10 mm long. The three stigmas are from 0.5 to 8 mm long, round in cross section, papillose on the adaxial side or all over, of uniform diameter except in Rostkovia magellanica, where they are much broader basally. The stigmas twine in various ways. In Luzula the placentation is basal and there are three ovules in a one-locular ovary. In the remaining genera the placentation may be parietal, on protruding septa, or axillary, and there are many ovules per ovary. In Juncus roemerianus the placentas are swollen and spongy. The ovules are anatropous, bitegmate, hanging or ascending except in Luzula where they are erect.

7. Pollen

The pollen grains of Juncaceae are united in tetrads surrounded by a common exine. The exine is derived from the pollen mother cell (Wille, 1882). The tetrads are usually tetrahedral and the four grains may be so closely appressed as to make it almost spherical. According to Buchenau (1890, 1906) and Selling (1947), tetragonal or rhomboidal tetrads also occur in the family. The exine is thin, usually about 1u, but lacking on the contact walls of the four grains. It is smooth or with small granules, and the sutures between the four grains are visible through it. The grains are (confusingly) said to be inaperturate (Cranwell, 1952), mono-sulcate (Huang, 1972), mono-porate (Heusser, 1971) or mono-aperturate [ulcer(oid)ate] (Erdtman, 1971). Woodehouse (1935) is more explicit in his description of the pollen of Luzula campestris (L.) DC.: 'The germinal furrow is not sharply defined but is represented by a thin area of the exine on the outer face of each grain....distinguished by....the more open distribution of its granular flecks. It is through (these areas) that the pollen tube emerges at time of germination. At best however, the germinal furrow of these grains is vestigial.'

The size range of the individual grains is from 20-57u, and of the tetrads from 24-70u, according to the literature (Table I). The absence of germinal pores is probably due to the thinness of the exine. A thin exine is often seen as adaptation to anemophily, which is the dominant mode of pollination in Juncaceae. The small South American genera Marsippospermum, Rostkovia, Oxychloe and Patosia have, on the average, larger tetrads than Juncus and Luzula, whereas Prionium from South Africa has smaller tetrads. The smaller tetrad size of Juncus,

TABLE I . SIZE OF POLLEN GRAINS AND TETRADES IN JUNCACEAE

Taxon	Individual Grain (μ)	Tetrad (μ)	Source
<i>Juncus acutiflorus</i> Hoffm.	26.6-31.4(28.8)	40.0-45.7(42.5)	Hyde & Adams, 1950 (111.)
<i>Juncus antarcticus</i> Hook.f.	30-36x25	50	Cranwell, 1952
<i>Juncus dombeyanus</i> Gay		41-48	Heusser, 1971 (111.)
var. <i>dombeyanus</i>			
<i>Juncus maritimus</i> Lamarck		36	Cranwell, 1952
var. <i>australiensis</i> Buch.			
<i>Juncus modicus</i> N. E. Br.	27-40x41-45x30-40		
<i>Juncus tenuis</i> Willd.	34x34-35x26-29		Huang, 1972 (111.)
Range of JUNCUS	26-45	36-50	
Average of JUNCUS	35	43	
<i>Luzula alopecurus</i> Desv.		43-48	Heusser, 1971 (111.)
<i>Luzula campestris</i> (L.) DC.	25.1-29.6		Woodhouse, 1935 (111.)
	23.8-28.6(25.6)	38.0-44.7(40.7)	Hyde & Adams, 1956 (111.)
		30-45	Kapp, 1969 (111.)
	35-38x38-43x30-33		Huang, 1972
<i>Luzula campestris</i> (L.) DC.			
var. <i>australasica</i> Buch.	28x20	34-40	Cranwell, 1952
<i>Luzula effusa</i> Buchenau	23-49x26-50x28-40		
<i>Luzula formosana</i> Ohwi	31-45x36-53x30-34		Huang, 1972
<i>Luzula multiflora</i> Lejeune	36x39-43x32-33		
<i>Luzula pilosa</i> L.		33.2x50 (dry)	Zander, 1935 (Cranwell, 1952)
		38.2x35.7 (moist)	Zander, 1935 (Cranwell, 1952)
		40	Erdtman, 1971
<i>Luzula taiwaniana</i> Satake	23-48x38-57x26-41		Huang, 1972 (111.)
Range of LUZULA	20-57	30-50	
Average of LUZULA	36	40	
<i>Marsippospermum grandiflorum</i> (L.f.) Hook.f.		58-65	Heusser, 1971 (111.)
<i>Oxychloe andina</i> Philippi		46-55	Heusser, 1971 (111.)
<i>Patosia clandestina</i> (Phil.) Buchenau		50-58	Heusser, 1971 (111.)
		55x50	Markgraf & D'Antoni, 1978 (111.)
Range		50-58	
Average		54	
<i>Rostkovia gracilis</i> Hook.f.		34-40(36)	
<i>Rostkovia magellanica</i> (Lam.) Hook.f.		44-50x44-30	Cranwell, 1952 (111.)
		65-70	Heusser, 1971 (111.)
Range		30-70	
Average		50	
<i>Prionium palmita</i> E. Meyer		24	Erdtman, 1971

Luzula and Prionium probably represent progressive adaptation to wind pollination. Apart from the size, the appearance of the pollen is uniform within the family, and has not been useful taxonomically below the family level. Above the family level however, the tetrad arrangement does show that Juncaceae is related to Thurniaceae, which has a similar arrangement. It has also been suggested that the Juncaceous tetrad, though advanced relative to most monocotyledons, is a primitive precursor to the Cyperaceous tetrad, in which three of the four derivatives from the pollen mother cell disintegrate. Otherwise the very reduced (=advanced) pollen morphology of Juncaceae sheds little light on its familial relationships.

8. Fruit

The fruit is a dry capsule. In Juncus, Luzula and Rostkovia dehiscence is loculicidal, in Distichia, Oxychloe and Patosia less well defined, but sometimes circumscissile. The capsule is globular in Rostkovia, otherwise longer than wide, ranging from 1.5-5.5 mm in length. The outline varies from ovoid to abovoid, and it may be apically truncate, obtuse, acute or acuminate, sometimes drawn out into a prominent beak. The cross section is round, trigonous or three-keeled, sometimes varying at different levels in the same capsule. The lumen is one-locular, three-septate or three-locular, and the placentation correspondingly parietal or central axillary (Buchenau, 1877). Juncus repens and sometimes J. uruguensis are unusual in having a central columella derived by the disappearance of partitions of a three-locular capsule late in ontogeny, and their placentation is thus free central. The cross section of the capsule and the placentation is constant in a given species, but should be observed carefully. Septa sometimes develop late in ontogeny, and immature capsules may dry up and appear mature in herbarium specimens. In addition the degree to which the septa protrude into the lumen vary along the length of the capsule; it may be three-locular basally but three-septate higher up (Schaeppi, 1974). Dehiscence is variable. In Luzula racemosa the three carpels completely reflex. Some beaked species dehisce by slits only, and the carpels remain connate at the apex of the beak, e.g., in J. densiflorus. In some populations of

J. microcephalus and J. marginatus the carpels inflex, whereas other species have rigid carpels that do not deform at dehiscence, but merely separate, e.g. J. imbricatus. A short gynophore is present in J. tenuis (Schaeppi, 1974), and probably in other species. Distichia muscoides has a distinct gynophore that elongates and lifts the capsule above the shoot apex at maturity (Fig. 3, 20B).

The ovules of Juncaceae are anatropous with two integuments and ascend from parietal or axillary placentas. Luzula differs in having basally attached erect ovules. The mature seeds are ovoidal, obovoidal, ellipsoidal, oblong, or fusiform, often oblique. In cross section they are terete or, when many seeds are crowded in one capsule, sometimes angular. The raphe is usually visible along one side as a fold in the outer seed coat (Fig. 10E). The ends of the seeds are rounded or more often drawn out into short apiculate extensions, or in some species drawn out into longer extensions so the seeds appear tailed. The length of the seeds of neotropical Juncaceae varies from 0.3 mm to 1.8 mm, and the width varies from 0.15 mm to 1 mm. The larger part of the seed is occupied by a starchy endosperm. The embryo is small, straight, cylindrical or conical, and located in the centerline near the micropyle. A single cotyledon occupies the larger part of the embryo (Buchenau, 1906). The derivation of the seed coat from the two integuments was described by Buchenau (1890). The two integuments each consist of two cell layers, at least near the middle of the seed, whereas there may be more layers near the micropyle and the chalaza. In Luzula the dark brown shell surrounding the endosperm and the embryo is derived from the inner integument. The outer integument changes into a more or less shrivelled outer seed coat at maturity. Many species of Luzula have carunculate seeds as an adaptation to ant dispersal.. Among the neotropical species L. campestris var. multiflora and L. caricina have carunculate seeds. In some Juncus the outer seed coat is entirely derived from the outer integument as in Luzula. It is then very loosely sheathing

and detached from the yellowish brown hard inner seed coat, which is derived entirely from the inner integument. In most species of Juncus, however, the two two-layered integuments are closely appressed. In these the inner wall of the inner cell layer of the outer integument and the inner wall of the outer cell layer of the inner integument thicken to become hard and suberized. The single cell layer between these two thickened layers disappears, and they fuse to form the yellow or brown 'inner seed coat'. Covering this inner seed coat is the 'outer seed coat' consisting of thin walled cells. When moistened the outer seed coat swells to form a sticky mucilaginous cover (Fig. 6C,D), which functions in seed dispersal, for instance in Juncus tenuis. In other species such as J. imbricatus the swelling of the outer seed coat causes the volume of the seed mass to increase and functions in opening the capsule. In J. effusus the swelling of the seed coat causes the entire inflorescence to become a slimy glob, the weight of which bends the culm to the ground where the seeds are deposited. It has been suggested that the slime functions in the protection of the seeds (Buchenau, 1906).

The sculpturing of the seed coat of Juncus attracted the attention of Engelmann (1866), who recognized three seed types: 1. 'Semina costata' - with longitudinal ribs only (or nearly so), 2. 'Semina lineolata' - with transverse ridges only (or nearly so), and 3. 'Semina reticulata' - with uniform longitudinal and transverse lines. Buchenau (1867) in a study of the German species of Juncus suggested two types of seeds, one of them subdivided: 1. 'Semina costata' - corresponding to Engelmann's type of the same name, 2a. 'Semina reticulata' - with longitudinal and

transverse ridges equally prominent, creating more or less regular meshes, and 2b. 'Semina transverse reticulata' - with transverse ridges most prominent creating meshes that are wider than long. Since these two pioneer studies most work on Juncus has included more or less detailed descriptions of the seeds. Satake (1933) discussed the seeds of Japanese Juncaceae in detail, and Lourteig (1968) placed much emphasis on the characters of the seeds when recognising five species in the Juncus stipulatus complex. Clemants (1979) studied the Minnesotan species of Juncus using Scanning Electron Microscope (SEM) technique, and distinguished three types of seeds defined as follows: 1. 'Transverse reticulate-scrobiculate' with longitudinal rows of uniform or irregular scrobiculae (transversally elongate depressions), 2. 'Costate-scalariform' with pronounced longitudinal ribs (costae) with light transverse lines giving the appearance of a ladder, and 3. 'Reticulate' with regular or irregular areoles, bounded by raised ridges, the areoles are or are not arranged in longitudinal rows. Buchenau's and Engelmann's studies were based dried but otherwise untreated seeds from herbarium specimens at magnifications from 50-X to 60-X. Clemants' SEM studies were made at magnifications from 100-X to 1000-X after having treated the seeds with ultrasonic vibrations to remove (supposedly only) the outer seed coat. The ultrasonic treatment was used because, according to Clemants, the sculpturing is produced only by the inner suberized seed coat. For the present study I surveyed the seeds of the neotropic taxa of Juncaceae using the SEM technique. The seeds were taken directly from dried herbarium specimens, placed on stubs with doublesided tape, coated with 200 Å gold or platinum and examined at magnifications from 100-X to

3000-X. No attempts were made to remove any part of the seed coat before examination. Occasionally the outer seed coat had detached itself spontaneously and could then be removed with a pair of forceps. In those cases comparison of the sculpturing of the outer and inner seed coat could be made (Fig. 6A,B).

From my observations it is obvious that the sculpturing of the seed coat is clearly visible under the SEM without removal of the outer seed coat. When comparing my photographs with those of Clemants it is also obvious that a good deal of the sculpturing is actually produced by the outer seed coat. It is still unclear to what extent, and in which manner the two seed coats interact to produce the sculpturing. The adaptive significance of the sculpturing is also unclear at this point, though it seems obvious that the answer must be sought in the swelling properties of the seed coat (Fig. 6C,D), and the sculpturing observed in dried seeds may thus be nothing but a byproduct without adaptive significance in itself. In the following I will describe the seeds of selected species of neotropical Juncaceae to illustrate the variation encountered. I do not accept the categories applied to Juncaceous seed coats by previous workers. Rather than defining different types I will discuss them in terms of evolutionary trends. The terms I use are descriptive and not to be taken as names of formal categories. Except for those of Luzula, each seed is shown at low magnification in the range from 100-X to 300-X, and in a higher magnification in the range from 600-X to 1400-X. These numbers refer to the original magnifications used on the SEM, and the plates reproduced here are slightly smaller. Instead of referring to actual magnification, which will be evident from the figure itself I will simply refer to 'low' and 'high magnification'.

FIGURE 6

SEM images of Juncus seeds.

6A. Whole seed of J. planifolius with the outer seed coat removed, showing the smooth inner seed coat (From Eyerdam 10604, NY).

6B. Detail of same.

6C. Whole seed of species of J. tenuis complex, showing swelling of wetted seed coat. The swollen seed was freeze dried before coated with gold (From Crutchfield 1638, NY).

6D. Detail of same.

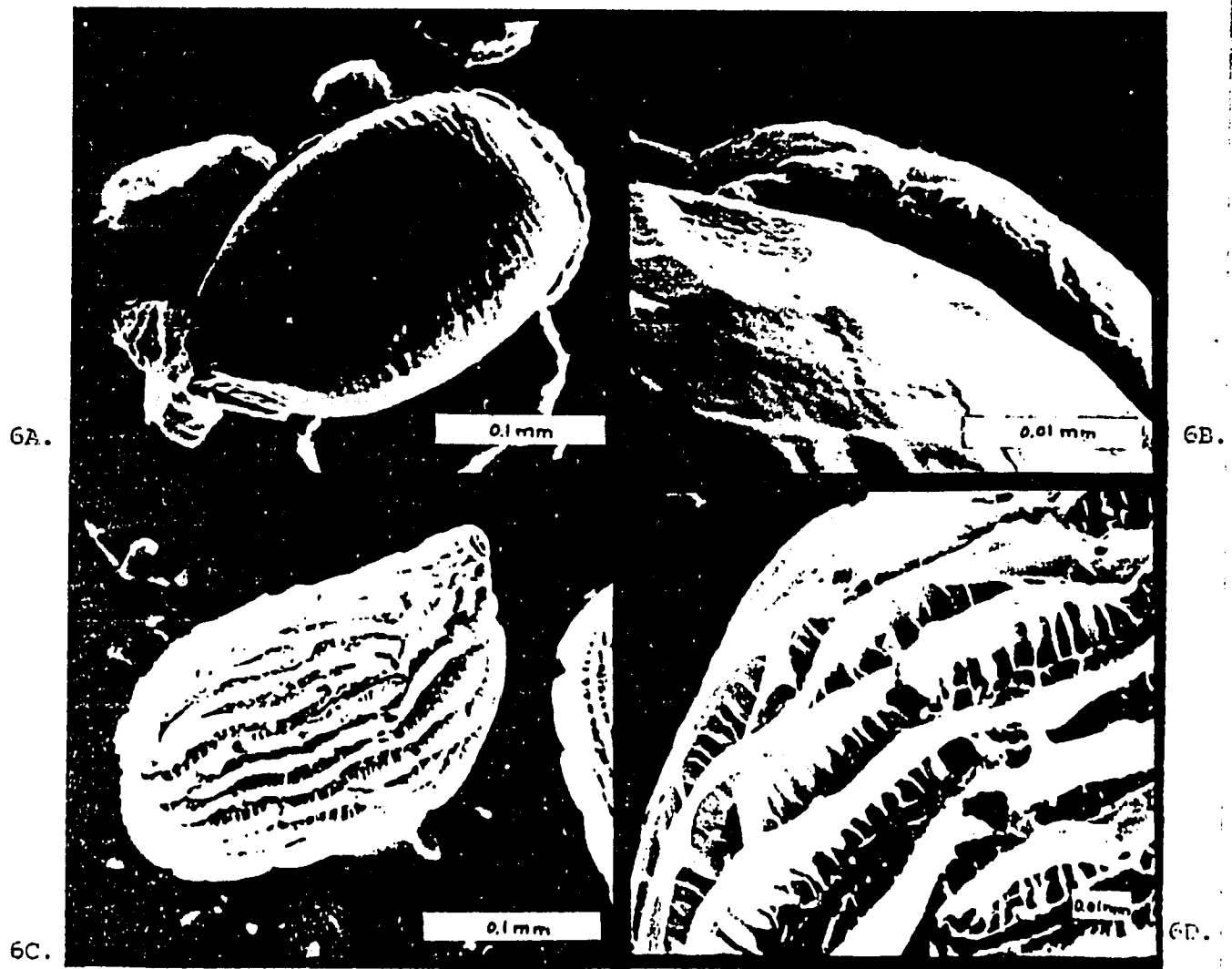


FIGURE 6

Rostkovia magellanica (Fig. 7A,B).

The seeds are obovoidal inapiculate and appear smooth at low magnification, whereas a slightly wavy surface created by the convex surface of elongated and apically pointed cells is seen at high magnification. The elongate cells of the outer seed coat are arranged longitudinally on the seed.

Oxychloe andina (Fig. 7C,D).

The seeds are obovoidal, slightly apiculate, and appear heavily and irregularly sculptured at low magnification. There is an external system of ridges creating a network of irregular polygonal meshes with a slight tendency to become elongate along the axis of the seed. Below the external system of ridges an internal system of narrow curved projections is seen. These projections fill out the meshes of the net created by the external ridges in some places, in others they appear to continue from one mesh to another. This pattern is amplified at high magnifications, but in addition the areas within the meshes show a ripple structure transverse to the long axis of the seed.

Distichia muscoides (Fig. 7E,F).

The seeds are irregularly shaped and sometimes (e.g. the one shown on the photograph) tailed by long extensions of the outer seed coat. At low magnification the seed appears irregularly wrinkled, but with a tendency for the wrinkles to be oriented longitudinally. The areas between the wrinkles are irregularly wavy when seen at high magnification.

FIGURE 7

SEM images of Juncaceae seeds.

7A. Whole seed of Rostkovia magellanica (From Skottsberg Ser. I 292, S).

7B. Detail of same.

7C. Whole seed of Oxychloe andina (From Johnston 4825, GH).

7D. Detail of same.

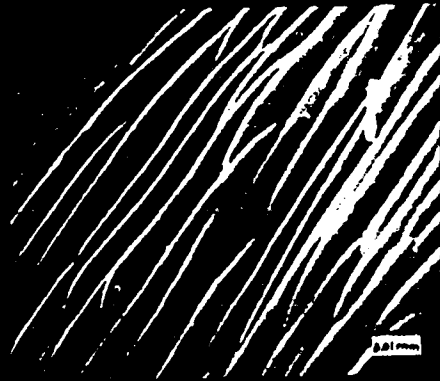
7E. Whole seed of Distichia muscoides (From Iltis & Ugent 1285, NY).

7F. Detail of same.

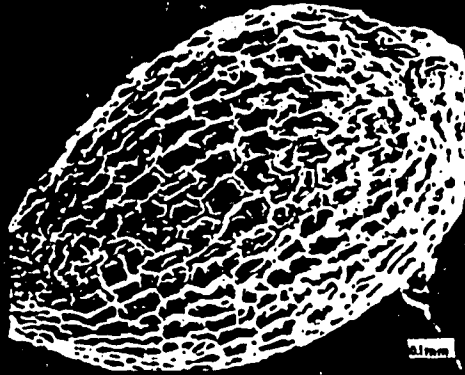
7A



7B



7C



7D



7E



7F

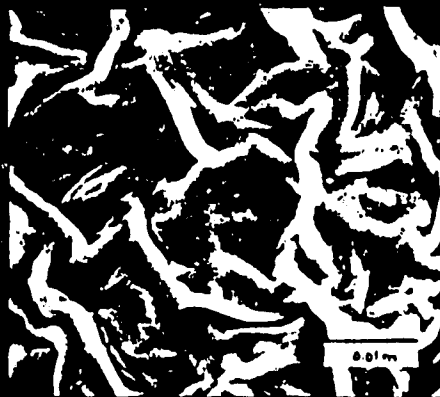


FIGURE 7

Luzula (Figs. 8A-G).

The seeds of six species of Luzula are all shown at low magnification only. Luzula gigantea has obliquely obovoidal slightly apiculate seeds (Fig. 8D). A completely smooth area represents the contact surface of the neighboring seed in the capsule. The larger part of the surface is irregularly wrinkled, but near the middle of the seed there is a reticulation of the outer seed coat. In L. denticulata the reticulation of the outer seed coat is more pronounced and covers a larger part of the seed surface (Fig. 8A). The reticulation appears somewhat regular, the meshes being arranged in longitudinal rows, but without regular shapes. The seed coat of a dried seed of L. denticulata was removed by forceps, and a much stronger reticulation was obvious on the inner seed coat (Fig. 8B). This reticulation was a distinct system of longitudinal rows of uneven meshes created by uniformly thick ridges lying over a smooth surface. Luzula ecuadoriensis has oblique obovoidal seeds with a smooth surface of longitudinal slightly bulging cells, but no obvious reticulation (Fig. 8C). Seeds of L. excelsa were not encountered in a fully ripe stage, so the longitudinally wrinkled surface seen on the photograph is probably not representative of that species (Fig. 8F). Luzula vulcanica (Fig. 8G) and L. racemosa (Fig. 8E) have very similar seeds. They are obovoidal with a longitudinal groove at the micropylar end surrounded by two lip like bulges. The surface of the seeds is almost completely smooth except for the lines indicating the circumference of the individual elongate rectangular or polygonal cells. Towards the micropylar and chalazal ends the surface cells are smaller and with bulging surfaces. Remnants of pollen tubes are seen sticking out of the micropyle of the L. vulcanica seed.

FIGURE 8

SEM images of Luzula seeds.

- 8A. Whole seed of L. denticulata with outer seed coat intact (From Burger & Leisner 7406, NY).
- 8B. Same with outer seed coat removed.
- 8C. Whole seed of L. ecuadoriensis (From Asplund 9685, S).
- 8D. Whole seed of L. gigantea (From Balslev AAU-24144, NY).
- 8E. Whole seed of L. racemosa (From Balslev AAU-24111, NY).
- 8F. Whole seed of L. excelsa (From Buchtien s.n., F).
- 8G. Whole seed of L. vulcanica (From Balslev AAU-23896, NY).

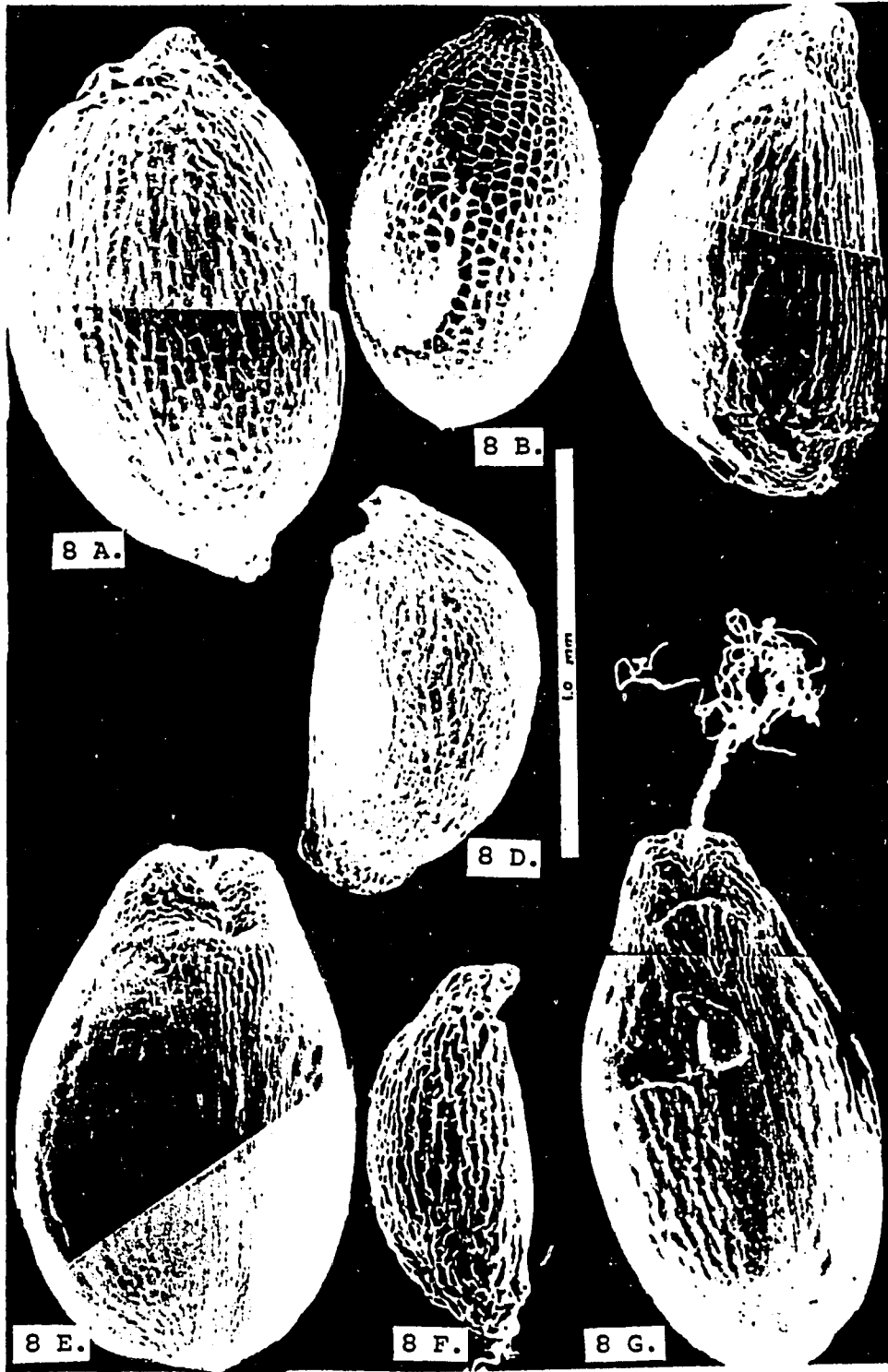


FIGURE 8

Juncus subgenus Juncus (Figs. 9A-F).

The seeds of Juncus roemerianus are obliquely ellipsoidal and shortly apiculate (Fig. 9A,B). The surface of a not fully ripe seed shown on the photograph has 13 longitudinal costae visible from one side. These are connected by less prominent transverse ridges lying much closer to one another. Thus four to seven transverse ridges occupy the length corresponding to the distance between two costae. At high magnification the costae appear superimposed upon the underlying layer of transverse ridges. A finer system of irregular wrinkles crosses freely over the costae. These wrinkles are separated by distances about as large as those between the costae. The seeds of J. maritimus (Fig. 9C,D) are oblong and distinctly tailed at both ends. One tail is turned to the side so the entire seed attains a strongly oblique shape, even if the central part is symmetrical. The central part of the seed exhibits about seven longitudinal ridges, not prominent enough to be called costae. They do not all run straight through, but some diverge. The longitudinal ridges are connected by transverse, unevenly-developed ones. The ridge system overlies a rather smooth and even surface. Towards the apices it changes into longitudinal wrinkles that run out into the seeds tails. At higher magnification the longitudinal and transverse ridges are seen overlying a smooth surface traversed by minute wrinkles. The seeds of J. acutus (Fig. 9E,F), have an ellipsoidal central part, and the outer seed coat is drawn out into two uneven tails at the ends of the seed. The chalazal tail of the seed is pointed and slightly oblique. The micropylar tail is flat and truncate. At low magnification the

FIGURE 9

SEM images of Juncus subg. Juncus seeds.

9A. Whole seed of J. roemerianus (From Oasting 3569, NY).

9B. Detail of same.

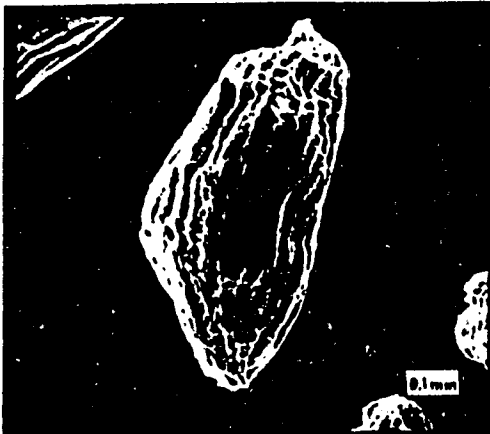
9C. Whole seed of J. maritimus (From Edinburg 514, NY).

9D. Detail of same.

9E. Whole seed of J. acutus subsp. leopoldii (From Schulz 6127, NY).

9F. Detail of same.

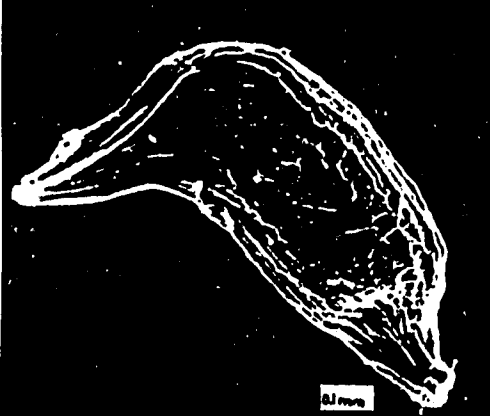
9 A.



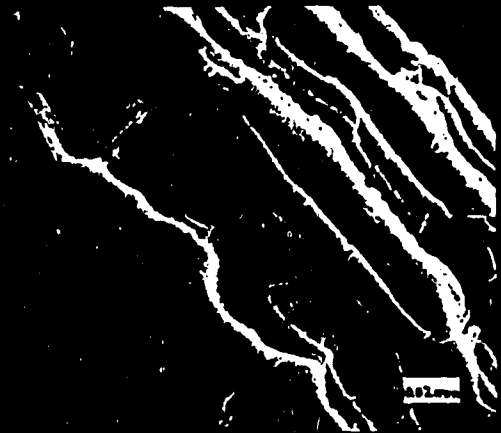
9 B.



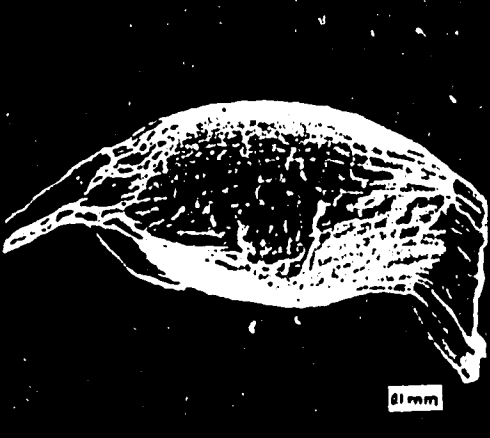
9 C.



9 D.



9 E.



9 F.

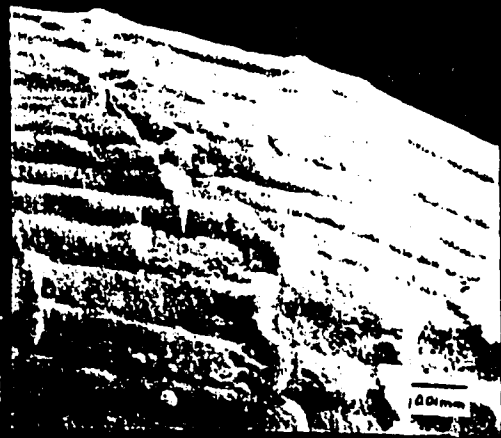


FIGURE 9

surface appears smooth. At high magnification a pattern of longitudinal cells is seen. These have a very slightly bulging surface. At regular intervals little transverse ridges spanning the width of the cells are seen. These may be lined up so a few of them create transverse ridges spanning more than one cell width.

Juncus subgenus Poiophylli (Figs. 10A-F).

The seeds of Juncus tenuis var. dichotomus (Fig. 10A,B) exhibit a honeycomb pattern of ten longitudinal rows of hexagons. The hexagons are not isodiametric but about one and a half times as wide as long. The margins of the hexagons are made up of elevated ridges. At high magnification the angles of the hexagons are seen to rise slightly higher. The areas between the ridges are smooth or slightly longitudinally wrinkled. The seeds of J. uruguensis (Fig. 10C,D) are oblong and slightly oblique. Weak traces of eight longitudinal rows of hexagons are seen below a thick outer seed coat. The hexagons are more compressed than those of J. tenuis var. dichotomus, and each one is about four times as wide as long. The outer seed coat shows a cell structure in the middle part of the seed. The cells are as wide as the underlying hexagons but seven to ten times as long. The ends of the outer seed coat cells are pointed or truncate. The seeds of J. bufonius (Fig. 10E,F) are ellipsoidal or barrel shaped, and shortly apiculate or truncate. The sculpturing comprises 20-25 rows of strongly longitudinally compressed hexagons. The compression has advanced to the point where the lateral ridges in the hexagons have fused to one longitudinal noded ridge, and the terminal ridges have approached so the space between them is reduced to a longitudinal groove or slit. At higher magnification

FIGURE 10

SEM images of Juncus subg. Poiophylli seeds.

10A. Whole seed of J. tenuis var. dichotomus (From Smith & Klein
13998, NY).

10B. Detail of same.

10C. Whole seed of J. uruguensis (From Herb. Parc. exper. 62, GH).

10D. Detail of same.

10E. Whole seed of J. bufonius (From Holm-Nielsen & Balslev 23586, NY).

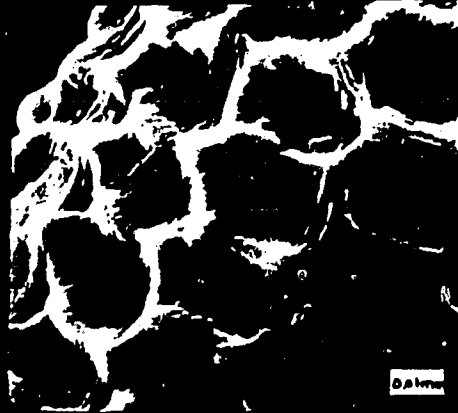
10F. Detail of same.

10 A.



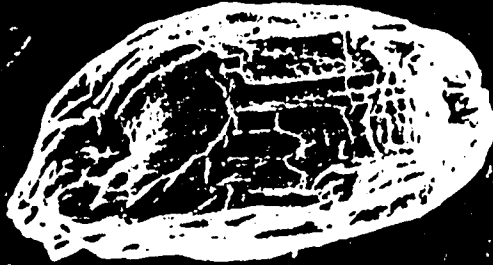
0.1mm

10 B.



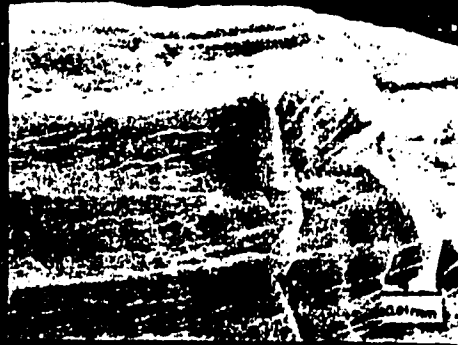
0.1mm

10 C.



0.1mm

10 D.



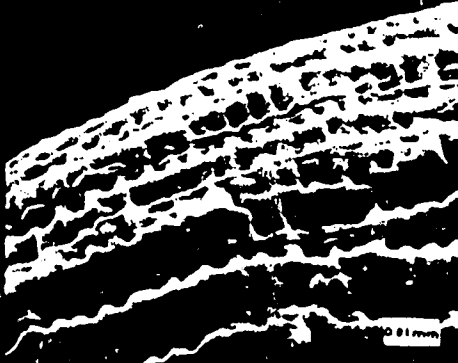
0.1mm

10 E.



0.1mm

10 F.



0.1mm

FIGURE 10

a delicate 'secondary longitudinal ridge' is seen running down the center of the line of compressed hexagons. The raphe is seen along the center line terminating in a little funiculus which attached the seed to the placenta. Immediately to the right of this the V-shaped micropyle is seen.

Juncus subgenus Genuini (Figs. 11A-F).

In this subgenus we also observe honeycomb pattern and modifications thereupon. Juncus procerus (Fig. 11A,B) has ellipsoidal distinctly apiculate seeds. The chalazal end of the seed has a large rounded and twisted appendage created by the extension of the outer seed coat, and the micropylar end has a truncate extension. Centrally the seed shows nine longitudinal rows of somewhat irregular hexagons. The longitudinal alignment is strict enough, but individual meshes are not always strictly hexagonal. In some cases an extra transverse ridge has developed in the center of the mesh. Under high magnification ridges similar to those of J. tenuis var. dichotomus are seen. They differ only in not having higher raised angles of the meshes. Delicate secondary longitudinal ridges run down the center of the row of meshes as in J. bufonius (subg. Poiophylli). In Juncus effusus (Fig. 11C,D) the seeds are obliquely ellipsoidal and slightly apiculate. The entire seed has a heavily wrinkled outer seed coat with seven to eight rows of hexagons near the middle of the seed. At higher magnification longitudinal wrinkles without signs of cell structure are seen. In the lower left corner weak indication of an underlying hexagon pattern is observed. Juncus arcticus (Fig. 11E,F) has obovoidal apiculate seeds with an outer seed coat which is even thicker than that of J. effusus. No sign of an underlying pattern is visible.

FIGURE 11

SEM images of Juncus subg. Genuini seeds.

11A. Whole seed of J. procerus (From Skottsberg 858, S).

11B. Detail of same.

11C. Whole seed of J. effusus (From Hermann 11342, US).

11D. Detail of same.

11E. Whole seed of J. arcticus var andicola (From Asplund 6910, NY).

11F. Detail of same.

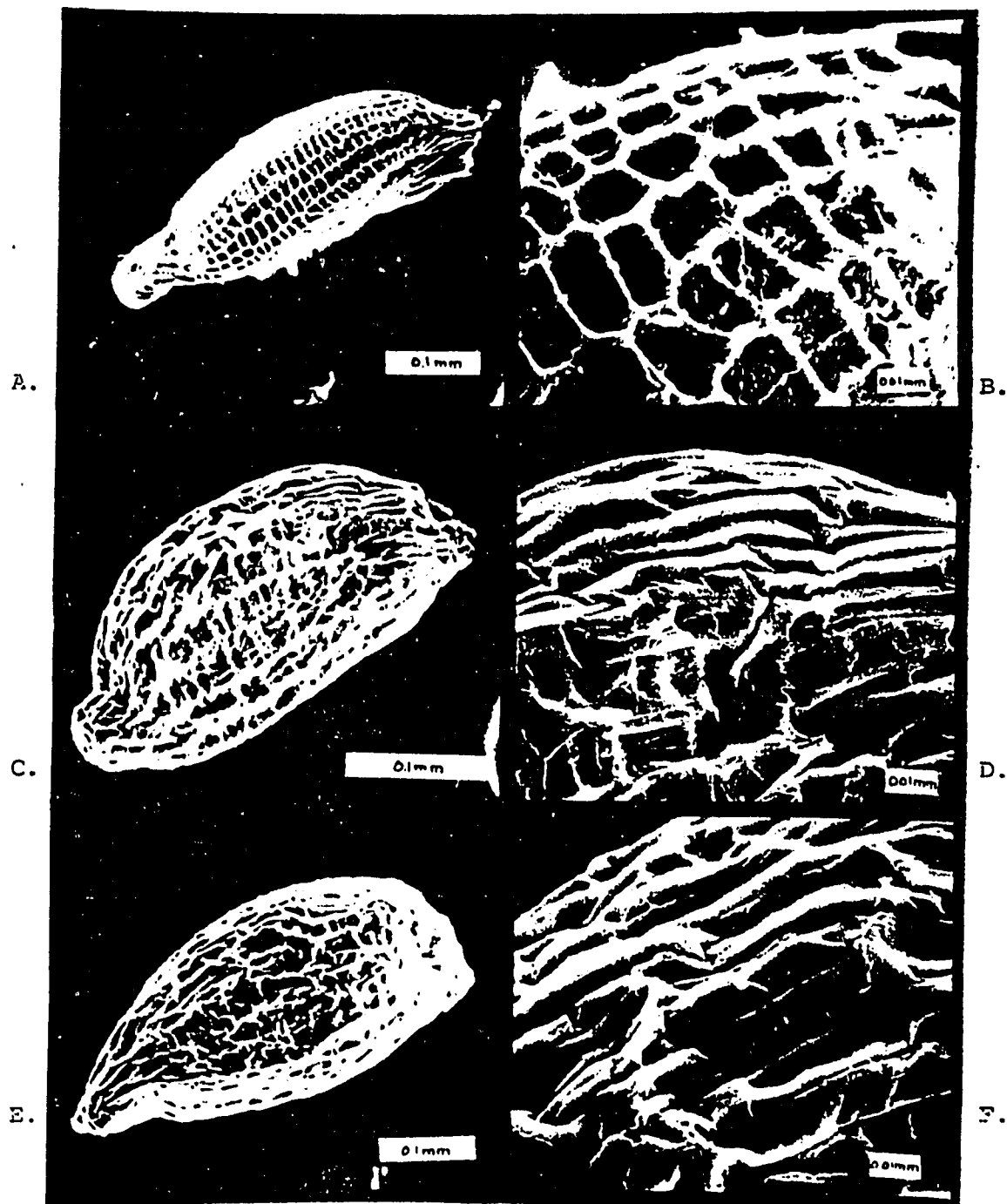


FIGURE 11

Juncus subgenus Graminifolii (Fig. 12A-F).

Juncus planifolius does not occur in the neotropical region but is included here to show that honeycomb patterns also occur in this subgenus, and that other species show modifications thereupon. The seeds of J. planifolius (Fig. 12A-B) are ellipsoidal and slightly apiculate. The photograph at low magnification shows a pattern of longitudinal rows of meshes. The high magnification photograph shows that in parts of the surface the meshes are in the shape of hexagons. In other parts it is obscured because the lateral sides of the meshes are straight and not V-shaped as in a hexagon. In still other parts there is an addition of extra transverse ridges. It is obvious that the ridge pattern is derived by only slight modifications of an original honeycomb pattern. Juncus marginatus (Fig. 12C,D) has obovoidal, clearly apiculate seeds. The seed coat exhibits eight to ten pronounced longitudinal costae, connected by thin transverse ridges. At high magnification delicate secondary longitudinal ridges are seen running down the seed midway between the costae. Juncus cyperoides (Fig. 12E,F) has ellipsoidal slightly apiculate seeds. The seed coat shows 10-12 longitudinal costae connected by transverse ridges which are about as prominent as the costae themselves, and separated by intervals as large as the distance between the costae, whereby a system of quadrat meshes emerges. The areas within the quadrat meshes are covered by transverse, less developed ridges or ripples lying so close that only a groove is left between them. A thin secondary longitudinal ridge runs down the seed just next to one of the costae.

FIGURE 12

SEM images of Juncus subg. Graminifolii seeds.

12A. Whole seed of J. planifolius (From Eyerdam 10604, NY).

12B. Detail of same.

12C. Whole seed of J. marginatus (From Smith & Reitz 995, NY).

12D. Detail of same.

12E. Whole seed of J. cyperoides (From Eyerdam 10137, NY).

12F. Detail of same.

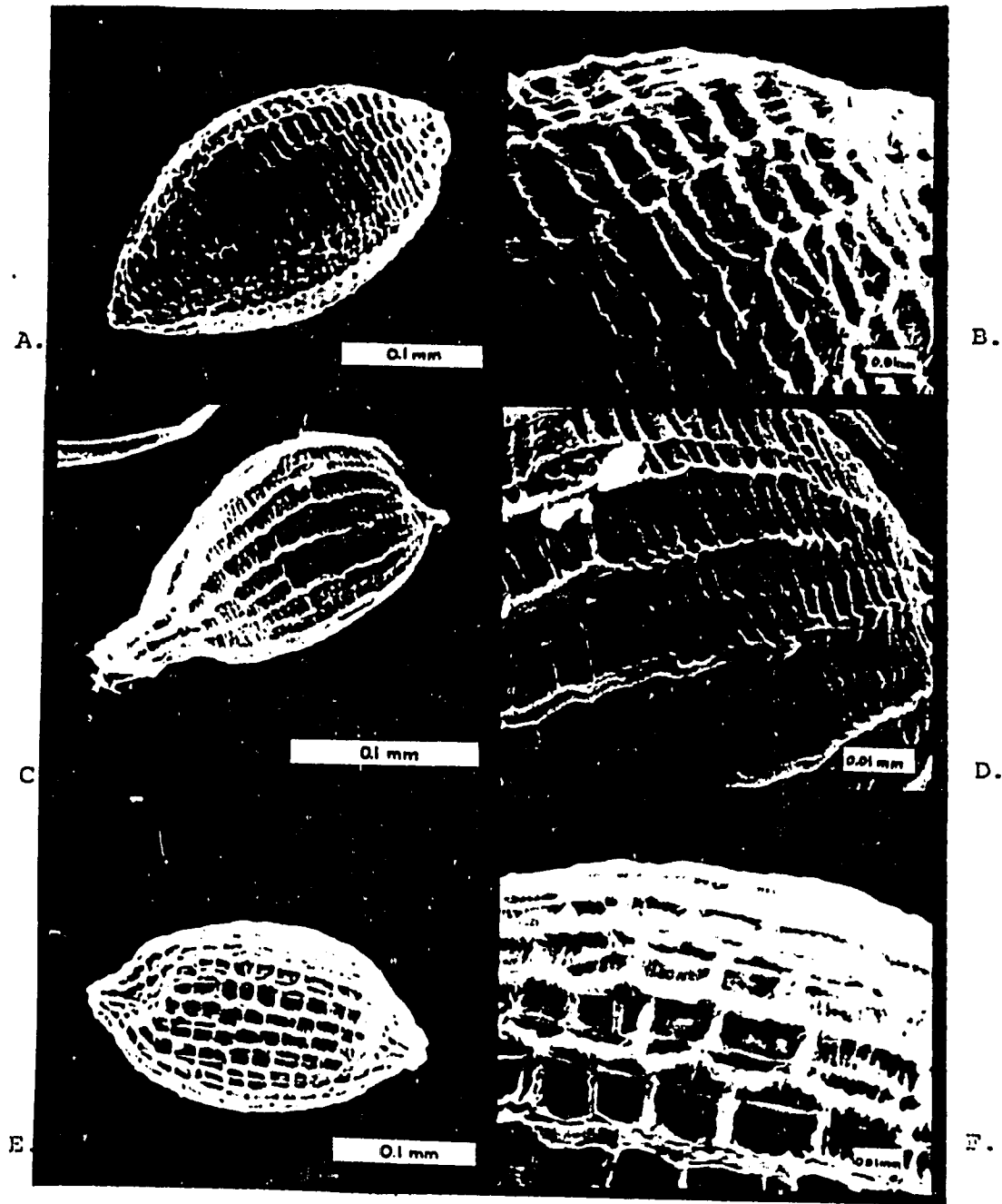


FIGURE 12

Juncus subgenus Septati (Figs. 13-15).

The seeds of this subgenus show variations upon the theme laid down by Juncus cyperoides of the subgenus Graminifolii. They are generally ellipsoidal or oblong and apiculate to various degrees. The seed coat sculpturing consists of a system of longitudinal costae connected by transverse ridges, some of which are usually thicker than the remaining. The costae and larger transverse ridges create a network of longitudinally arranged quadrangular or rectangular meshes. The areas delimited by costae and transverse ridges are striped by smaller transverse ridges or lines. Secondary longitudinal ridges run either down the center of a row of meshes or closer to one of the costae. The seeds of Juncus pallescens are ellipsoidal and apiculate (Fig. 13C,D). Costae and transverse ridges are well developed. There is no clear differentiation in two types of transverse ridges, though some are somewhat larger than the rest. The transverse ridges are thicker than the average in the subgenus, and secondary longitudinal ridges are lacking. Juncus ecuadoriensis has distinct longitudinal costae and well developed transverse ridges (Fig. 13E,F). This species lacks differentiation of stronger transverse ridges, but secondary longitudinal ridges occur, sometimes midway between two costae or sometimes closer to one costa. A distinct feature of the seeds of J. ecuadoriensis is small knobs where transverse ridges cross the costae, making the costae appear as long rows of knobs. Between the transverse ridges a smooth surface can be seen. Juncus microcephalus has ellipsoidal apiculate seeds (Fig. 13A,B). The sculpturing shows longitudinal costae and transverse ridges. The latter showing differentiation into larger and smaller ones. Secondary

FIGURE 13

SEM images of Juncus subg. Septati seeds.

13A. Whole seed of J. microcephalus (From Holm-Nielsen et al. 6943, NY).

13B. Detail of same.

13C. Whole seed of J. pallescens (From Prescott 781, NY).

13D. Detail of same.

13E. Whole seed of J. ecuadoriensis (From Idrobo et al. 431, MO).

13F. detail of same.

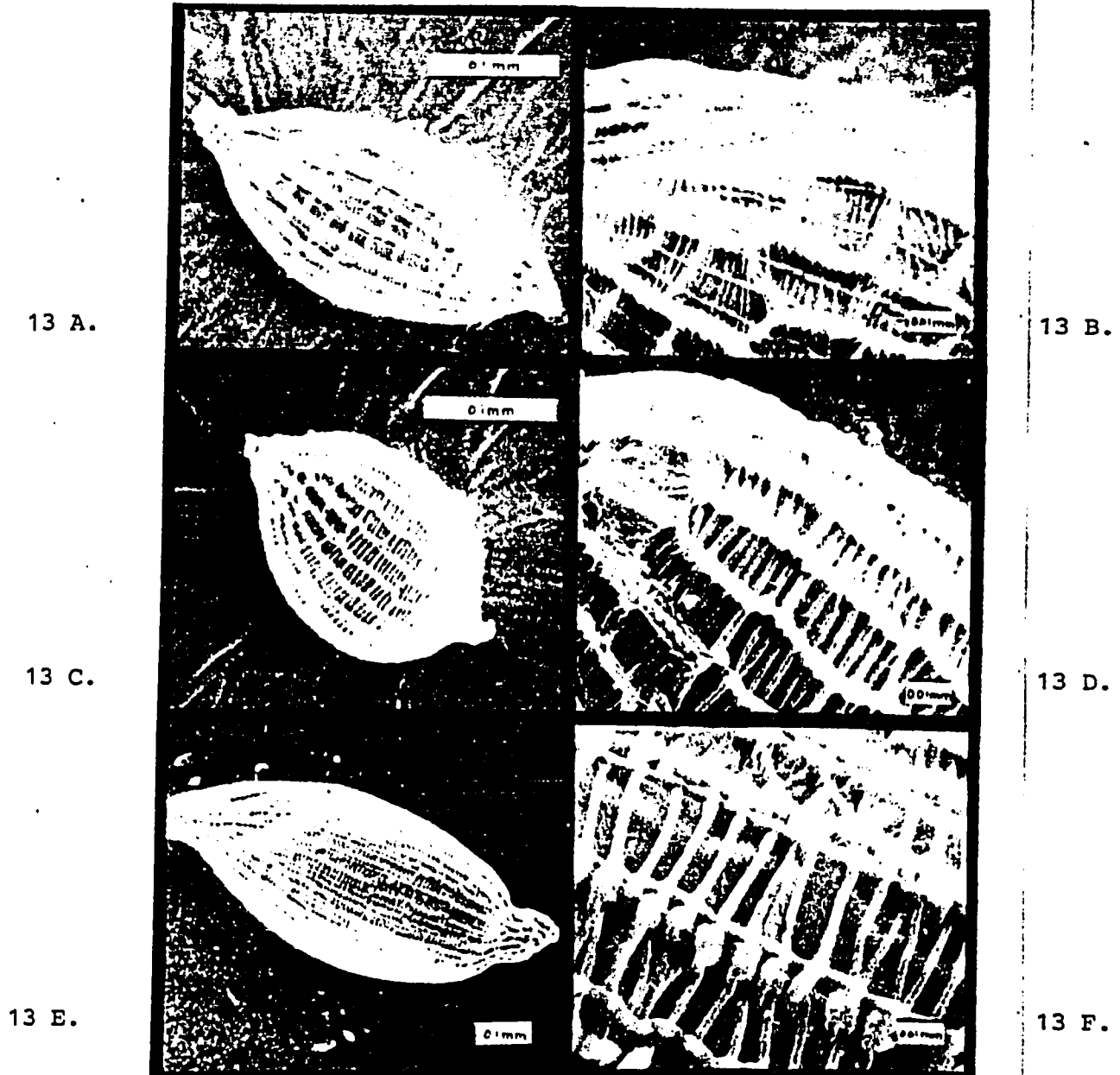


FIGURE 13

longitudinal ridges are well developed, sometimes up to three in each row of meshes, and then with one central and one along each of the bordering costae. Juncus stipulatus has ellipsoidal apiculate seeds (Fig. 14). The sculpturing shows longitudinal costae which tend to become obscured. Transverse ridges show differentiation in larger and smaller ones. Secondary longitudinal ridges run parallel to the costae, either midway between them or closer to one of them. Sometimes two secondary longitudinal ridges occur for each row of meshes. The distance between the small transverse ridges is reduced so only grooves or slits remain. The seeds of J. liebmannii var. liebmannii are ellipsoidal and apiculate (Fig. 15A,B). The sculpturing shows conspicuous longitudinal costae connected by equally prominent transverse ridges. There are no smaller transverse ridges and the meshes are occupied by a smooth surface, traversed only by two secondary longitudinal ridges per row of meshes. Juncus ebracteatus has obovoidal apiculate seeds (Fig. 15C,D). The sculpturing shows longitudinal rows of meshes, but longitudinal costae are not or barely discernible. The meshes are occupied by smaller densely lying ridges. Secondary longitudinal ridges run down the center of the rows of meshes.

Juncus subgenus Ensifolii (Fig. 15E,F).

Only one species, Juncus xiphioides, of this subgenus is represented in the neotropical flora, but no seed material was available. Instead the closely related Juncus ensifolius was examined. It has ellipsoidal, apiculate seeds (Fig. 15E,F). The sculpturing shows obvious longitudinal costae connected by large transverse ridges creating a network with smaller transverse ridges inside the meshes. One or two secondary longitudinal

FIGURE 14

SEM images of Juncus subg. Septati seeds.

14A. Whole seed of J. stipulatus (From Buchtien s.n. 11/2 1905, S).

14B. Detail of same.

14C. Whole seed of J. stipulatus (From Mexia 7884, S).

14D. Detail of same.

14E. Whole seed of J. stipulatus (From Dusén 5819, S).

14F. Detail of same.

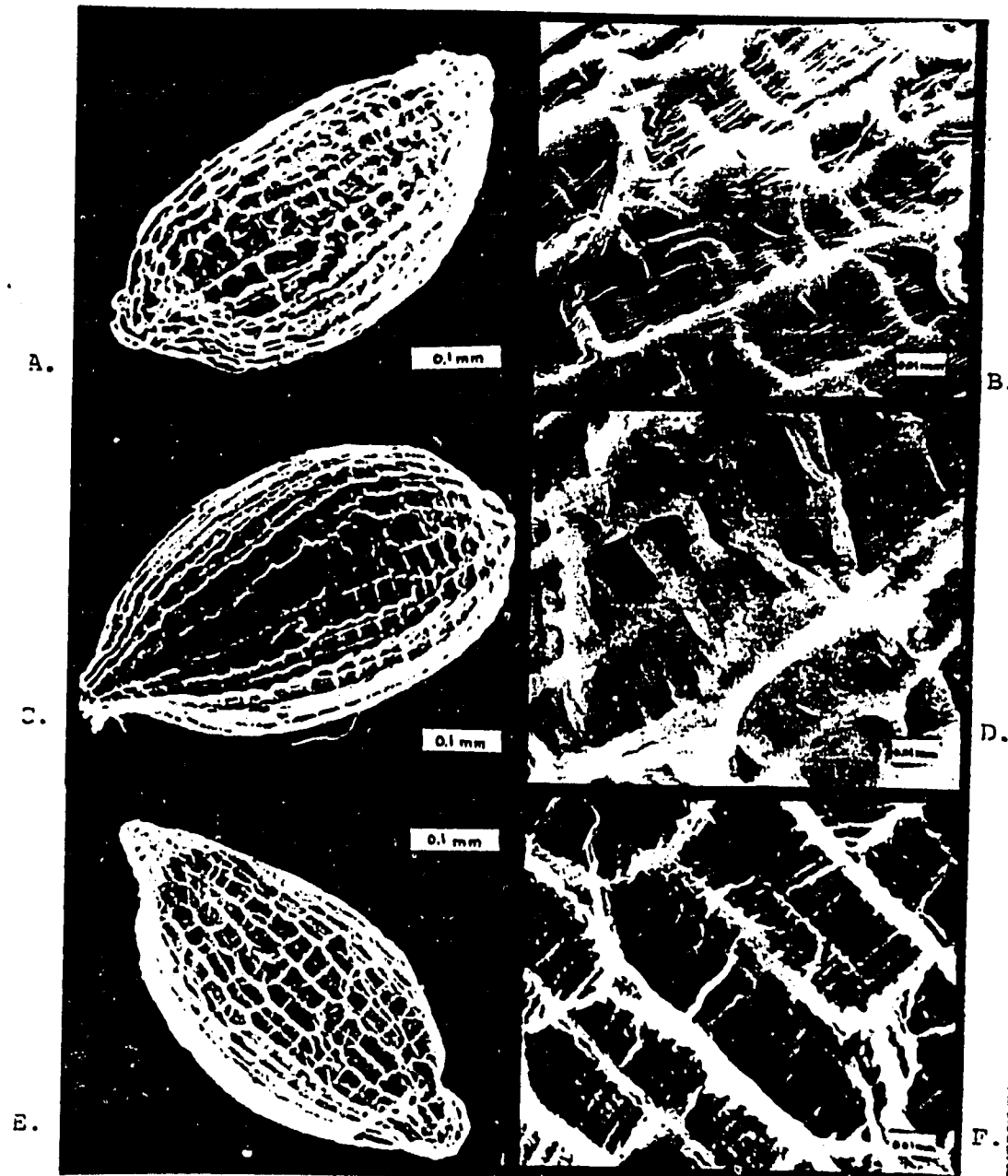


FIGURE 14

ridges run down each row of meshes. Some meshes also have strongly developed longitudinal ridges which are not part of the longitudinal costae. These are tertiary longitudinal ridges.

From the foregoing description of seeds of selected neotropic Juncaceae it is obvious that a tremendous diversity exists. Some of this diversity clearly shows evolutionary trends and phylogenetic relationships, other parts of it can at this point merely be interpreted as useful taxonomic distinctions between taxa. The smooth seeds of Rostkovia magellanica are very distinct and unlike any other seeds of neotropic Juncaceae, except for a superficial similarity to the seeds of certain species of Luzula. The seeds of Distichia muscoides and Oxychloe andina are similar in their very thick outer seed coat, and differs only in that Oxychloe shows a tendency towards regular net patterning, whereas Distichia is completely irregular in its sculpturing. On the basis of seed coat sculpturing Distichia and Oxychloe may thus be considered related, which is in accordance with other morphological data. In Luzula it is interesting to note that the two neotropic species of subgenus Anthelaea (L. gigantea and L. denticulata) show at least some reticulation of the outer seed coat, whereas reticulation was not observed in the remaining species which all belong to the subgenus Luzula. It is also noteworthy that the seeds of L. racemosa and L. vulcanica are practically indistinguishable. These two names have previously been considered synonymous. In Juncus I consider the honeycomb pattern so clearly shown by J. tenuis var. dichotomus and J. procerus as primitive. Within the subgenus Poiophylli there is

FIGURE 15

SEM images of Juncus subg. Septati and subg. Ensifolii seeds.

15A. Whole seed of J. liebmannii var. liebmannii (From Breedlove 15276, MO).

15B. Detail of same.

15C. Whole seed of J. ebracteatus (From Beck 1902, NY).

15D. Detail of same.

15E. Whole seed of J. ensifolius (From Wynd & Mueller 509, MO).

15F. Detail of same.

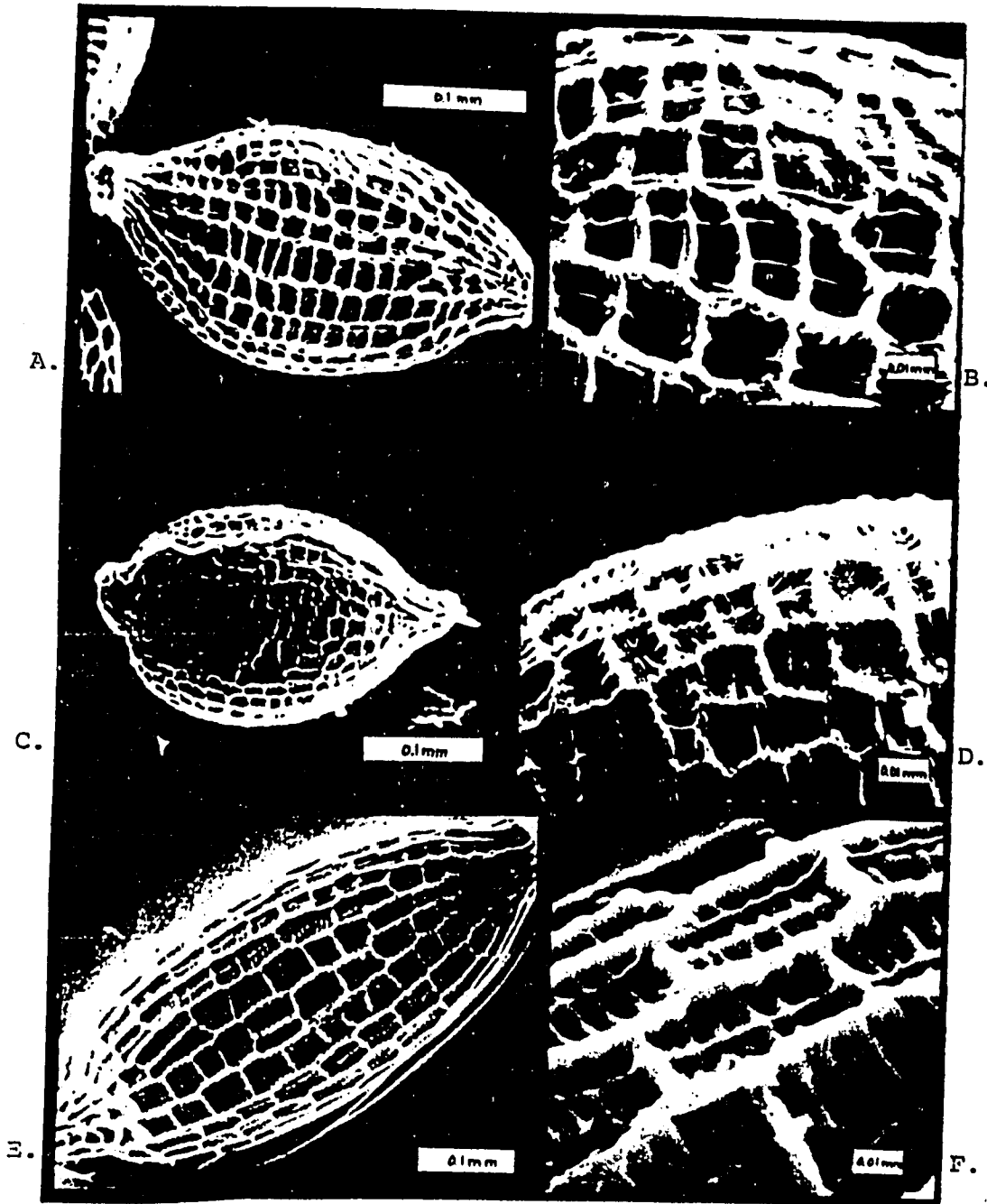


FIGURE 15

an evolutionary trend towards compression of the hexagons along the longitudinal axis of the seed, and another trend towards thicker outer seed coats obscuring the honeycomb pattern. Juncus bufonius shows the extreme degree of longitudinal compression. Juncus uruguensis shows some degree of longitudinal compression and a high degree of thickening of the outer seed coat. In Juncus subg. Genuini the primitive honeycomb pattern is observed in J. procerus. In J. effusus and J. arcticus there is both longitudinal compression and thickening of the outer seed coat. Juncus subg. Graminifolii also has honeycomb pattern as shown by J. planifolius. In this subgenus there is a trend towards development of longitudinal costae through the enforcement of the lateral ridges in the meshes of the honeycomb pattern, and the reduction of the terminal ridges of the meshes to become weakly developed transverse ridges. This is seen in J. marginatus. A further trend is the reinforcement of some of the transverse ridges to become large transverse ridges which together with the longitudinal costae creates a network of rectangles and quadrats, as seen in J. cyperoides. Development of secondary longitudinal ridges is observed in J. marginatus and J. cyperoides. In Juncus subg. Septati no major new inventions relative to subg. Graminifolii were observed, though it is evident that only sculpturing corresponding to the more advanced types of subg. Graminifolii is present. Thus all species observed in Juncus subg. Septati have a network of meshes created by longitudinal costae connected by large transverse ridges, with secondary (small) longitudinal ridges are present in most species. Some modifications upon this theme are obvious from the photographs and the above descriptions. Tertiary

longitudinal ridges may be considered a minor new invention in Juncus subg. Septati. Juncus subg. Ensifolii, as far as known from the observation of a single species, falls well within the variation seen in Juncus subg. Septati, from which it is considered derived for other reasons. Juncus subg. Juncus is treated first in the above descriptive section to follow the Systematic Treatment applied below.

As far as seed sculpturing goes it is more easily discussed at this point because of its derived seed sculpturing characteristics. Juncus roemerianus exhibits a sculpturing that is more similar to that of J. marginatus of the subg. Graminifolii than to any other species. Longitudinal costae are obvious, if not as prominent as in J. marginatus. These are connected by small transverse ridges. Large transverse ridges are lacking. Juncus maritimus exhibits a smoother surface with less prominent longitudinal and transverse ridges. Juncus acutus exhibits almost completely smooth seed surface. Subg. Juncus therefore exhibits an evolutionary trend towards smooth seed surface, and this trend seems originate in a pattern which corresponds to medium developed species in the subg. Graminifolii exemplified by J. marginatus. The seed sculpturing characteristics therefore link subgenus Juncus closer to the subgenera Septati, Graminifolii and Ensifolii, which are those with racemose inflorescences, than it links the subgenus to the cymose subgenera Poiophylli and Genuini.

CYTOLOGY

Chromosome numbers of Juncaceae show polyploidy and aneuploidy. The diffuse centromere, found at least in Luzula, makes chromosome fragmentation a possible evolutionary alley.

The diffuse centromere.

Malheiros & Castro (1947) reported diffuse centromeres in Luzula purpurea Link. They observed the chromosomes in anaphase taking the shape of a U with the ends towards the pole, rather than a V with the tip towards the pole. They could not observe any constrictions along the chromosomes. Such chromosome behavior was until then unknown in plants. Malheiros and Castro suggested it was related to a phenomena called 'diffuse centromere', which at that time had recently been reported in scorpions and Hemiptera. Malheiros & Garde (1947) studied chromosome numbers and dimensions in Luzula. They found chromosome dimensions of tetraploid Luzulae being little less than half of diploid ones, and those of octaploid half of the tetraploid. This led to suggestions that chromosomal evolution in Luzula is accomplished in part by the fragmentation of chromosomes. With a diffuse centromere spread over the length of the chromosome the spindle will attach itself at several points along the chromosome arms. Segments which for some reason break off the chromosomes will therefore be pulled to poles during anaphase in the same way as the main part of the chromosomes. The fragments can therefore remain functional in the genome rather than being lost. The suggestion of fragmentation as an evolutionary process led to a series of experiments, mainly by Nordenskiöld (1955, 1957a, 1957b,

1961, 1963, 1964). She artificially induced chromosome breakage and damage by X-irradiation and observed the subsequent chromosome behavior. One of the experiments showed that Luzula tolerates much higher X-ray doses than most other plants. This is easily explained if broken chromosomes remain functional in the genome. Additional chromosome counts, studies of chromosome size, and hybridization experiments have strengthened the hypothesis of fragmentation as a process involved in the chromosomal evolution of Luzula. Though diffuse centromeres are often said to occur "in Juncaceae", I have seen evidence for it only in Luzula.

Chromosome numbers.

Published diploid chromosome numbers in Juncus vary between 18 and 130 (Table II and Fig. 16). About one-third of the known species of the genus have been counted. The predominant numbers are $2n=40$, which occurs in about two-thirds, and $2n=80$, which occurs in about one-third of the counted species. The remaining diploid numbers have been reported from one or few species only. Löwe & Löwe (1944) suggested the basic number $x=5$, and Darlington & Wylie (1955) $x=8$ or 10 for Juncus. Snogerup (1963), however, suggested a series of nine secondary basic numbers within Juncus, ranging from $x=9$ to $x=25$. Within each subgenus he found one or two basic numbers. Harriman & Redmond (1976) suggested further basic numbers, so up to three basic numbers were reported in each subgenus. With the increasing number of species in which the chromosome numbers becomes known the number of basic numbers keeps increasing if designated according to such criteria as previously applied. Subgenus Poiophylli would now have seven basic numbers. This seems absurd

TABLE II. Diploid chromosome numbers in *Juncus*. Extracted from Fedorov, 1969; Harriman & Redmond, 1976, and Löwe, IOPB. Chromosome number reports in TAXON vol. 20-29.

Subgenus Juncus:

<i>Juncus acutus</i> (*)	46, 48
<i>maritimus</i> (*)	40, 48

Subgenus Subulati:

<i>Juncus subulatus</i>	42

Subgenus Poiophylli:

annuals:

<i>Juncus bufonius</i> (*)	30, 60, 80, 106, 108, 120
<i>ranarius</i>	30, 120
<i>sphaerocarpus</i>	36

perennials:

<i>Juncus compressus</i>	40, 44
<i>dichotomus</i> (*)	80
<i>dudleyi</i>	80
<i>greenii</i>	80
<i>gerardi</i>	80, 84
<i>interior</i>	80
<i>squarrosus</i>	40, 42
<i>tenuis</i> (=macer) (*)	30, 32, 40, 80
<i>trifidus</i>	30

Subgenus Genuini:

<i>Juncus arcticus</i> (*)	74, 80, 100
<i>balticus</i>	40, 80
<i>conglomeratus</i>	
(=leersii) (*)	40, 42
<i>coriaceus</i>	80
<i>effusus</i> (*)	40, 42
<i>effusus</i>	
v. <i>brunneus</i>	40
<i>filiformis</i>	40, 70, 80
<i>inflexus</i>	
(=glaucus)	20, 40

Subgenus Juncinella:

<i>Juncus capitatus</i>	18

Subgenus Alpini:

<i>Juncus biglumis</i>	100, 120 130 + 10
<i>castaneus</i>	40, 60
<i>membranaceus</i>	60
<i>triglumis</i>	50, 130

Subgenus Graminifolii:

<i>Juncus biflorus</i>	40
<i>covillei</i>	38
<i>filipendulus</i>	40
<i>marginatus</i> (*)	38, 40

Subgenus Septati:

<i>Juncus acuminatus</i> (*)	40
<i>acutiflorus</i>	40
<i>acutiflorus</i>	
x <i>articulatus</i>	60
<i>alpigenus</i>	40
<i>alpinus</i>	40, 80
<i>alpinus</i>	
v. <i>nodulosus</i>	40
<i>anceps</i>	40
<i>articulatus</i>	80
<i>atratus</i>	40
<i>atricapillus</i>	40
<i>brachycarpus</i>	44
<i>brachycephalus</i>	80
<i>brevicaudatus</i>	80
<i>bulbosus</i>	40
<i>canadensis</i>	80
<i>elliottii</i>	40
<i>lampocarpus</i>	60
<i>nodosus</i> (*)	40
<i>nodulosus</i>	40, 80
<i>pelocarpus</i>	40
<i>pygmaeus</i>	40
<i>rugulosus</i>	40
<i>scheuscherioides</i> (*)	40
<i>scirpoides</i>	44
<i>subnodulosus</i>	40
<i>subtilis</i>	40
<i>supinus</i>	40
<i>torreyi</i>	40
<i>trigonocarpus</i>	40
<i>validus</i>	40

Subgenus Ensifolii:

<i>Juncus ensifolius</i>	40
<i>xiphioides</i> (*)	40

Neotropical species marked with an (*)

FIGURE 16

Histogram of diploid chromosome numbers in Juncus.

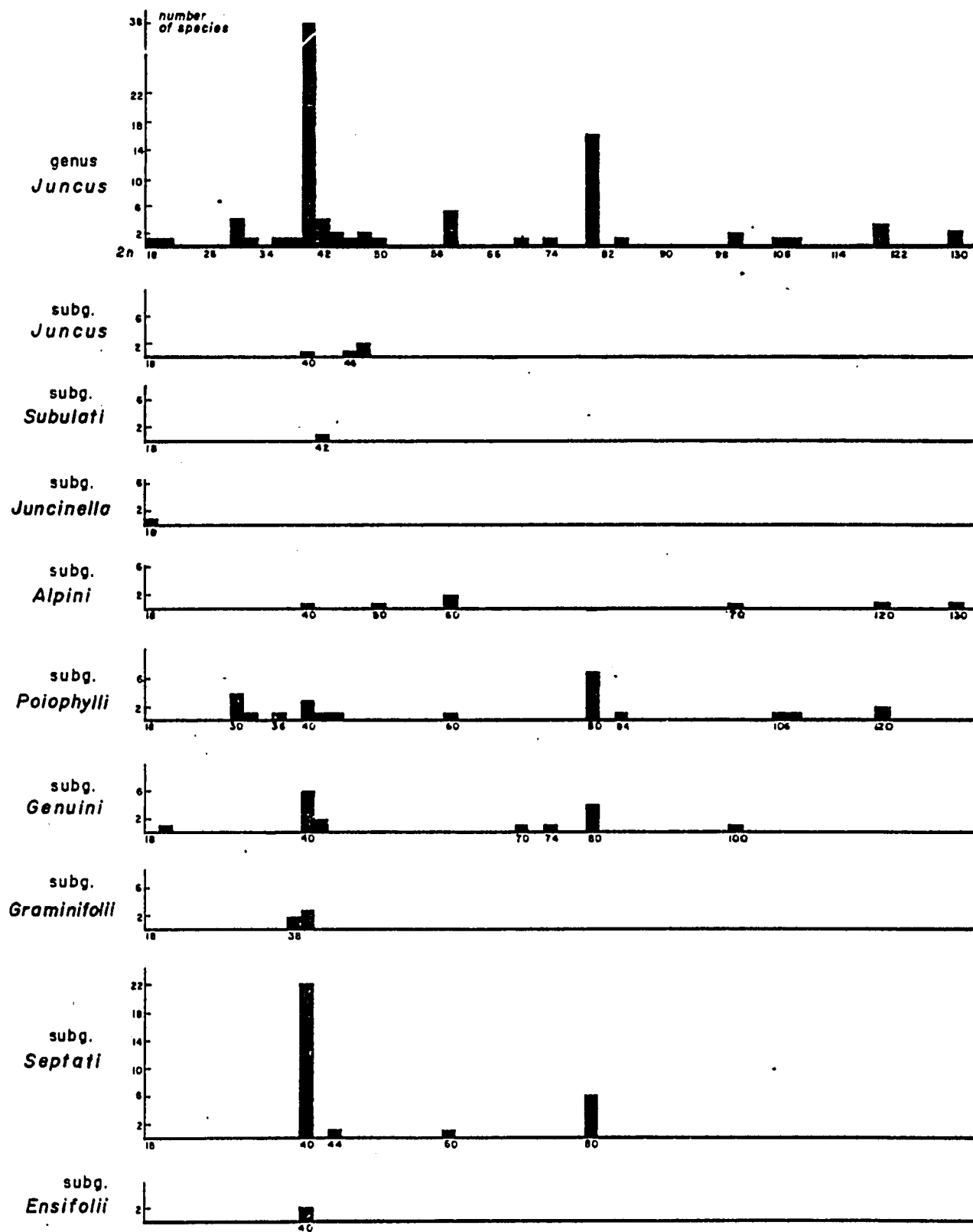


FIGURE 16

if the basic number is defined as the lowest haploid number in a polyploid series (Löwe & Löwe, 1975). From the data presented in Table II and Fig. 16, it is obvious that $2n=40$ is the most common diploid number in Juncus. It is found in seven of the nine subgenera, or all subgenera where more than one species been counted. $2n=80$ is likewise very common, and is easily derived from the doubling of $2n=40$. I favor the view of accepting only one basic number in Juncus, which may be $x=10$ or $x=20$. The numbers that cannot be derived by polyploidy from one of these basic numbers can then be regarded as aneuploid changes, superimposed on the polyploid series.

Chromosome numbers in Luzula vary between $2n=6$ and $2n=84$ (Table III and Fig. 17). From Fig. 17 it is obvious that multiples of 6 and 12 are overwhelming and a base number of $x=3$ or $x=6$ seems logical. Subgenus Marlenia is monotypic and seems derived because of its pseudorachis in the inflorescence. The diploid number of $2n=6$ in Luzula purpurea may thus be derived, even if it is the lowest in the genus. Subgenus Pterodes accounts for a high proportion of the higher numbers. Both subgenera Anthelaea and Luzula have $2n=12$ in the majority of their species, and exclusively or predominantly multiples of 12 in the remaining species. Some of the polyploidy in Luzula seems to have arisen through fragmentation of chromosomes.

Oxychloe andina is reported to have the diploid number $2n=16$ (Sasaki, 1937 in Fedorov, 1969).

The remaining genera of Juncaceae are unknown cytologically.

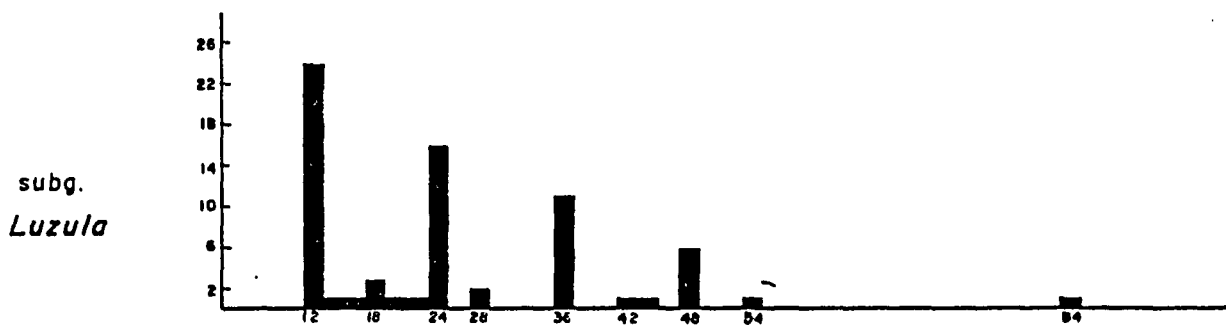
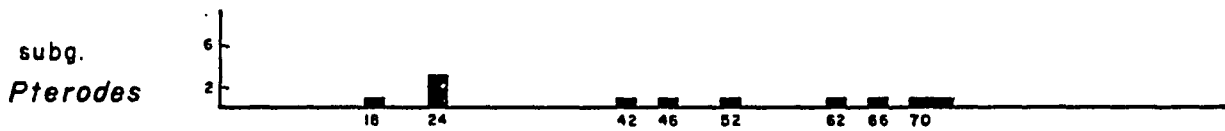
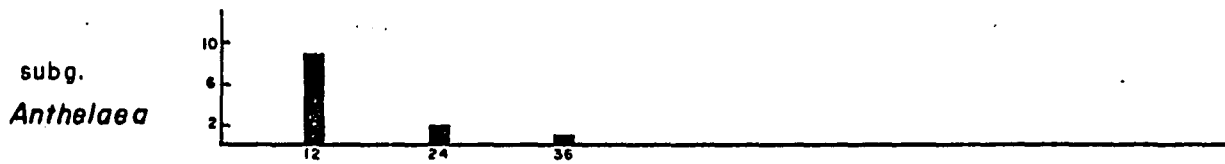
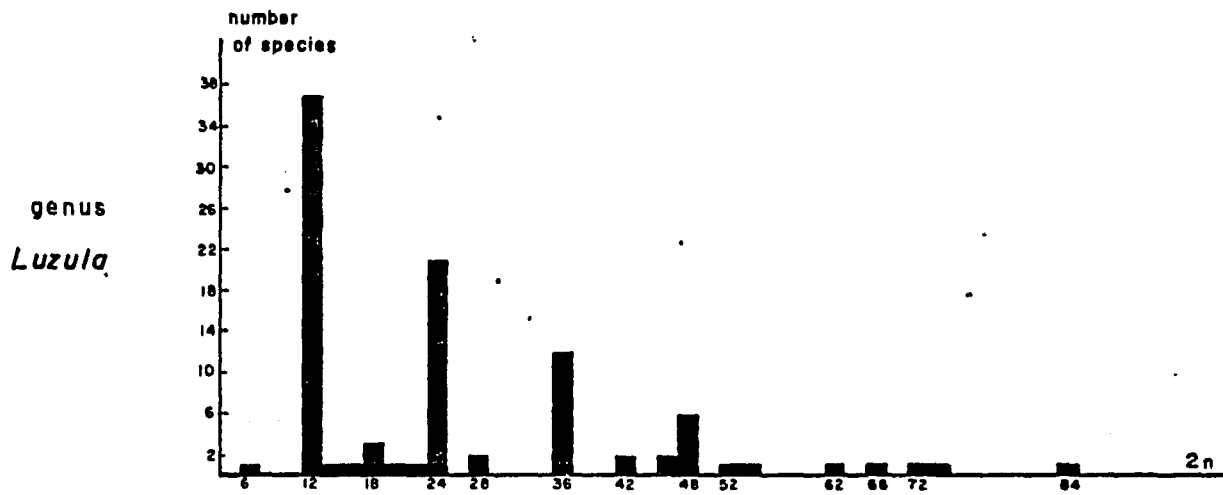
TABLE III. Diploid chromosome numbers in Luzula. Extracted from Fedorov, 1969, and Löve, IOPB Chromosome number reports in TAXON vol. 20-29.

<u>Subgenus Anthelaea:</u>		<u>Luzula celata</u>	12
<u>Luzula lutea</u>	12	<u>chilensis</u>	24
nemorosa	12	<u>colensoi</u>	12
silvatica	12	<u>columbiana</u>	12
canariensis	12	<u>comosa</u>	12, 24
lactea	12	<u>confusa</u>	36, 48
nivea	12	<u>congesta</u>	36, 48
seubertii	12	<u>crenulata</u>	12
glabrata	12	<u>decolor</u>	24
parviflora	24	<u>echinata</u>	12
spadicea	12	<u>frigida</u>	36
wahlenbergii	24, 36	<u>groenlandica</u>	24
<u>Subgenus Marlenia:</u>		<u>hawaiiensis</u>	28
<u>Luzula purpurea</u>	6	<u>henriquesii</u>	12, 84
<u>Subgenus Pterodes:</u>		<u>laxa</u>	12
<u>Luzula acuminata</u>	18	<u>leptophylla</u>	12
flavescens	24	<u>lutescens</u>	12
forsteri	24	<u>luzuloides</u>	12
johnstonii	42	<u>macrantha</u>	12
luzulina	24	<u>maxima</u>	12
pilosa	62, 66, 70, 72	<u>multiflora</u>	12, 18, 24, 28, 36, 48
plumosa	46	<u>nemorosa</u>	24
rufescens	52	<u>nivalis</u>	24
<u>Subgenus Luzula:</u>		<u>orestra</u>	20, 22
<u>Luzula abyssinica</u>	24	<u>pallescens</u>	12, 12-18, 36
arctica	24	<u>picta</u>	12
arcuata	36, 42, 48	<u>pumila</u>	12
alopecurus	24	<u>racemosa (*)</u>	24
australasica	24	<u>rufa</u>	12
banksiana	12	<u>spicata</u>	12, 14, 18, 24
beringensis	36	<u>subcongesta</u>	24
bulbosa	12	<u>sudetica</u>	12, 36, 48, 54
campestris (*)	12, 12+B, 16, 18, 24, 36	<u>traversii</u>	46
capitata	12	<u>tundricola</u>	24
		<u>ulophylla</u>	48
		<u>unalaschkensis</u>	36
		<u>vallesiaca</u>	36

Species occurring in the neotropical region marked with an (*).

FIGURE 17

Histogram of diploid chromosome numbers in Luzula.



Bate-Smith (1968) reported caffeic acid in Juncus ensifolius, J. effusus, J. inflexus and Luzula silvatica, and in addition quercetin in the latter. Stabursvik (1969, cited in Williams & Harborne, 1975) reported luteolin and its 7-glucoside in flowers of J. effusus and ten other species of Juncus and in L. silvatica. Fredga et al. (1973) identified several anthocyanins based on luteolinidin in L. pilosa, L. multiflorus, J. effusus, J. articulatus and J. bulbosus var. fluitans. Howard Miles et al. (1973, 1978) reported and described the cytotoxic phenol compound juncosol $C_{18}H_{18}O_2$ from Juncus roemerianus, and Pelletier et al. (1978) further analyzed this compound. Williams & Harborne (1975) surveyed 38 species in six genera of Juncaceae and found luteolin 5-methyl ether, both free and as the 7-glucoside, 7-glucosidephosphate of luteolin, 7,3',4'-Trihydroxyflavone and its 7-glucoside, 7,8-dihydroxycoumarin, daphnetin and its 8-methyl ether. Stasiak (1978) compared flavonoid patterns among populations of two species of Juncus.

The presence of luteolin 5-methyl ether and the coumarin daphnetin, and the absence of tricetin and C-glycosylflavones distinguishes Juncaceae from Poaceae and Cyperaceae. Williams & Harborne (1975), however, suggest that the mode of flavonoid synthesis is as advanced in Juncaceae as in Poaceae and Cyperaceae.

POLLINATION

Juncaceae are generally wind-pollinated and proterogynous. A syndrome of features adapts them to anemophilous pollination: small flowers in many-flowered inflorescences, dull-colored tepals, prominent and projecting stigmatic surfaces, plentiful pollen production and an exine which is thin and lacks sculpturing. Temporal separation of stigmatic receptivity and pollen production is the most common apparent isolating mechanism, though there is often overlap between the two. Self fertilization appears to be common. From this condition both cleistogamy and insect pollination has evolved. Insect pollination is known in some central European Luzulae with bright white flower heads and exposed anthers (Buchenau, 1892). Cleistogamy is well documented in Juncus bufonius and J. capitatus Buchenau, (1892, 1906), but occurs in several other species. It is usually found in combination with wind pollination in the same population. Reduction in the number of stamens accompanies development of cleistogamy. Opening of non-cleistogamous flowers is accomplished by turgor swelling of tissue basally in the flower, including the base of the filaments. There may be causal relationship between reduction in number of stamens and lack of opening of cleistogamous flowers (Buchenau, 1892).

The cushion-forming genera have developed unisexuality and dioecy as isolating mechanisms. Female flowers are hidden in leaf axils, and only the stigmas project above the cushions. Male flowers are lifted on 1-2 cm long pedicels above the cushion, and exposed to pollinating vectors. Distichia muscoides has male and female plants separated in different cushions. A cushion constitutes a clone, and can therefore

produce flowers of one sex only. Cushions of opposite sex may grow right next to one another, male and female flowers being only a few centimeters apart. Because of the sometimes considerable size of the cushions a flower may, however, be separated from the nearest one of opposite sex by several meters. When blooming, the flowers are specked over the entire surface of the cushion. Female flowers in the center of the cushion do become pollinated, as proven by the presence of capsules with seeds. The pollen vector is most likely wind, but flowering cushions are in some cases submerged in water, and the water may consequently transfer some pollen. No data is available as to the relative position of male and female plants in Patosia clandestina and Oxychloe andina. The former I have observed only in its sterile stage. The latter I have observed fertile in the field, but I never encountered more than one of the sexes in a given place.

ECOLOGY

All neotropical Juncaceae are terrestrial or semiaquatic and occur in sunlit places in the highlands, or sometimes at lower altitudes towards the northern and southern limits of the tropical region. In Ecuador, which lies on the equator, the lowest record of a Juncaceae comes from 1000 m altitude and the highest from 4800 m, but most collections were made between 2500 m and 4300 m (Fig. 18).

Oxychloe, Patosia and Distichia all grow at very high altitudes, usually between 3500 m and 4500 m. They are conspicuous elements of the páramo and puna vegetation, where they sometimes dominate in wet places. Distichia may form floating islands in bogs, or it may grow at the margin of creeks. It is also found near the highest limits of the vegetation, as one of the few plants that survives diurnal freezing and thawing. Oxychloe likewise is found at the margin of creeks, and Patosia is found in the humid so-called 'bofedal' vegetation in wet depressions over 3400 m.

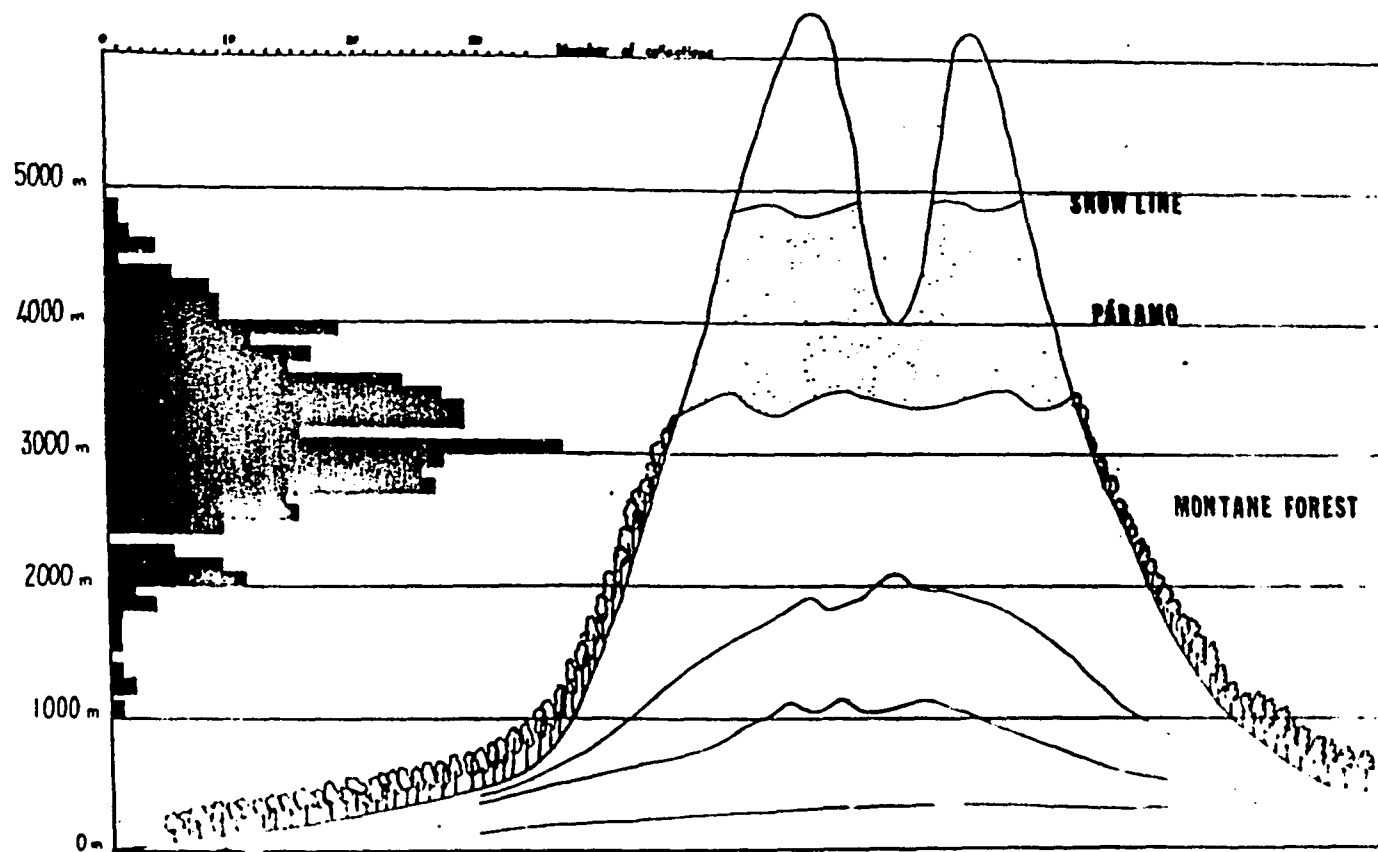
Luzula usually occur at lower altitudes than the cushion-forming genera, and is most often found in the drier bunch-grass páramo or puna. Luzula vulcanica is not typical of the genus, being restricted to boggy areas. Luzula gigantea is found mostly below the timberline, where it is a pioneer plant on newly cut roadbanks and landslides.

Juncus is quite different in that it is found mostly in habitats under human influence. Some species are obvious weeds, such as J. bufonius and J. tenuis, which are usually encountered in the gravel along the roadsides. Others seem to depend on the eutrophication by cattle farming in the páramos and montane valleys. Juncus arcticus

FIGURE 18

The altitudinal distribution of Juncaceae in Ecuador. The figure shows a diagrammatic transect of the two Andean cordilleras with the main vegetation types indicated. On the left side the total number of collections of Juncaceae made in any interval of 100 meters altitude is indicated in the form of a histogram.

FIGURE 18



var. andicola and J. echinocephalus belong to these plants that are often found in grazed areas. South American collections of J. arcticus var. mexicanus often come from the surroundings of old Inca ruins.

Juncus imbricatus and J. capillaceus are frequently encountered on hard soils in the dry interandine valleys. I often collected Juncus cyperoides in silt deposits in road ditches, and J. pallescens was once collected in a shallow mudlayer which had accumulated on top of the paved Panamerican Highway in Cuenca, Ecuador. In general, Juncus is thus anthropochorous, even if some species, such as J. stipulatus and J. ecuadoriensis, are often found in natural bogs in the páramos.

Rostkovia is only known from a few collections in the tropical region. They all come from natural and relatively untouched páramo vegetations, one of them from the margin of a lake. The ecology of Rostkovia magellanica was discussed in a previous publication (Balslev, 1979).

GEOGRAPHIC DISTRIBUTION

Juncaceae occur on all continents except Antarctica. The highest concentration of species is found in the temperate regions of both hemispheres. At tropical latitudes the family is found in the highlands only. In Ecuador, for example, the lower altitudinal limit is about 1000 m, but most collections come from above 2500 m altitude.

The monotypic Prionium is restricted to South Africa. Marsippospermum with three species occurs in Patagonia, the Falkland Islands and New Zealand. Rostkovia with two species likewise occurs in Patagonia, the Falkland Islands and New Zealand, but also on Tristan da Cunha, Gough Island, South Georgia, Campbell Island, and disjunctly in Ecuador (Fig. 19). Patosia is monotypic and occurs at high altitudes in the southern Andes from Bolivia to Nequen in Argentina. Oxychloe with possibly six species is also southern Andean, occurring from Ayacucho in Peru to Mendoza in Argentina. Distichia has one species along the Andes from Colombia to northern Argentina, and one species endemic to Bolivia.

Juncus covers the distributional range of the family, and is highly developed in both the north and south temperate regions. It extends into the neotropical mountains and occurs along the entire Mexican mountain range, and on all Central American mountains that reach above some 1200 meters altitude. In South America Juncus is found along the entire Andes chain, and spreads out into the lowlands in Paraguay, Argentina and Uruguay. In southeastern Brazil the genus occurs north to Bahia at altitudes above some 800 meters. I have seen one collection of Juncaceae only from the Guayana Highlands. That

FIGURE 19

Examples of north temperate and south temperate elements of Neotropical Juncaceae. The total distribution of Juncus effusus is indicated with a dotted signature, showing its wide occurrence in the north temperate regions of both the old and new worlds, and with scattered occurrences in the tropics and south temperate regions. The total distribution of the genus Rostkovia is indicated with a broken line. Rm is Rostkovia magellanica with a subantarctic distribution, and a disjunct occurrence in Ecuador. Rt is R. tristaniensis which is endemic to Tristan da Cunha.

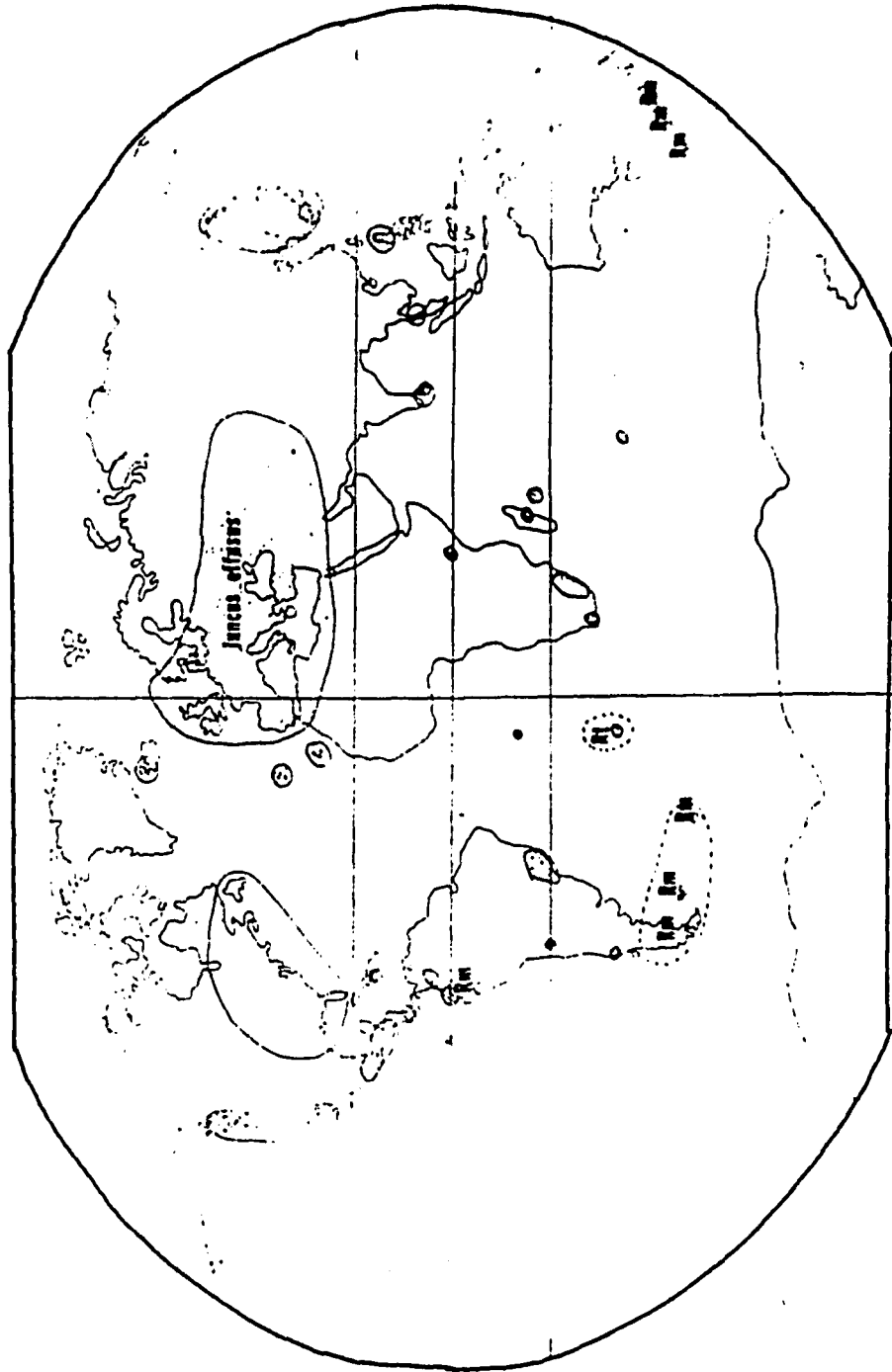


FIGURE 19

was a specimen of Juncus densiflorus from Soropán Tepui. Many species of Juncus are widespread. The halophytic subgenus Juncus has populations of the same species scattered along far removed seacoasts, and in the case of J. acutus also in inland salt deserts. Some weedy species, such as J. bufonius, are cosmopolitan. Other neotropic species are introduced widespread temperate ones such as J. effusus (Fig. 19). A number of species are widespread, but restricted to the neotropical region of South America, such as J. cyperoides and J. densiflorus. Other species have a restricted distribution within the neotropical region or South America, such as J. ramboi subsp. colombianus, J. uruguensis and J. breviculmis.

Luzula like Juncus is a mainly temperate genus with most of its species in the temperate regions. Luzula denticulata of the subgenus Anthelaea occurs in the Mexican and Central American mountains and is most closely related to the circumpolar Luzula parviflora complex, whereas the Andean L. gigantea of the same subgenus is most closely related to the eastern Asian L. effusa. In the subgenus Luzula there is the widespread and variable cosmopolitan species L. campestris which barely makes it into the neotropical region. Luzula racemosa is widespread in the neotropical region and most closely related to the circumpolar L. spicata. Luzula caricina, L. ecuadoriensis, L. excelsa and L. vulcanica are restricted to the neotropical region.

In general the neotropical Juncaceae have both north temperate and south temperate elements (Fig. 19), and some evolution has occurred within the neotropical region so there are a number of species which are restricted to or occurring mainly within the neotropical region (Table IV).

TABLE IV. Geographic affinities of neotropical Juncaceae. Three columns represent, 1. Mainly north temperate species, which have most of their area of distribution to the north of the neotropical region, 2. Mainly neotropical species, which have most or all of their area of distribution within the neotropical region, and 3. Mainly south temperate species, which have most of their area of distribution to the south of the neotropical region.

GENUS	Mainly North Temperate	Mainly Neotropical	Mainly South Temperate
<u>Rostkovia</u>			<u>magellanica</u>
<u>Distichia</u>		<u>muscoides</u> <u>filamentosa</u>	
<u>Patosia</u>			<u>clandestina</u>
<u>Oxychloe</u>			<u>andina</u>
<u>Luzula</u>	<u>campestris</u> <u>var. multiflora</u>	<u>gigantea</u> <u>denticulata</u> <u>campestris</u> <u>var. ulei</u> <u>caricina</u> <u>ecuadoriensis</u> <u>excelsa</u> <u>racemosa</u> <u>vulcanica</u>	
<u>Juncus</u>	<u>acutus</u> <u>roemerianus</u> <u>maritimus</u> <u>bufonius</u> <u>tenuis</u> <u>var. tenuis</u> <u>var. dichotomus</u> <u>effusus</u> <u>conglomeratus</u> <u>patens</u> <u>arcticus</u> <u>var. mexicanus</u> <u>var. montanus</u> <u>marginatus</u> <u>repens</u> <u>acuminatus</u> <u>debilis</u> <u>nodosus</u> <u>xiphioides</u>	<u>tenuis</u> <u>var. platycaulos</u> <u>arequipensis</u> <u>aemulans</u> <u>arcticus</u> <u>var. andicola</u> <u>ramboi</u> <u>subsp. colombianus</u> <u>microcephalus</u> <u>ecuadoriensis</u> <u>breviculmis</u> <u>guadeloupensis</u> <u>liebmannii</u> <u>var. liebmannii</u> <u>var. quitensis</u> <u>ebracteatus</u> <u>densiflorus</u> <u>echinocephalus</u> <u>ustulatus</u>	<u>imbricatus</u> <u>capillaceus</u> <u>uruguensis</u> <u>procerus</u> <u>cyperoides</u> <u>pallescent</u> <u>achalensis</u> <u>stipulatus</u> <u>micranthus</u>

USES

Few uses of Juncaceae are known. Standley (1937) reported that Juncus effusus is used in Dota, Costa Rica, for weaving mats which are used as mattresses. Standley & Steyermark (1952) reported that the same species is used in Coban, Guatemala, likewise for weaving mats. An Indian woman at Huancayo, Peru, told me when asked, that J. arcticus var. andicola has no particular use there, but that the cattle may eat it. Distichia muscoides is sometimes used by the highland indians for making fires because blocks of this cushion forming plant, when cut out and dried, are easily ignited (Ferreyra, 1979).

SYSTEMATIC TREATMENT

JUNCACEAE A. Jussieu, Gen. pl. 43. 1789 ("Junci"); Rostkovius, de

Iunco 1-59. 1801; Laharpe, Essai monogr. junc.

1-93. 1825, also published in Mém. Soc. Hist. Nat. Paris 3: 88-

181. 1827; Kunth, Enum. pl. 3: 293-378. 1841; Buchenau, Abh.

Naturwiss. Vereine Bremen 6: 353-431. 1879; Buchenau, Bot. Jahrb.

Syst. 12: 1-498. 1890; Buchenau in Engler, Pflanzenreich IV, 36

(Heft 25): 1-284. 1906. Type genus. Juncus Linnaeus.

Perennial and usually rhizomatous or rarely annual herbs, leaf margins glabrous or hairy. Rhizome creeping, ascending or erect, unbranched or branched, naked or covered by scales of splitting leaf bases. Culms erect or ascending, rarely procumbent, terete, smooth or longitudinally ridged, naked or leaf bearing. Leaves linear or filiform, with an open and sometimes auriculate or closed sheath, spirally arranged or rarely distichous, blades sometimes reduced. Inflorescence terminal, sometimes pseudolateral, compound, cymose or racemose, usually in heads or spike-like clusters, rarely reduced to a single terminal or lateral flower. Flowers generally small, tepals less than 8 mm long, rarely up to 40 mm long, perfect or imperfect, actinomorphic. Perianth segments 6, in two whorls of three, glumaceous, equal or almost equal, free. Stamens 6 in two whorls of three, opposite the perianth segments, inner whorl sometimes reduced. Filaments filiform, sometimes somewhat flattened and widened at the base. Anthers oblong to linear, basifixed, obtuse or mucronate, dehiscent by two longitudinal lateral slits.

Carpels 3, connate. Ovary superior, 1-locular, 3-septate or 3-locular. Style 1, usually short but sometimes up to 10 mm long. Stigmas 3, terete and of equal diameter throughout or sometimes tapering upwards, twining, with adaxial papillae. Fruit an orbicular to oblong or ellipsoidal, trilobed, round or trigonous, loculicidal capsule. Seeds usually many per capsule, sometimes 3; outer seed coat hyaline, whitish or light brown, sometimes drawn out into tail like appendages, often with distinct sculpturing; inner seed coat brown to castaneous or yellow.

A family of eight genera and about 300 species, most of which are confined to temperate or cold regions of the world. In the tropics the family is found only at high elevations, usually above 2000 m but sometimes as low as 1000 meters altitude. At the generic level Juncaceae is highly developed in South America with seven genera occurring there. Only one genus, the shrubby monotypic Prionium of southern Africa, is restricted to the old world. Of the seven South American genera one does not reach the tropical region (Marsippospermum, 3 species), three are mainly south temperate but reach into the neotropical region (Rostkovia, Patosia and Oxychloe), one is confined to the neotropical region (Distichia), and two are cosmopolitan (Juncus, Luzula).

Key to the neotropical Genera of Juncaceae

1. Flowers solitary; anthers mucronate.
2. Plants not cushion forming, culms erect naked 10-25 cm long.
Flowers terminal on the culms, bisexual, supported by two herbaceous bracts, one clearly overtopping the flower, and one about as long as the flower. 1. Rostkovia.
2. Plants cushion forming, culms not developed. Flowers on slender pedicels in the axils of subapical leaves, usually unisexual, with 1-2 membranaceous bracteoles which are shorter than the flower.
3. Leaves distichously arranged. Capsule lifted on gynophore at ripening. 2. Distichia.
3. Leaves spirally arranged. No gynophore at ripening.
4. Flowers with one bracteole. Leaf apex acute but not hard and stinging. 3. Patosia.
4. Flowers with two bracteoles. Leaf apex acute and stinging. 4. Oxychloe.
1. Flowers in many flowered (or rarely few flowered) inflorescences; anthers not mucronate.
5. Leaf sheaths closed; blades with hairy margins. Capsule with three seeds. 5. Luzula.
5. Leaf sheaths open; blades glabrous. Capsule with many (up to 120) seeds. 6. Juncus.

1. *Rostkovia* Desvaux, J. Bot. (Desvaux) 1: 324. 1809; J. D. Hooker, Fl. antarct. 1: 81. 1844; Gay, Fl. chil. 6: 149. 1853; Buchenau, Abh. Naturwiss. Vereine Bremen 6: 375. 1879; Bentham & Hooker, Gen. pl. 3: 867. 1883; Buchenau, Bot. Jahrb. Syst. 12: 69. 1890; Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 39. 1906; Hauman. An. Mus. Nac. Hist. Nat. Buenos Aires 27: 300. 1915; Barros, Darwiniana 10: 312. 1953; Moore, Brit. Antarct. Surv. Sci. Rep. 60: 142-143. 1968; Barros in Correa (ed.), Fl. Patagonica 2: 114. 1969; Moore & Edgar, Fl. New Zealand 2: 56. 1970; Balslev, Fl. Ecuador 11: 5. 1979. Type species. *Rostkovia magellanica* (Lamarck) J. D. Hooker.

Erect, glabrous, perennial herbs. Culms naked. Leaves all basal, spirally arranged, linear or with reduced blade, stomata restricted to two narrow, abaxial bands of lighter color, one on each side of the midrib. Inflorescence reduced to a single, large, terminal, bisexual flower. Stamens 6, with linear, mucronate anthers. Ovary sessile. Style with 3 tapering, twining stigmas. Capsule sub-orbicular, unilocular or slightly 3-septate, sessile. Seeds many.

The name *Rostkovia* honors F. W. G. Rostkovius, a medical counselor from Stettin, who published a monograph of *Juncus* in 1801.

Distribution. Two species. One (*R. tristaniensis*) is endemic to Tristan da Cunha, and the other (*R. magellanica*) occurs on the subantarctic islands from New Zealand to South Georgia, and on the mainland of South America, disjunct between Patagonia and Ecuador (Fig. 19).

Rostkovia was separated as a genus by Desvaux (1809) to accommodate the single species, Juncus magellanicus, described by Lamarck (1789). He gave it the new name Rostkovia sphaerocarpa. The most important diagnostic features mentioned were the globose, unilocular and non-dehiscing capsule. Rostkovia was not immediately accepted, and several authors retained the name Juncus magellanicus (e.g. Meyer, 1822; Laharpe, 1827; Gaudichaud, 1825, d'Urville, 1826; Roemer & Schultes, 1829; Kunth, 1841). Hooker (1844) re-established the genus Rostkovia, and made the correct combination with the original Lamarckian specific epithet. He included the species now referred to Marsippospermum in the genus, because they also have "singularly large and solitary flowers...together with the elongated style and the disproportionate size of the stigmata (which are) characters peculiar to all of these, and appear of sufficient importance to warrant retaining them under a separate generic name" (Hooker, 1844). Buchenau (1879, 1890, 1906) treated Rostkovia as a monotypic genus, as it was originally described. He distinguished it from Marsippospermum on its long leaf-like floral bracts (vs. small and membranaceous), one cm long flower (vs. 1.5-4 cm), obovate seeds (vs. scobiform), and canaliculate leaf blade (vs. terete). I apply the same generic concept as Buchenau. To the characters peculiar to Rostkovia can now be added the restriction of the stomata to two narrow bands, one on each side of the midrib, which is unique in the family. Christophersen (1944) described a second species, R. tristanensis, from Tristan da Cunha. (Type. Mejland 1516. Holotype, O, n.v.; Isotypes, BM, GH, K). In our area only one species is represented.

1. *Rostkovia magellanica* (Lamarck) J. D. Hooker, Fl. antar. 1: 87.

1844.

Figs. 19, 20 D-E, 22 A.

Juncus magellanicus Lamarck, Encycl. 3: 266. 1789. Type.

Chile. Magellan, Commerson s.n. (holotype, P; photo of holotype, AAU; isotypes, P, US).

Rostkovia sphaerocarpa Desvaux, J. Bot. (Desvaux) 1: 327, pl. 12,

f. 2. 1809. Basionym. *Juncus magellanicus* Lamarck.

Rostkovia magellanica (Lamarck) J. D. Hooker forma *pumila* Alboff,

Rev. Mus de La Plata 7: 353. 1896. Type. Argentina. Source

gauche du Río Grande, region alpine, 1896, Alboff 808 (n.v., possibly at CORD, LP or SI).

Loosely caespitose herb, 15-30 cm high. Rhizome erect or ascending, sometimes short creeping, 1.5-2.5 mm diam., occasionally with runners covered with brown, 1-1.5 cm long scales, 0.5-1 cm apart. Culms erect, 0.5-1 mm diam., with unevenly spaced longitudinal ridges. Cataphylls 2-4 per culm, to 7 cm long, longitudinally ridged, light brown, with smooth reddish brown margin; rudimentary blade to 4 mm long. Blade bearing leaves 15-25 cm long; sheaths resembling cataphylls, sometimes slightly longer, auricles ca. 1 mm long, rounded; blade flat, slightly trigonous or channeled adaxially, narrowly grooved along abaxial midrib. Pedicel 1-3 mm long. Flower subtended by a long, leaf like lower bract to 4 cm long, and a scale like upper bract to 1 cm long. Tepals equal, lanceolate, 6-7 mm long, dark reddish brown, gradually membranaceous towards the margin, appearing acuminate, but obtuse with inflexed margins; inner tepals with inflexed apex also. Stamens ca.

4.5 mm long; filaments linear, flat; anthers ca. 2.5 mm long, mucronate. Style ca. 4 mm; stigmas ca. 2.5 mm long. Capsule ca. 4 mm wide, thick walled, dark brown to blackish. Seeds oblong to ovoidal, ca. 1.3 x 0.8 mm, shiny, smooth with fine color pattern of longitudinal blackish rectangles.

Distribution. A mainly subantarctic and trans-Pacific species. . The western Pacific occurrence includes the mainland of New Zealand, the Auckland Islands and the Campbell Islands. East of the Pacific Ocean it occurs in Patagonia, the Falkland Islands and South Georgia, and disjunctly in Ecuador. Collections of this species are plentiful from Patagonia and the Falkland Islands, whereas more scanty material exists from the other areas. The distribution, ecology and history of discovery of R. magellanica were discussed by Balslev (1979b)(Fig. 22A).

Specimens examined. ECUADOR. Chimborazo: Condorasto, 3950 m, 1859, Jameson s.n. (K). Cotopaxi: Mulatos páramo, 3950 m, 7 Mar 1953, Prescott 685 (NY). Loja: Amaluza, 10-12 km ENE of the village (nr Laguna Negra), 3000-3400 m, 23 Sep 1976, Øllgaard & Balslev 9772 (AAU). Apart from these specimens many extratropical collections have been examined and annotated.

EXCLUDED NAMES

Rostkovia (?) brevifolia Philippi, Linnaea 29: 76. 1857. = Patosia
clandestina (Philippi) Buchenau.

Rostkovia (?) clandestina Philippi, Linnaea 29: 76. 1857. = Patosia
clandestina (Philippi) Buchenau.

Rostkovia ensiformis J. D. Hooker, Fl. Brit. India 6: 396. 1892 nom.
in syn. = Juncus prismatocarpus R. Brown.

Rostkovia gracilis J. D. Hooker, Fl. antarct. 1: 83. 1844. = Marsippo-
spermum gracile (J. D. Hooker) Buchenau.

Rostkovia gracilis Philippi, Linnaea 29: 75. 1857. = Marsippospermum
grandiflorum (Linnaeus f.) J. D. Hooker var. philippi Buchenau.

Rostkovia grandiflora J. D. Hooker, Fl. antarct. 1: 82. 1844. = Mar-
sippospermum grandiflorum (Linnaeus f.) J. D. Hooker.

Rostkovia Novae Zeelandiae Buchanan, Trans. & Proc. New Zealand Inst.
4: 227, t.16, 10. 1871. = Marsippospermum gracile (J. D. Hooker)
Buchenau var. Novae Zeelandiae (Buchanan) Buchenau.

FIGURE 20

Habit and details of Distichia muscoides and Rostkovia magellanica
(From Balslev, 1979a).

20A. Habit of D. muscoides (Drawn from Holm-Nielsen et al. 6732, AAU).

20B. Fruiting shoot of same (Drawn from Øllgaard & Balslev 8435, AAU).

20C. Male flowering shoot of same (Drawn from Jameson s.n., K).

20D. Habit of R. magellanica (Drawn from Øllgaard & Balslev 9772, AAU).

20E. Flower of same.

20F. Fruit of same.



DISTICHIA

2. *Distichia* Nees & Meyen in Meyen, Reise um die Erde, Theil 4 (Beiträge zur Botanik): 128. 1843, also published as Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 16 Suppl. 2, which is at the same time vol. 19 Suppl. 1; Steudel, Syn. pl. glum. 2: 309. 1855; Buchenau, Abh. Naturwiss. Vereine Bremen 6: 369. 1879; Benthams & Hooker, Gen. pl. 3: 866. 1883; Buchenau in Engler & Prantl, Nat. Pflanzenfam. 2 (5): 4. 1887; Buchenau, Bot. Jahrb. Syst. 12: 60. 1890; Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 33. 1906; Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 27: 300. 1915; Hauman & Vanderveken, Cat. phan. Argentine 1: 254. 1917; Castillon, Bol. Mus. Hist. Nat. Tucumán 7: 6. 1926; Vierhapper in Engler & Prantl, Nat. Pflanzenfam. 2 ed., 15a: 221. 1930; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 610. 1936; Barros, Darwiniana 10: 288. 1953; Balslev, Fl. Ecuador 11: 4. 1979. Type species. *Distichia muscoides* Nees & Meyen.

Goudotia Decaisne, Ann. Sci. Nat. (Paris), Ser. 3. 4: 83. 1845.

Type species. *Goudotia tolimensis* Decaisne.

Agapatea Steudel, Bot. Zeitung (Berlin) 14: 391. 1856, nom. nud.;

Buchenau, Abh. Naturwiss. Vereine Bremen 4: 124. 1874.

Distichia Nees & Meyen section *Goudotia* (Decaisne) Benthams &

Hooker, Gen. pl. 3: 367. 1883.

Perennial, glabrous, cushion-forming herbs. Stems more or less regularly forked and covered with persisting leaves. Leaves regularly, densely and strictly distichous, inserted along the stem, with a wide sheath clasping the leaf above. Blade shorter than the sheath, terete. Inflorescence reduced to a single lateral, subapical flower. Plants dioecious. Flowers supported by 2-4 minute membranaceous bracteoles. Tepals lanceolate. Male flower long pedicellate; stamens 6, with linear mucronate anthers about 10 times as long as the filaments. Female flower short pedicellate; ovary on a short gynophore; style with 3 filiform stigmas, covered with sticky papillae. Capsule unilocular, lifted on a gynophore at ripening. Seeds many.

The name Distichia refers to the distichous arrangement of the leaves.

Distribution. A small genus with only two known species. Distichia muscoides is distributed at high altitudes in the Andes from Colombia to northern Argentina, and D. filamentosa is endemic to Bolivia.

Taxonomic History of Distichia

Distichia was described by C. G. Nees ab Esenbeck (in Meyen, 1843) in a treatment of the Juncaceae that Meyen collected on a voyage around the world. A single specimen, collected at Pisacoma in Peru, was given the name D. muscoides, drawing attention to its distichous leaf arrangement and its moss-like habit. Only two years later Decaisne (1845) described Goudotia tolimensis as a new genus and species, based on

Goudot material from Tolima in 'Nouvelle-Grenade' (=Colombia). Steudel (1856) invalidly published the genus name Agapatea in a list of plants sent to Berlin from Peru by Lechler. Simultaneously (in Lechler, 1857) he published the species name A. peruviana as a nomen nudum. Buchenau (1874) in his treatment of Mandon's Juncaceae from Bolivia took up the name Agapatea. He identified one plant as 'A. peruviana Steudel' and an other as 'A. filamentosa Buchenau n. sp.' creating another nomen nudum. He was apparently unaware of the name Goudotia of Decaisne, and he believed that Distichia Nees & Meyen belonged in the Poaceae. Five years later, in his account of the South American Juncaceae (Buchenau, 1879), he accepted Distichia as belonging to Juncaceae, and placed A. peruviana in synonymy under D. muscoides. He also transferred A. filamentosa and Rostkovia clandestina to Distichia. This latter species has since been removed from the genus. The following year Buchenau (1880) became aware of Decaisne's genus Goudotia. He realized the generic relationship to Distichia and made the new combination D. tolimensis (Decaisne) Buchenau. Bentham & Hooker (1883) accepted Distichia, but included the genus Oxychloe (Philippi, 1860) in it. In his monograph of the entire Juncaceae Buchenau (1890) removed Oxychloe, and treated Distichia as a genus of three species: D. tolimensis, D. muscoides, and D. filamentosa. That situation was accepted until Balslev (1979) treated the genus as having two species, considering D. tolimensis and D. muscoides conspecific.

Farr et al. (1979) took up 'Distichia' in their Index Nominum Genericorum, as having been published at the generic level by Bridel (1827), and they treated it as a synonym of Neckera in the Neckeraceae (Musci). It thus seems that the name was preoccupied when Nees &

Meyen (1843) published the genus Distichia in the Juncaceae. However, even if "Distichia" is included in the index to the genera and species of Bridel's *Bryologia Universa* (1827, p. 787), the name was clearly treated as that of a subgenus in the main text of the same work (p. 238), and it cannot, therefore, be considered as preoccupied at the generic level.

Key to the Species of Distichia

1. Leaf apex bluntly acute, without hair-like extension.

1. D. muscoides.

1. Leaf apex drawn out into a hair-like extension. 2. D. filamentosa.

1. *Distichia muscoides* Nees & Meyen in Meyen, *Reise um die Erde*, Theil 4 (Beiträge zur Botanik): 129. 1843, also published as *Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur.* 16 Suppl. 2, which is at the same time vol. 19 Suppl. 1. Type. Peru, Pisacoma, 15.000', Apr 1831, Meyen s.n. (holotype, n.v., probably destroyed at B; isotype, P). Figs. 3, 20 A-C, 21.

Goudotia tolimensis Decaisne, *Ann. Sci. Nat. (Paris)* ser. 3, 4: 85. 1845. Type. Colombia. Tolima, 4600-5000 m, Feb 1828, Goudot s.n. (holotype, P; isotypes, G, K, P).

Agapatea peruviana Steudel in Lechler, *Berberid. amer. austral.*

1: 56. 1857, nom. nud. Original collection. Peru. Agapata, Jul 1854, Lechler 1954 (G, GOET, K, M, P, mixed collection).

Distichia tolimensis (Decaisne) Buchenau, Bot. Jahrb. Syst.

1: 141. 1880. This combination is incorrectly attributed to
Bentham & Hooker (1883) in Index Kewensis 1: 782. 1895.

Perennial herb, forming dense, hard cushions up to several meters in diameter. Single plants consisting of 5-15 cm long, $\pm$ regularly forked shoots, covered by short, strictly distichous, persistent, stramineous or rarely dark brown, wilted leaves; only 2 or 3 apical leaves green and projecting above the cushion. Leaves 1-2 cm long, inserted 1-2 mm apart; sheaths usually $2/3$ of entire leaf length, open, wide, V-shaped, with narrow and membranaceous margin, almost completely clasping the sheath of the leaf above; blade bluntly acute. Flowers in leaf-axil, near shoot apex. Tepals subequal, 4-7 mm long. Male flowers on filiform pedicels, 1-2 cm long. Stamens 2-3.5 mm long; filaments $1/10$ - $1/5$ as long as the anthers; anthers 1.8-3 mm long. Female flowers hidden in the sheath of the supporting leaf, only the stigmas projecting above the shoot apex; style filiform, exceeding the tepals; stigmas half as long as the style. Gynophore stretching at fruit-ripening, lifting the capsule slightly above the cushion. Capsule ellipsoidal to ovoidal, apically acute to slightly apiculate or obtuse, 5-7 x 2.5-3.5 mm irregularly dehiscent, yellowish brown, unilocular. Seeds oblong, 1-1.5 x 0.5-1 mm, covered by a thick white outer seed coat.

Distribution. In the Andes from Colombia to northern Argentina.

Distichia muscoides is a characteristic plant of the high altitude páramo and puno vegetation. It has been collected at altitudes as low as 3600 m, but it is more common above 4000 m and up to 4600 m. It

FIGURE 21

- 21 A. The neotropical distribution of Distichia muscoides, corresponding to the total distribution except for a few localities in northern Argentina.
- 21 B. Total distribution of Distichia filamentosa, endemic to Argentina.

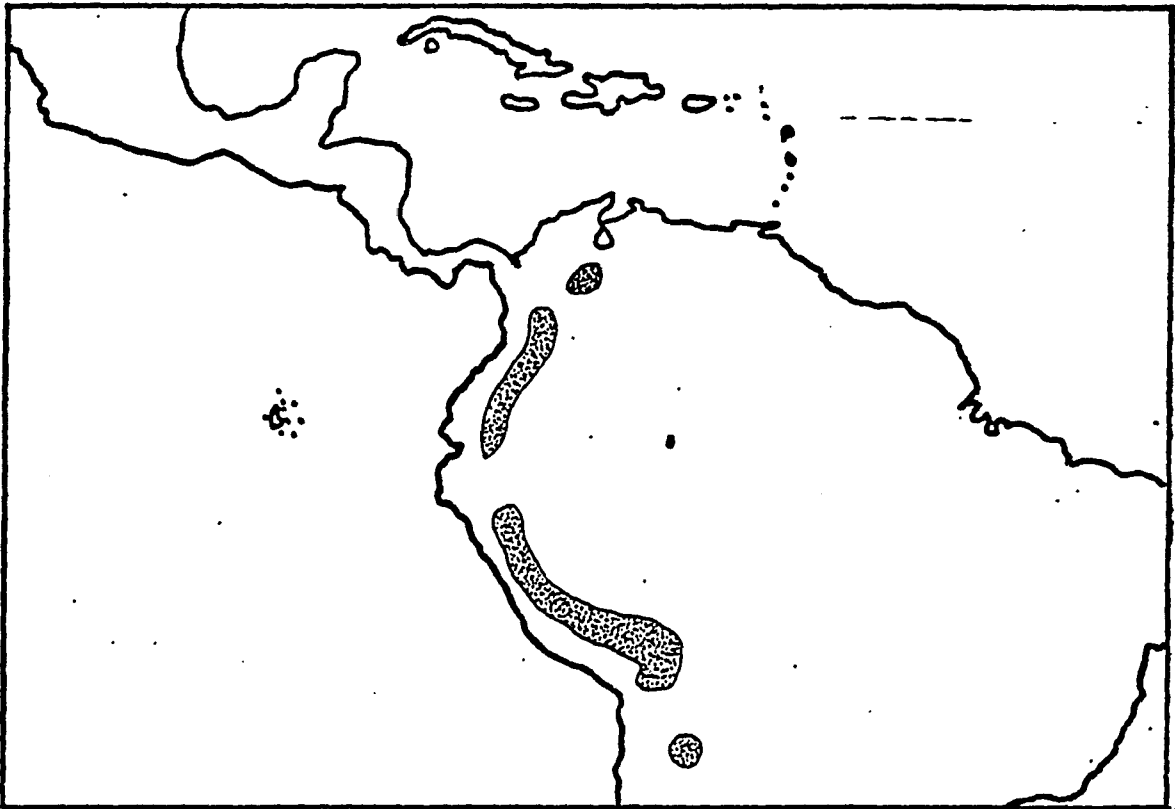


FIGURE 21 A.



FIGURE 21 B.

forms dense and very hard cushions up to several meters in diameter, which in boggy depressions often provide the only secure foothold for the wanderer. On slopes with high precipitation it may create bizarre protruding formations.

Representative specimens. COLOMBIA. Arauca: Sierra Nevada del Cocuy, Quebrada El Playon, Patio Bolos, 4190-4285 m, Cleef 8914 (P), 9018B (COL). Boyacá: Sierra Nevada del Cocuy, 4000-4300 m, Cuatrecasas 1516-D (F), 1518 (COL, F). Caldas: Nevado de Santa Isabel, Río Otún, 3820 m, Cuatrecasas 23232 (F); Páramo del Quindío, 4100-4300 m, Pennell & Hazen 9860 (COL, GH, K, NY, S); Nevado del Ruíz, Termales, 4200-4500 m, Humbert 27076 (COL, GH, NY, S, U, W). Cauca: Mt Puracé Río Vinagre, 3800 m, Cleef 617 (P). Santander: Páramo de Santurbán nr Vetás, 3950-4160 m, Killip & Smith 17576 (COL, GH, NY, S).

ECUADOR. Azuay: Páramo nr Toreador between Molleturo & Quinoas, 3810-3930 m, Steyermark 53204 (NY); Páramo El Cajas W of Sayausí & Cuenca, 4100 m, Balslev 1444 (NY). Carchi: Tulcán-Maldonado rd, km 38, 4000 m, Øllgaard & Balslev 8435 (AAU); Nudo de Boliche, Voladero, 4000 m, Penland & Summers 928 (F). Chimborazo: E slope Mt Chimborazo, 4200 m, Asplund 7807 (K, NY, S); Páramo Laguna Negra NE of Alaó, 4100 m, Barclay & Jujibioy 8786 (US). Cotopaxi: Laguna Salayambo Cocha E of Latacunga, 3800-4050 m, Øllgaard & Balslev 9905 (AAU). Imbabura: Mt Cayambe NE slope, Drew E-232 (US). Napo: Páramo de Guamaní nr Antennas, 4260 m, Øllgaard & Balslev 10121 (AAU). Pichincha: Páramo de Guamaní, 4300 m, Balslev 1620, 1621 (NY), Holm-Nielsen et al. 6732 (AAU, NY, S). Mt Cayambe NE slope, 4000 m, Holm-Nielsen & Balslev 23685 (AAU, NY). Tungurahua: Sachafilo, Cazagual, 4000-4200 m, Acosta-Solis 8779 (F).

PERU. Ancash: Huaraz, Cajamarquilla, 4200-4300 m, Ferreyra 14328 (USM). Arequipa: Pichu Pichu, 4100 m, Stafford 691 (BM, K). Ayacucho: Puqui-Chalhuanca rd, 3600-4500 m, Iltis & Ugent 510 (GH, NY, U, WIS). Cuzco: Canchis, La Raya pass, 4250 m, Iltis & Ugent 1285 (GH, K, NY, U, US, USM, WIS). Huánuco: Dos de Mayo, Valle de Vizcarra, 3000-4800 m, Llanos s.n. (USM). Junín: Mt La Juntay nr Huancayo, 4700 m, Killip & Smith 22050 (GH, NY, S). La Libertad: Nevado de Cajamarquillo, Ferreyra 1282 (USM). Lima: Abra Anticona 45 km W of La Oroya, 4800 m, Balslev 1078 (NY). Puno: Maso Crus-Pasto Grande, 4300 m, Tovar 5099 (USM).

BOLIVIA. La Paz: Mina Caluyo-Cumbre rd, km 6 (ca 25 km N of La Paz), 4700 m, Balslev & Beck 1163, 1164 (LPB, NY); La Paz-Mina Caluyo rd 15 km N of La Paz, 4300 m, Balslev & Beck 1154, 1155 (LPB, NY); Lago Songo S side of Huayna Potosí, 4700 m, Balslev & Beck 1145 (LPB, NY); Chacaltaya 130 km from La Paz, 4800 m, Buchtien 9359 (GH, HBG, K, MO). Oruro: Carangas, Sajama, 5000 m, Asplund 3904, 3984 (NY, S).

Common name. "Champa" in Peru (Ferreyra, 1979).

Uses. Blocks of the dense cushions of Distichia muscoides are cut out by the highland Indians of Peru and kept near the houses and used as fuel for cooking and heating (Ferreyra, 1979).

2. *Distichia filamentosa* Buchenau, Abh. Naturwiss. Vereine Bremen 6: 369.

1879. Type. Bolivia. Prov. Larecaja (Viciniis Sorata): Laguna de Juriquana prope Anilaya, in paludosis; reg. alpina, 4500 m; Febr. - Apr. 1860, Mandon 1443 p.p. (holotype. n.v.; isotypes, G, GH, K, NY, P). Fig. 21 B.

Agapatea filamentosa Buchenau, Abh. Naturwiss. Vereine Bremen

4: 124. 1874, nom. nud. Original collection. Bolivia.

Viciniis Sorata, San Pedro, in paludosis; alt. 4500 m - 1860,

Mandon 1443 p.p. (GOET).

Distichia filamentosa (Buchenau) Grisebach, Symb. fl. argent.

318. 1879, also issued as Abh. Königl. Ges. Wiss. Göttingen

24: 318. 1879. Invalid combination based on Agapatea fila-

mentosa Buchenau nom. nud.

Similar in general habit to Distichia muscoides, from which it is distinguished by a less rigid and hard appearance, and mainly by the leaves which have the apex drawn out to a hair-like filamentous tip, rather than having bluntly acute tips.

Distribution. Very local north of La Paz in the Andes of Bolivia. Ecologically similar to D. muscoides, but it does not form so large and dense cushions as that species. Instead, it grows in soft tufts at the margin of small ponds in the alpine bogs at altitudes about 4500 m, or it grows intermixed with other plants.

Specimens examined. BOLIVIA. La Paz: Slopes of Mt Sorata, 4400 m, Hill 487 (B, K); Ulla Ulla, 3400 m, Lara & Parker 11-24 (NY); Lago Zongo on S side of Huayna Potosí, 4700 m, Balslev & Beck 1146 (LPB, NY)

The nomenclature of this species is somewhat complicated and needs explanation. Buchenau (1874) in his treatment of Mandon's Juncaceae from Bolivia, was the first to mention this species. The collection Mandon 1443 is listed as "Agapatea filamentosa Buchenau" in one place, and as "Agapatea filamentosa n. sp." elsewhere, but no description is provided and the name is therefore a nomen nudum. Grisebach (1879) in his listing of Argentinian plants intended to clarify the generic limitations of the pulviniform Juncaceae. In a discussion of Oxychloe he wrote: "...et in D[istichia] filamentosa Gr. (Syn. Agapatea Buchen. in Mandon pl. boliv. 1443)". Grisebach therefore made a new combination, but since based on a nomen nudum it is illegitimate. Buchenau (1879) in his review of South American Juncaceae intended to make the same new (invalid) combination of Distichia filamentosa as he cited Agapatea filamentosa. However, the collection he cited, though having the same number as the original collection of Agapatea filamentosa (Mandon 1443) is from a different locality (see under synonymy for details). Furthermore Buchenau provides a Latin diagnosis distinguishing Distichia filamentosa from D. muscoides. Distichia filamentosa Buchenau (1879) is therefore to be considered a validly published new species and not an invalid new combination based on Agapatea filamentosa Buchenau (1874).

EXCLUDED NAMES

Distichia andina (Philippi) Benth. & Hooker, Gen. pl. 3: 867.

1883. =Oxychloe andina Philippi.

Distichia bisexualis Clarke in schedis =Oxychloe bisexualis Kuntze.

? Distichia brevifolia Philippi ex Benth. & Hooker, Gen. pl.

3: 867. 1883. =Oxychloe sp.

Distichia ? clandestina (Philippi) Buchenau, Abh. Naturwiss. Vereine

Bremen 6: 370. 1879. =Patosia clandestina (Philippi) Buchenau.

Distichya macrocarpa Weddell ex Buchenau, Abh. Naturwiss. Vereine

Bremen 4: 123. 1874. =Oxychloe andina Philippi.

PATOSIA

3. *Patosia* Buchenau, Bot. Jahrb. Syst. 12: 63. 1890; Buchenau in Engler, Nat. Pflanzenfam. Nachtr. zum II-IV teil: 71. 1897; Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 35. 1906; Fuentes, Bol. Mus. Nac. Hist. Nat. Santiago 10: 3. 1917; Castillon, Bol. Mus. Hist. Nat. (Univ. Nac.) Tucumán 7: 8. 1926; Barros, Darwiniana 10: 291. 1953; Barros in Correa (ed.), Fl. Patagonica 2: 110. 1969.
- Type species. *Patosia clandestina* (Philippi) Buchenau.

Perennial cushion-forming, glabrous herbs. Stems + regularly forked, dying back from the base, densely covered with persisting wilted leaves. Leaves regularly, densely and alternately inserted along the stem. Blade equal to or slightly shorter than the sheath, flat or canaliculate, usually finely dentate along the margin. Inflorescence reduced to a single lateral, subapical flower. Plants dioecious or rarely with a few bisexual flowers. Tepals linear-lanceolate. Male flowers long pedicellate, lifted above the cushion, surrounded by one clasping bracteole at the base; stamens 6, with long, linear, mucronate anthers on short filaments. Female flowers sessile in axil of a subapical leaf; ovary sessile; style long, filiform with 3 filiform, papillose stigmas. Capsule triseptate, sessile. Seeds many.

The name *Patosia* is derived from 'los Patos', the type locality of *Rostkovia* ? *clandestina* Philippi (= *P. clandestina*).

Distribution. One species in the Andes from Bolivia to Neuquén in Argentina.

FIGURE 22

- 22 A. The neotropical distribution of Rostkovia magellanica, which in addition occurs in the subantarctic region from Patagonia to New Zealand (compare Fig. 19).
- 22 B. The neotropical distribution of Patosia clandestina, which in addition occurs southwards in the Andes until Neuquén in Argentina.

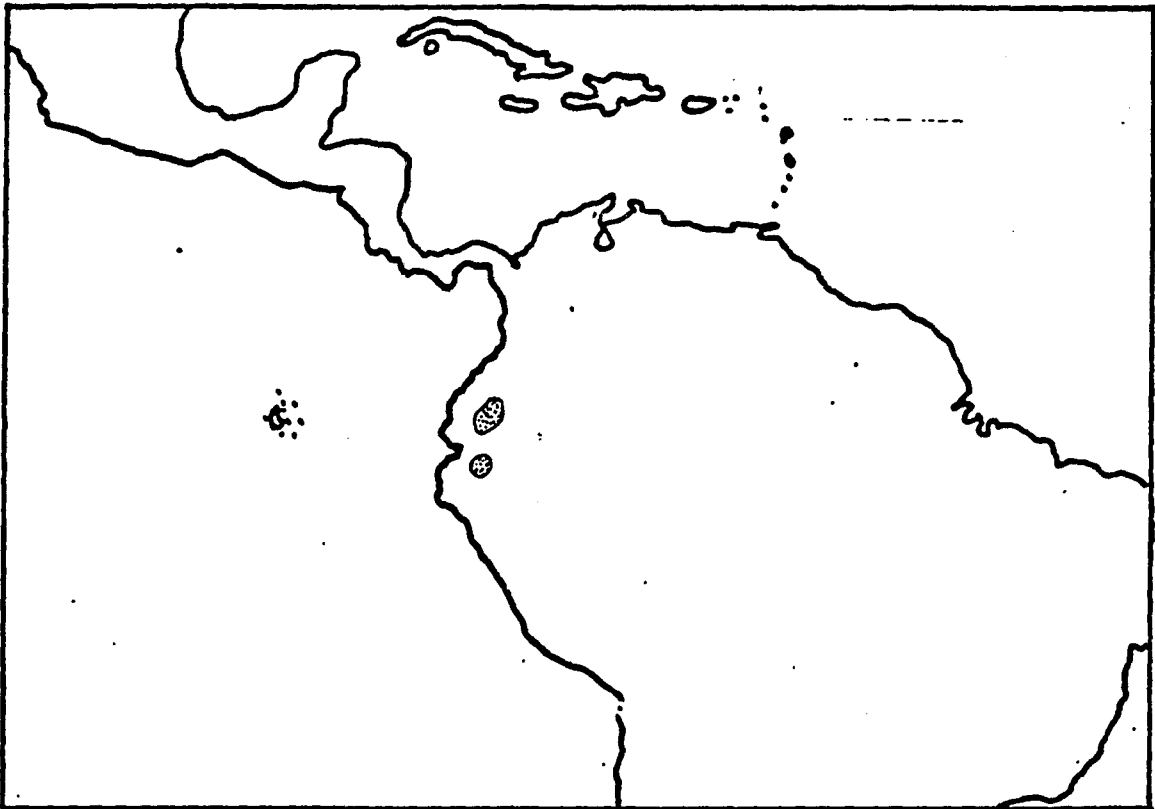


FIGURE 22 A.

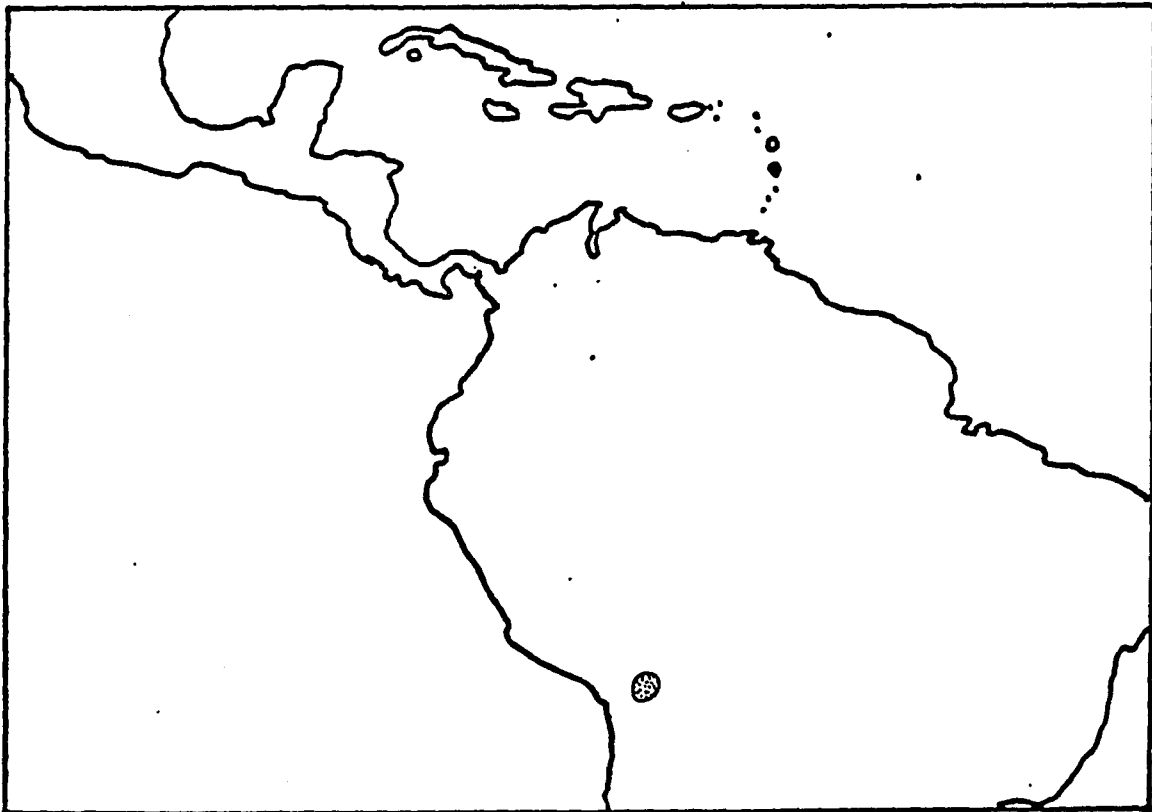


FIGURE 22 B.

Taxonomic History of Patosia

The sole species of Patosia was, when first described, assigned to Rostkovia with some doubt (Philippi, 1857). Two available collections were described as different species: 'Rostkovia ? clandestina' and 'Rostkovia ? brevifolia'. Buchenau treated them as one species and united them under the specific epithet brevifolia in the genus Oxychloe in one publication (Buchenau in Grisebach, 1879), and under the epithet clandestina in the genus Distichia in another almost simultaneous, publication (Buchenau, 1879). In his monograph of Juncaceae he established the genus Patosia to accommodate this species (Buchenau, 1890). Hauman (1915) transferred the species back to Oxychloe under the epithet clandestina, but this generic assignment has not been accepted by subsequent workers. Castillon (1926) described a second species of Patosia, P. tucumanensis. This was reduced to varietal status under P. clandestina by Barros (1953). Patosia is here treated as monotypic.

1. Patosia clandestina (Philippi) Buchenau, Bot. Jahrb. Syst. 12: 64. 1890. Figs. 22 B, 23.

Rostkovia ? clandestina Philippi, Linnaea 29: 76. 1857. Type. Chile. In Andibus prov. Coquimbo loco los Patos dicto habita, Philippi s.n. (holotype, n.v., probably at SGO; at K there is a probable isotype).

Rostkovia ? brevifolia Philippi, Linnaea 29: 76. 1857. Type. Chile. In Cordillera de Sant Jago, Philippi s.n. (syntype, BREM, GOET); Laguna Malvarco, Germain or Philippi s.n. (syntype, K).

Oxychloe brevifolia (Philippi) Buchenau in Grisebach, Symb. fl.

argent. 318. 1879, also issued as Abh. Königl. Ges. Wiss.

Göttingen 24: 318. 1879.

Distichia (?) clandestina (Philippi) Buchenau, Abh. Naturwiss.

Vereine Bremen 6: 370. 1879.

Oxychloe clandestina (Philippi) Hauman, Anales Mus. Nac. Hist.

Nat. Buenos Aires 27: 294. 1915.

Patosia tucumanensis Castillon, Bol. Mus. Hist. Nat. (Univ. Nac.)

Tucumán 7: 8, 1926. Type. Argentina. Tucumán: valle de Tafí,

cerro Muños, entre la Piedra Pintada y la laguna de los Patos,

4100 m, Dec 1916, Castillon 6039, n.v.

Patosia clandestina (Philippi) Buchenau var. tucumanensis

(Castillon) Barros, Darwiniana 10: 295. 1953.

Perennial herb, forming dense, very hard cushions up to several meters in diameter and 1/2 meter high. Single plants consisting of 5-15 cm long, + regularly forked shoots covered with short, alternate, stramineous or brown persisting, wilted leaves, only a few apical leaves green and projecting above the cushion. Leaves 1.5-2 cm long, inserted 1-2 mm apart; sheath constituting 1/2-2/3 of entire leaf length, to 5 mm wide, terminated in two rounded auricles which sometimes run together adaxially to form a ligule; blade linear, 0.5-0.7 mm wide, acuminate, basally canaliculate becoming terete, apical 1/2-1/3 flat, bent somewhat adaxially and the blade therefore appearing jointed, margin usually finely dentate. Flowers in leaf axils near shoot apex. Male flower protruding above the shoot on 1-2 cm long, filiform pedicels, basally clasped by one bracteole which is 1/3-1/2 as long as the tepals;

FIGURE 23

Habit and details of Patosia clandestina (Drawn from Johnston 4925).

- 23A. Habit showing the dense arrangement of the clone of which only the upper part is exposed to the environment.
- 23B. Habit of a single shoot showing the spiral arrangement of the leaves and the bifurcating branching pattern.
- 23C. Single leaf showing the basal sheath, the channeled central part, and the slightly dorsiventrally flattened apical part with finely serrate margin.
- 23D. Female flower with protruding stigmas.
- 23E. Gynoecium showing the ovary, the filiform style, and the long filiform and papillose stigmas.
- 23F. Male flower showing the six tepals and the single bracteole.
- 23G. Androecium showing the six stamens with short filaments and long, mucronate anthers, and vestigial gynoecium.

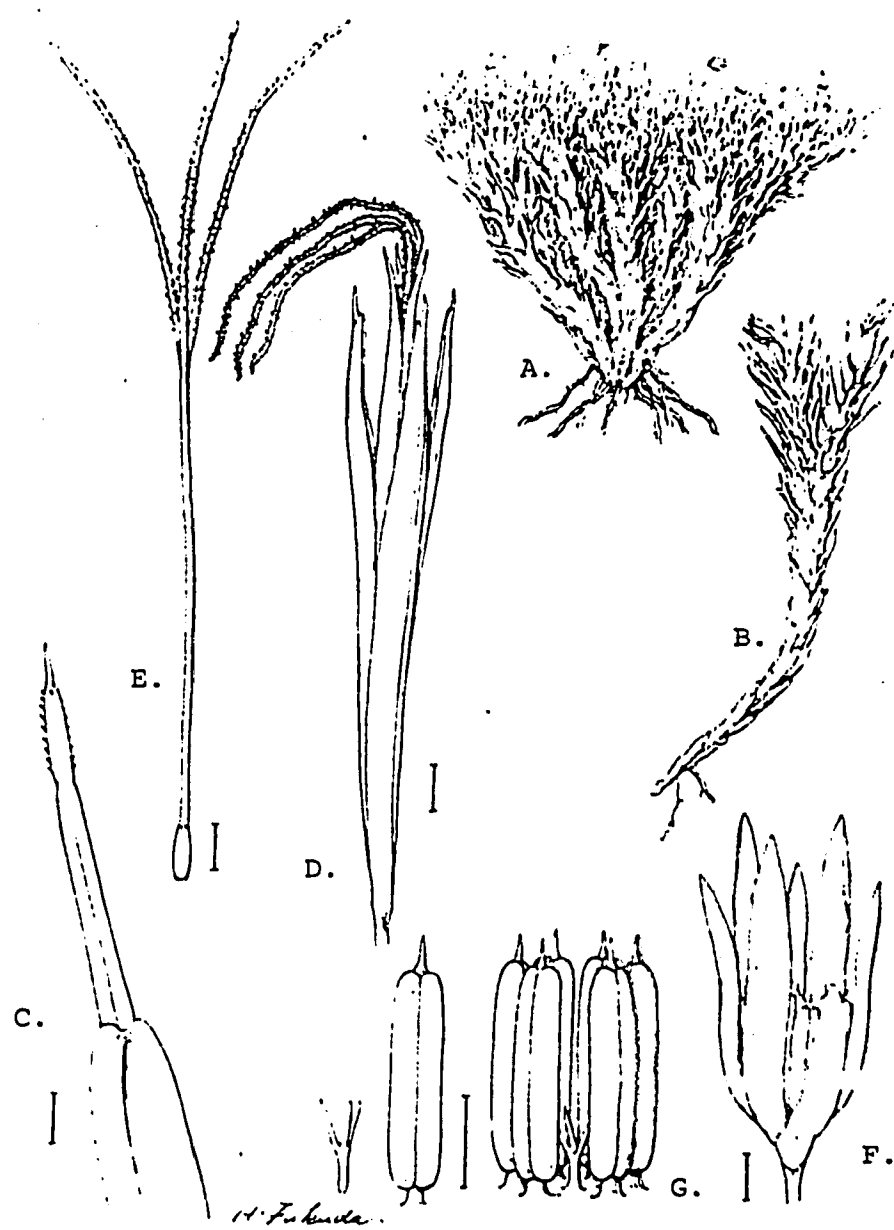


FIGURE 23

tepals equal 5-7 mm long; stamens 6; filaments very short, less than 1/10 of anther length; anthers 2.5-3.5 mm long, linear, mucronate. Female flowers sessile and hidden in axil of supporting leaf, only the stigmas protruding above the shoot; tepals linear-lanceolate, to 18 mm long; ovary ellipsoidal to 2 mm long, gradually merging into the filiform, up to 10 mm long style; stigmas 3, filiform, to 8 mm long, papillose, exceeding the tepals. Capsule ellipsoidal, acuminate, ca 10 x 2 mm, triseptate. Seeds variable in shape, obovate, ovoidal, conical, pyriform, etc., with a spongy white outer seed coat and a hard, thick, castaneous inner seed coat.

Distribution. In the Andes from Bolivia to Neuquén in Argentina. It is found in alpine bogs at altitudes between 3000 and 4000 m, and may form very dense almost spherical cushions along small streams (cf. photo attached to Grandjot s.n. (S) from Santiago, Chile), or it may form more flat undulating cushions dominating extensive areas in the so called 'bofedal' vegetation in humid depressions. At Comanche in Bolivia, which is one of the only two known localities of Patosia within the neotropical region, it is the dominant cushion-forming plant in the 'bofedal'.

Specimens examined. BOLIVIA. La Paz: Pacajes, Comanche, 4000 m, Balslev & Beck 1085 (LPB, NY); Beck 2351 (LPB, NY); Asplund 6502 (US).

CHILE. Atacama: Copiapo, Sierra San Miguel, 3200 m, Johnston 4925 (F, GH, K, P, S). Apart from these specimens several extra-tropical ones have been examined and annotated.

OXYCHLOE

4. *Oxychloe Philippi*, *Florula Atacamensis* 52, t.6c. 1860; Buchenau, *Abh. Naturwiss. Vereine Bremen* 6: 368. 1879; Grisebach, *Symb. fl. argent.* 318. 1879; Buchenau in Engler, *Nat. Pflanzenfam.* 2 (5): 4. 1887; Buchenau, *Bot. Jahrb. Syst.* 12: 65. 1890; Kuntze, *Revis. gen. pl.* 3 (2): 321. 1898; Post & Kuntze, *Lex. gen. phan.* 182. 1904; Buchenau in Engler, *Pflanzenreich IV*, 36 (Heft 25): 36. 1906; Hauman, *Anales. Mus. Nac. Hist. Nat. Buenos Aires* 17: 293. 1915; Hauman & Vanderveken, *Cat. phan. Argentine* 1: 261. 1917; Fuentes, *Bol. Mus. Nac. Hist. Nat. Santiago* 10: 4. 1917; Castillon, *Bol. Mus. Hist. Nat. (Univ. Nac.) Tucumán* 7: 12. 1926; Macbride, *Field Mus. Nat. Hist., Bot. Ser.* 13: 610. 1936; Barros, *Lilloa* 23: 417. 1950; Barros, *Darwiniana* 10: 295. 1953; Barros, *Lilloa* 28: 2. 1957; Barros in Correa (ed.), *Fl. Patagonica* 2: 110. 1969. Type species. *Oxychloe andina* Philippi.

Distichia sectio *Oxychloe* Benthams & Hooker, *Gen. pl.* 3: 867. 1883.

Andesia Hauman, *Anales Mus. Hist. Nat. Buenos Aires* 27: 287.

1915. Type species. *Andesia bisexualis* (Kuntze) Hauman

=*Oxychloe bisexualis* Kuntze.

Perennial cushion-forming, glabrous herbs. Stems ± regularly forked, dying back from the base, densely covered with persisting wilted leaves. Leaves regularly, densely and alternately inserted along the stem; blade equal to or longer than the sheath, terete, smooth

with hard pointed prickly apex. Inflorescence reduced to a single, lateral subapical flower, clasped by two membranaceous bracteoles, bisexual or, unisexual and the plants then dioecious, without differentiation in long pedicellate male flowers and short pedicellate female flowers. Male flowers with narrowly lanceolate tepals; stamens 6, with long, linear, mucronate anthers on short filaments. Female flowers with broadly lanceolate tepals; ovary sessile, with pronounced style and 3 slightly tapering, papillose stigmas. Capsule trilocular or triseptate, sessile, dehiscent or indehiscent. Seeds many.

The name Oxychloe is derived from the greek *ὄξυς* (=acute) and *χλόη* (=grass), referring to the hard pointed and prickly leaves.

Distribution. Six species in the Andes from the department of Ayacucho in Peru to the province of Mendoza in Argentina. They all occur at high altitudes, being dominant parts of the cushion-plant communities in alpine bogs and along rivers and brooks. Only one species, O. andina, reaches into the neotropical region.

Taxonomic History of Oxychloe

Oxychloe was described as a monotypic genus by Philippi (1860) in his account of the flora of the Atacama desert in northern Chile.

Bentham and Hooker (1883) accepted only one genus of pulviniform Juncaceae, and treated Oxychloe as a section of Distichia, but this was not accepted by any later worker. Kuntze (1898) described O. bisexualis as the second species in the genus. Hauman (1915) segregated O. bisexualis into a separate genus, Andesia, because of its bisexual flowers, and his segregation was accepted in most papers up to

and including Barros (1950). In his treatment of Juncaceae of Chile, Argentina and Uruguay, Barros (1953) merged Andesia with Oxychloe. I agree with Barros and treat Andesia as a synonym of Oxychloe. Barros (1950, 1953) described four additional species in the genus so that a total of six species have now been proposed. Oxychloe andina Philippi, the type species of the genus, is the only one that reaches into the neotropical region. I have seen very little material of the remaining five species, but they all seem very closely related, and a critical re-evaluation of more material may result in taxonomic changes.

1. Oxychloe andina Philippi, Florula Atacamensis 52, t.6c. 1860.

Type. Chile. Antofagasta: Ad initium vallis Zorras 24°4' lat. m. et 10700 p.s.m. inveni, and iterum ad Riofrio 25°50' lat. m. et (10500 p.s.m.), (holotype, n.v., probably at SGO; two collections at K labelled "Atacama" and "desertum Atacama" respectively by Philippi are probably syntypes). Figs. 24, 25.

Distichya macrocarpa Weddel in sched. ex Buchenau, Abh. Naturwiss.

Vereine Bremen 4: 123. 1874. Type. Bolivia. Viciniis Sorata: Vancuiri prope Chuchu, in paludosis, Regio. temp.; 4500-5000 m. Jan.-Mart. 1857, Mandon 1442 (holotype, LUB; n.v.; isotypes, G, GH, K, NY, P, S).

Distichia andina (Philippi) Benth & Hooker, Gen. pl. 3:

867. 1883.

FIGURE 24

Habit and details of Oxychloe andina (A, B, D, E, drawn from Balslev 1150; C, from Werderman 937; F, G, from Balslev 1147).

- 24A. Habit showing the loose arrangement of the shoots.
- 24B. Leaf showing the basal, auriculate sheath, the channeled basal part of the blade, and the hardly visible joint near the apex.
- 24C. Female flower showing the two bracteoles, the wide tepals, and a mature fruit with remaining style and stigmas.
- 24D. Extracted gynoecium showing the ovary, the short style and the papillose stigmas.
- 24E. Young female flower showing the two bracteoles, the tepals, and the projecting stigmas.
- 24F. Male flower showing the two bracteoles, the six tepals, and some of the stamens.
- 24G. Stamen showing the very short filament, the long, mucronate anther.

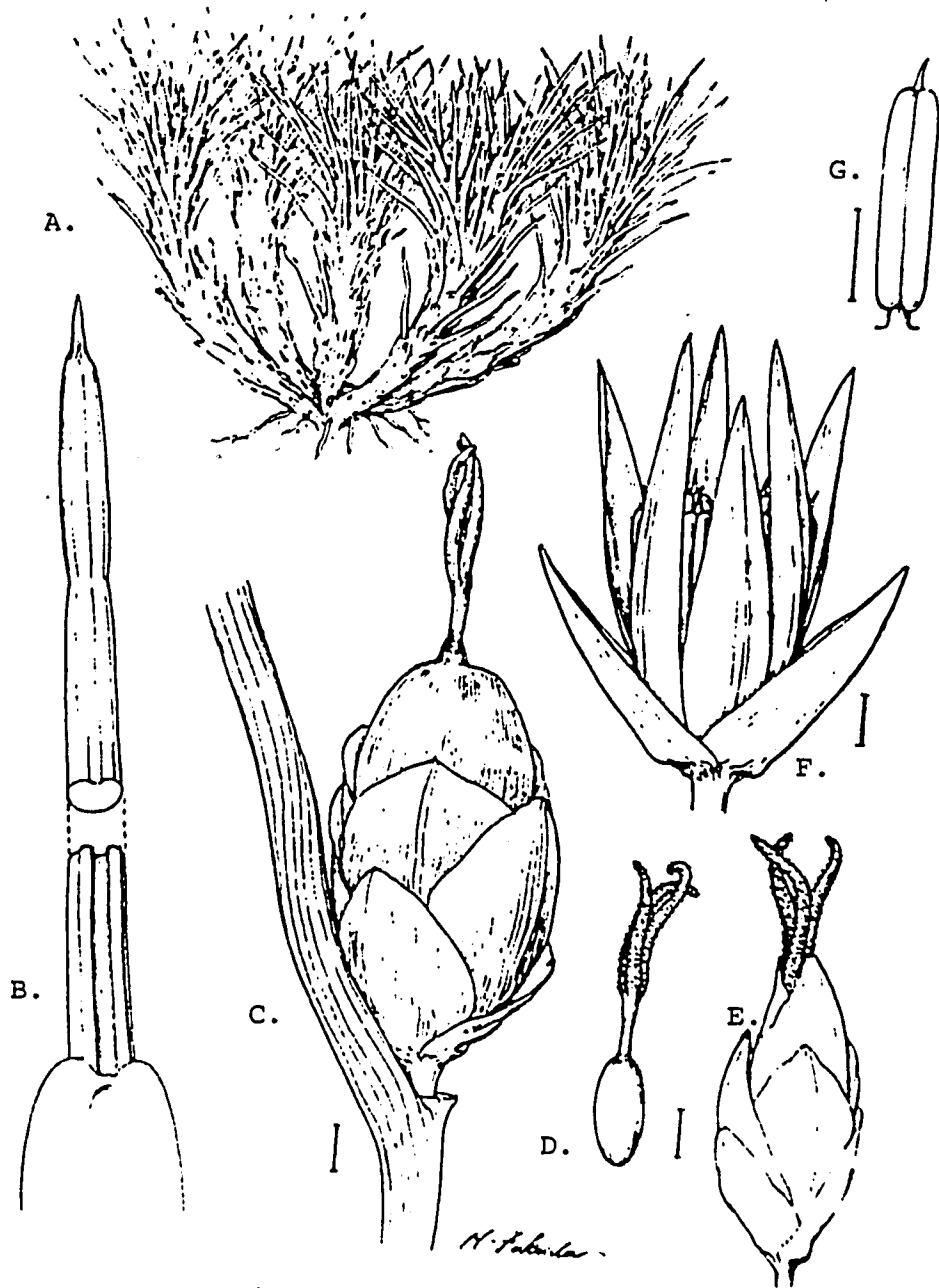


FIGURE 24

Perennial herb, forming loose, large, prickly cushions up to several meters in diameter and 1/2 meter high. Single plants consisting of 5-30 cm long, ± regularly forked shoots covered with alternate, stramineous or brown persisting wilted leaves and leaf bases, progressively more degraded downwards. Leaves 5-8 cm long, inserted 1-3 mm apart; sheath constituting about 1/2 of the entire leaf length, with membranaceous margin terminated in two rounded auricles which sometimes run together adaxially to form a ligule; blade linear, to 1.2 mm wide, apically hard pointed and prickly, basally adaxially channeled, then terete and finally very slightly dorsiventrally flattened on the apical 1/4 of its length. Flowers in leaf axils near shoot apex, on 1-3 cm long pedicels, unisexual, clasped by two triangular membranaceous bracteoles to 5 mm long; tepals 6-8 mm long, membranaceous, stramineous to castaneous. Male flowers with narrowly lanceolate tepals; stamens 6; filaments ca 0.3 mm long and less than 1/10 of anther length; anthers 4-5 mm long, linear, mucronate. Female flowers with broadly lanceolate tepals; ovary ellipsoidal ca 2 mm long; style ca 2 mm long; Stigmas 2-3 mm long, terete, papillose. Capsule oblong, apically obtuse, 8-11 x 4-5 mm, castaneous, 3-septate or 3-locular. Seeds ovoidal, pyriform, etc., or irregularly shaped from being crowded in the capsule, 1-1.3 mm long, covered by a thick white or very light brown irregularly patterned outer seed coat, over a dark brown inner seed coat.

Distribution. In the Andes from the department of Ayacucho in Peru to the province of San Juan in Argentina. Found at very high altitudes, usually between 4000 and 5000 meters, where it is dominant

FIGURE 25

The neotropical distribution of Oxychloe andina. In addition this species occurs southwards in the Andes until San Juan in Argentina.

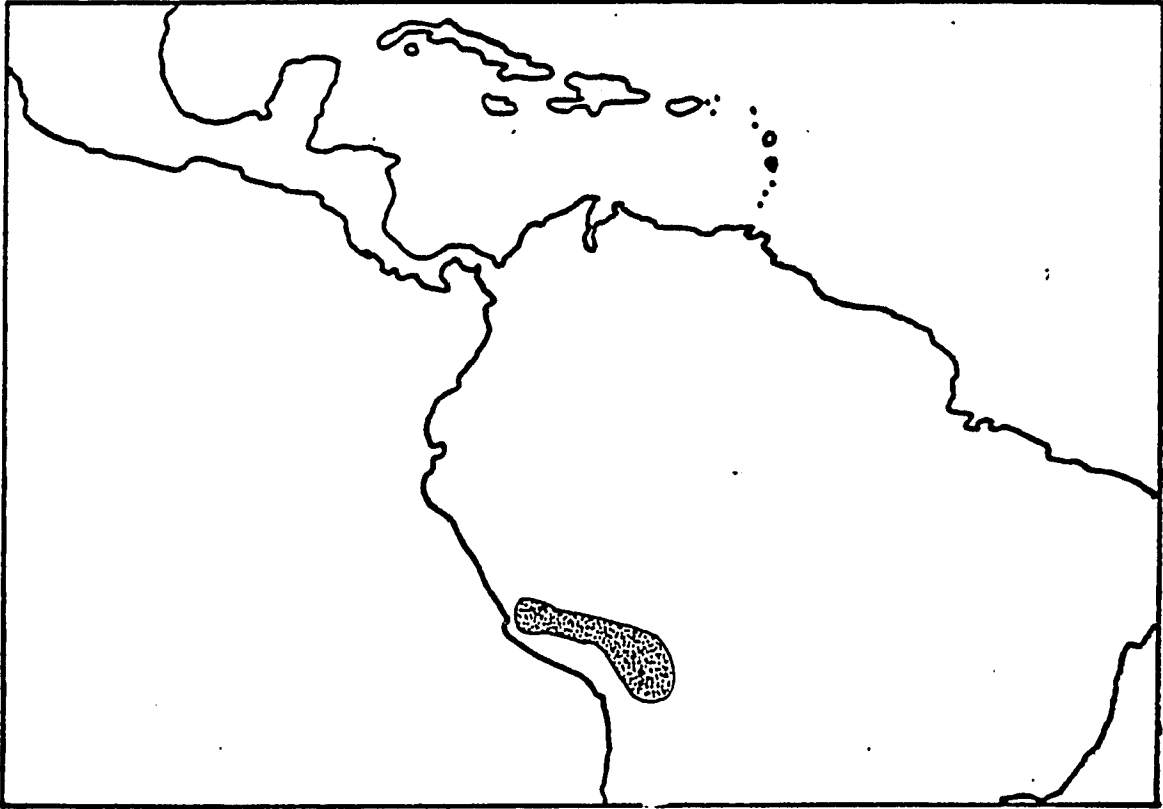


FIGURE 25

in the cushion plant formations in humid bogs together with Distichia muscoides. This species is known from many collections and is quite common within its area of distribution in contrast to the remaining five species of the genus.

Specimens examined. PERU. Ayacucho: Poquio-Chalhuanca rd, km 61, 3600-4500 m, Iltis et al. 509 (WIS). Puno: San Antonio de Esquilache, 4700 m, Stafford 736 (F, K, WIS); Caccachara ca 50 mi SW of Ilave, 4900-5000 m, Pearson 96 (US); Lalue of Sahuas between Puno and Arequipa, 4400 m, Sandeman 3841 (K); Sandia, 400-4500 m, Weberbauer 987 (F, G).

BOLIVIA. La Paz: Lago Zongo, S side of Huayna Potosí, 4700 m, Balslev & Beck 1147 (LPB, NY); Mina Milluni-Tuni Condoriri rd, km 15 on W slope of Huayna Potosí, 4700 m, Balslev & Beck 1150 (LPB, NY); La Paz, 4350 m, Graf 471 (NY); Los Andes, Laguna Soro Kkota, 56 km from La Paz towards Mina Palcoco, 4320 m, Beck 1975 (LPB, NY); Murillo, Palca Lago Choquecola, 4400 m, Asplund 897 (NY, S); Valle de ChuquiagUILLO Pacocota Pampa, 4200 m, Asplund 1878 (NY, S); Pacajes, Charaña, 4050 m, Asplund 2668 (NY, S); Chacaltaya, 130 km from La Paz, 4750-4800 m, Graf 286 (NY), Buchtien 1240 (US), 9360 (HBG). Oruro: Carangas, Sajama, 4800 m, Asplund 3947 (S), 4200 m, Asplund 3985 (NY).

CHILE. Atacama: Chanaval, 7 km NE of Cerro Valiente, 3400 m, Johnston 4825 (F, GH, K, P, US); Vallenar nr Laguna Valeriano, 4000 m, Johnston 6052 (GH, S); Copiapo, Río Turbio Co. Cadillal, 3300 m, Werdermann 937 (F, GH, MO, NY, S, U, US); Copiapo, Maricanga, 3700 m, Werdermann 453 (F, G, K, MO, NY, S, U).

EXCLUDED NAMES

Oxychloe brevifolia (Philippi) Buchenau in Grisebach, Symb. fl. argent.

318. 1879. =Patosia clandestina (Philippi) Buchenau.

Oxychloe clandestina (Philippi) Hauman, Anales Mus. Nac. Hist. Nat.

Buenos Aires 27: 294. 1915. =Patosia clandestina (Philippi) Buchenau.

LUZULA nom. cons.

5. *Luzula* A. P. de Candolle, Fl. franç. 3 ed., 1: 198. 1805; *ibid.* 3: 158. 1805; Desvaux, J. Bot. (Desvaux) 1: 129-165, t. 5-6. 1808; Meyer, Linnaea 22: 383-420. 1849; Buchenau, Abh. Naturwiss. Vereine Bremen 6: 413-424. 1879; Buchenau, Bot. Jahrb. Syst. 12: 74-167. 1890; Buchenau in Engler, Pflanzenreich IV 36 (Heft 25): 42-98. 1906; Barros, Darwiniana 10: 313-358. 1953. Type species: *Luzula campestris* (Linnaeus) A. P. de Candolle, typ. cons.

Juncoides Moehring, Primae Lineae Horti Privati. 1736; Sabatti, Synops. pl. Roma 23: 1745; Seguiet, Pl. Veron. 3: 88. 1754; Adanson, Fam. pl. 2: 47. 1763.

Luciola Smith, Engl. fl. 2 ed., 177. 1824.

Juncodes Kuntze, Revis. gen. pl. 2: 722. 1891.

Perennial, rhizomatous herbs, hairy at the margin of leaves and bracts. Culms erect. Leaves alternate, scale-like on runners and rhizomes, blade bearing basally and on the culm, and bracteous in the inflorescence; sheaths closed, without auricles at the junction to the blade; blades linear to narrowly lanceolate, flat, concave or with involute margins. Inflorescence with many individually inserted flowers arranged in a loose, much-branched panicle, or with the flowers congested into dense clusters, which are then arranged in a panicle, an anthela, a raceme or contracted into dense spike-like structure. Each flower subtended by a bract at the base of the pedicel and clasped by 1-2 bracteoles inserted on the pedicel just below the flower. Flowers

bisexual. Tepals unequal or subequal, lanceolate, margin entire, sometimes membranaceous or dissolved into ciliate lobes. Stamens 3-6; filaments filiform, rarely linear and flattened; anthers oblong, rarely linear. Ovary sessile. Style short, filiform. Stigmas 3, filiform, twining, covered with sticky papillae. Capsule trigonous, sometimes basally 3-lobed, unilocular. Seeds 3 per capsule, ellipsoidal to oblong, brown to reddish brown below a hyaline, whitish to very light brown outer seed coat, attached to the placenta by a long, fine silky thread.

The name Luzula is a corruption of the Italian verb 'lucciola' for shining, referring to the shiny appearance of the inflorescences which are overlaid with hairs.

Distribution. A cosmopolitan genus of ca. 75 species, most of which occur in the north temperate region. In the tropical region the genus is totally absent in the lowlands, but present at higher altitudes, mostly above 2500 meters altitude. Tropical America has eight species, tropical Africa three, and tropical Asia one. Fig. 26 A.

Taxonomic History of Luzula

Of the species now referred to Luzula three were included under Juncus in Species Plantarum by Linnaeus (1753). Though several generic names have been used for various species of Luzula, A. P. de Candolle (1805) was the first to circumscribe the genus as we now define it.

FIGURE 26

26 A. The distribution of the genus Luzula in the neotropical region.

26 B. The distribution of Luzula denticulata.

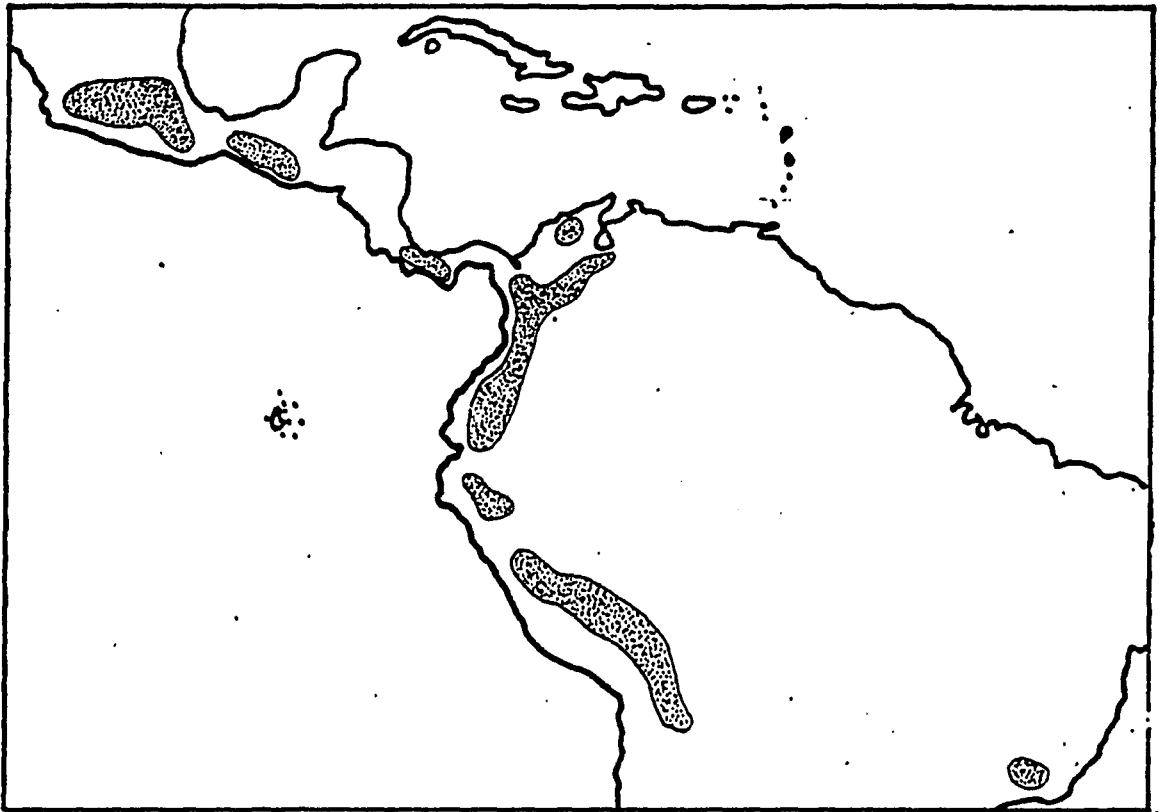


FIGURE 26 A.

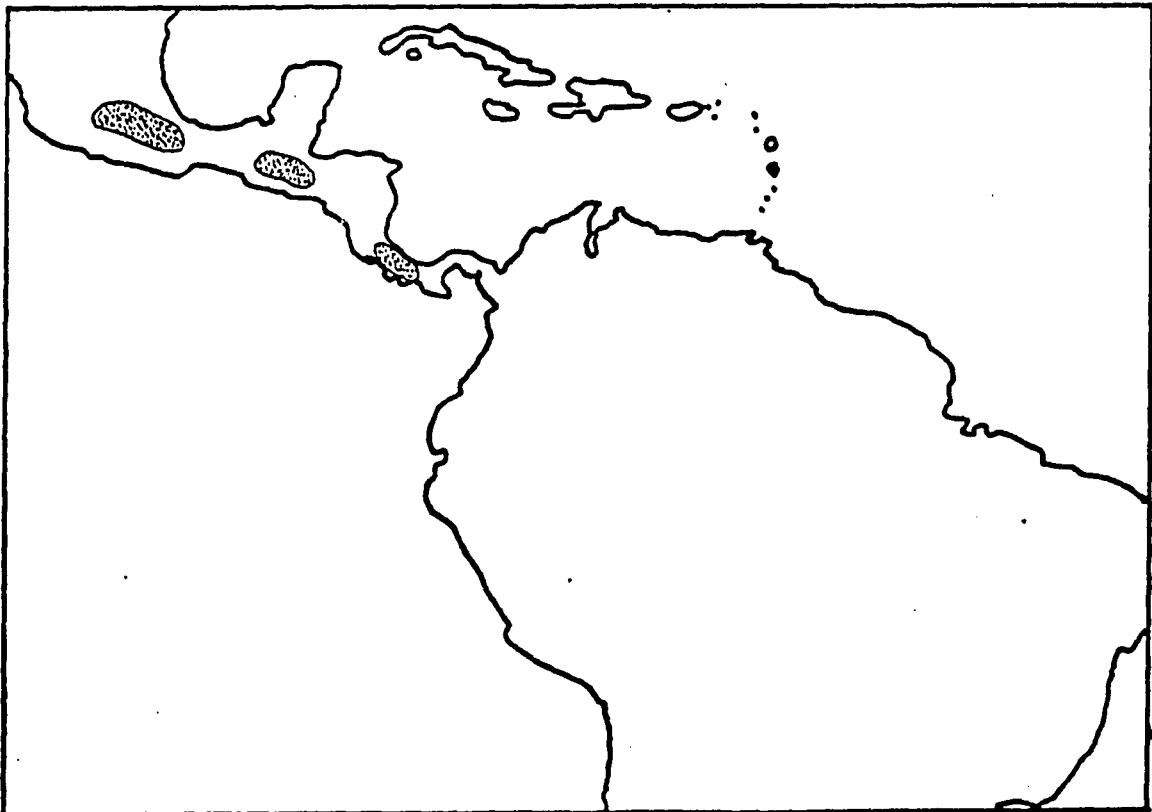


FIGURE 26 B.

Desvaux (1808) in his monograph of Luzula accepted 24 species, Meyer (1823) 24 species, and Laharpe (1825, 1827) only 20 species. Buchenau (1890, 1906) included 51 and 61 species, respectively. Since 1906 there has been no treatment of the entire genus. Ebinger (1964) revised subg. Pterodes, and there have been several revisions of the genus in geographically restricted areas.

Desvaux (1808) arranged Luzula synoptically based on inflorescence characters, but he did not name his subdivisions. Meyer (1823) divided the genus into four unnamed sections based on seed characters. Laharpe (1825, 1827) combined seed and inflorescence characters to divide the species into four, likewise unnamed, sections. Again based on seed and inflorescence characters, Grisebach (1845) formally proposed three sections: Pterodes, Anthelaea, and Gymnodes. These were taken up by Fourreau (1869) as genera, and by Buchenau (1890, 1906) as subgenera. These subgenera, though apparently quite artificial, have not been challenged, except for the segregation of Luzula elegans Lowe (= L. purpurea Buchenau ex Meyer) from subg. Anthelaea into the monotypic subg. Marlenia (Ebinger, 1963).

Key to the neotropical Subgenera and Species

of Luzula

1. Flowers inserted individually on visible pedicels, not in clusters or heads (subg. Anthelaea).
2. Rachis segments 5-15 cm long, the inflorescence divided into 4-5 subequal nodding panicles, one above the other. 1. L. gigantea.
2. Rachis segments less than 1 cm long, the inflorescence consisting of one terminal, loose, much-branched panicle 2. L. denticulata.
1. Flowers in round or oblong heads or elongate clusters; clusters arranged in anthelae, loose panicles, racemes, or spike-like structures (subg. Luzula).
3. Leaf apices obtuse, callose tipped.
 4. Inflorescence anthelate, with the flowers congested into several round or oblong heads. 3. L. campestris.
 4. Inflorescence a terminal, erect, somewhat interrupted spike, and a lower smaller spike usually on a long pedicel, but not bending away from the inflorescence. 4. L. caricina.
3. Leaf apices acute, not callose tipped.
 5. Flower clusters on distinct peduncles and arranged in loose much branched panicles. Leaf blades greater than 5 mm wide.
 6. Tepals 2.3-2.6 mm long, flowers dark. Ecuador. 5. L. ecuadoriensis.
 6. Tepals 1.3-2.5 mm long, flowers stramineous. Southern Peru to northern Argentina. 6. L. excelsa.

5. Flower clusters sessile in spikes, or at most on short

peduncles in racemes. Leaf blades less than 4 mm wide.

7. Runners present. Bracts of flower clusters all membra-

naceous and not exceeding the cluster. Culms usually

straight.

7. L. vulcanica.

7. Runners not present. Bracts of (at least lower) flower

clusters herbaceous and exceeding the cluster. Culms

usually curved.

8. L. racemosa.

Luzula subg. Anthelaea (Grisebach) Buchenau, Bot. Jahrb. Syst. 12:

76, 86. 1890.

Luzula sectio Anthelaea Grisebach, Spic. fl. rumel. 2: 404.

1845.

Perennial, caespitose or stoloniferous herbs, 30-100 cm high.
Leaf-blades apically acute. Inflorescence with many solitary flowers
inserted on distinct pedicels, arranged in loose anthelae or panicles.

Distribution. About 15 species, mostly circumboreal but one
species in Central America, one in the Andes, and one on the tropical
east Asian mountains and southern China.

Subg. Anthelaea is most easily recognized by the inflorescence
in which the flowers are inserted individually on distinct pedicels,
and not congested into round or elongate clusters or flower heads.
The plants are usually quite large (60-100 cm) and with long and wide
leaf-blades (1-2 cm wide and to 25 cm long).

1. *Luzula gigantea* Desvaux, J. Bot. (Desvaux) 1: 145. 1808. Type.

Colombia. Quindio in regno Santa-fe de Bogota, Humboldt &

Bonpland s.n. (holotype, P).

Figs. 27, 29 A.

Luzula paniculata Desvaux, J. Bot. (Desvaux) 1: 147. 1808.

Type. America calidior, (holotype, P).

Juncodes spadiceum Kuntze var. giganteum (Desvaux) Kuntze,

Revis. gen. pl. 2: 724. 1891.

Juncodes giganteum (Desvaux) Sheldon, Minnesota Bot. Stud.

1: 62. 1894.

Perennial herb, 20-90 cm high. Rhizome ascending, 1.5-3 mm diam., often covered with wilted leaves and giving rise to ascending runners terminated by leaf rosettes. Culms erect and apically nodding, terete, 2-4 mm diam. Basal leaves up to 25 in a rosette; sheath short; blade bending away from the culm, linear to narrowly lanceolate, (5-)10-20 mm wide, flat, margin hairy in young leaves. Cauline leaves resembling basal ones, but sheath to 6 cm long, and the blade shorter and more erect. Inflorescence a loose much-branched panicle constituting more than 1/3 of total plant height, storied and subdivided into 4-5 subequal, nodding parts, one above the other, by 5-15 cm long rachis segments, the flowers solitary on distinct delicate pedicels. Bracts supporting primary branches of the inflorescence resembling cauline leaves, basal one to 20 cm long, upper ones progressively smaller. Bracteoles and more distant bracts in the inflorescence linear to lanceolate, membranaceous, margin entire or dissolved into ciliate lobes. Tepals unequal,

FIGURE 27

Habit of Luzula gigantea showing the wide leaves and the storied inflorescence (Drawn from Fagerlind and Wibom 1405^{bis}, S; from Balslev, 1979a).



light brown to blackish brown, outer ones 2-3(-3.5) mm long, inner ones 1.5-2.5 mm long, narrower. Stamens 6, 1-1.5 mm long; anthers oblong, 0.3-0.6 mm long. Capsule broadly ellipsoidal, apiculate, 1.3-2 x 0.8-1.6 mm, first light green, becoming reddish brown and glossy at dehiscence. Seeds ellipsoidal to oblong, broadly apiculate, 0.9-1.3 x 0.4-0.6 mm, smooth to rugose, reddish brown below a whitish to light brown outer seed coat.

Distribution. In the Andes from Venezuela to northern Argentina at altitudes between (2700-)3000 m and 4000 (-4500) m. In Ecuador it is a pioneer plant on disturbed soil along roadcuts, etc.

Representative specimens. COLOMBIA. Antioquia: Páramo de Frontino, Río Urrao, 3200m, Core 415 (NY). Boyacá: Sierra Nevada de Cocuy, Quebrada de las Playas, 4100 m, Grubb et al. 321 (K, US). Caldas: Páramo de Quindio, 3200-4500 m, André 2244 (K, NY), Pennell & Hazen 9900 (GH, NY), 9901 (NY). Cauca: Mt Puracé, 3300-4000 m, Cleef 543 (U), Cuatrecasas 14720 (F, G), Pennell & Killip 6531 (GH), von Sneidern 1740 (GH, NY, S), 1741 (S), 2082 (F, G, S), 2083 (S); Chapa-Río Blanco, 3000 m, Core 908 (GH). Cundinamarca: Páramo de Palacio, 3300-3800 m, Cleef 5134A, 5237A, 6690A, 9619 (COL); Páramo de Chisacá, 3300-4000 m, Schultes 20167 (NY), Barclay & Juajibioy 6208 (US); Páramo de Guasca, Ariste-Joseph A386 (GH, NY); Páramo de Choachí, 3700 m, Killip & Ariste-Joseph 11921 (GH); Páramo de Sumapaz, 3800-4000 m, Cleef 1589 (U), 8360A (COL), 1630 (U); Páramo de Cruz Verde, 3100-3500 m, Pennell 2079 (GH, NY). Magdalena: Sierra Nevada de Santa Marta, Río Sevilla, 3370 m, Barclay & Juajibioy 6614 (US); Sierra de Perija E of Manuare, 3000 m,

Cuatrecasas & Castañeda 25089 (US). Meta: Páramo de Sumapaz, 3600-4100 m, Cleef 992 (U), 8092 (COL). Nariño: Mt Galeras, 4000 m, Plowman 1965 (COL, GH, K, S); Páramo Cumbal, 4000 m, von Sneider A375 (S). Norte de Santander: Páramo de Tamá, La Cueva, 3000-3200 m, Cuatrecasas et al. 12717 (F). Tolima: Páramo de Ruíz, Rosalito, 2900-3200 m, Pennell 3105 (GH, NY).

VENEZUELA. Mérida: Laguna Mucubají above Los Apartaderos, 3600 m, Steyermark 57495 (F), 57496 (NY), Aristeguieta 940 (NY); Trujillo, Linden 412 (BM, F, G, P); Sierra Nevada de Santo Domingo, Laguna Negra, 2700-2900 m, Steyermark 96971 (NY).

ECUADOR. Azuay: 10-15 km W of Sayausí W of Cuenca, 3200-3400 m, Balslev 1573 (NY). Carchi: Tulcán-El Carmelo rd, km 10, 3350 m, Balslev & Quintana AAU-23835 (AAU, NY); El Angel-Tulcán rd, km 7, 3700 m, Balslev & Quintana AAU-23911 (AAU, NY). Chimborazo: Páramo de Cusnopaccha E of Alaó, 3400 m, Acosta-Solis 7205 (US). Cotopaxi: Pilaló-Latacunga rd, timberline W andean slope, 3400 m, Holm-Nielsen & Jeppesen 1468 (AAU, S). Imbabura: Laguna Mojanda-Otavalo, 3400 m, Balslev & Quintana AAU-24144 (AAU, NY). Loja: Amaluza-Pallanda trail nr pass, 3100-3400 m, Øllgaard & Balslev 9661 (AAU); Loma de Oro 10 km S of Saraguro, 3200-3300 m, Balslev 1365, 1371 (NY). Morona-Santiago: Sevilla de Oro-Méndez trail at El Castillo, 3000-3250 m, Øllgaard & Balslev 9547 (AAU). Napo: Mt Cayambe NNE slope, 3900 m, Prescott 330 (NY); Mt Sumaco, 3700 m, Madison 6779 (NY). Pichincha: Mt Pichincha, N slope, Yanacocha, 3300 m, Balslev et al. 1723 (NY); Páramo de Guamaní, Balslev AAU-24188, AAU-24189 (AAU, NY); Mt Cayambe,

NE slope, 3600-4000 m, Holm-Nielsen & Balslev 23680, 23707 (AAU, NY).

Tungurahua: Mt Tungurahua, Spruce 5976 (G, GH, K, NY, P).

PERU. Amazonas: Chachapoyas, Jalca de Calla-Calla, 3400 m, Sagástegui 7485 (NY). Apurimac: Abancay, towards Cuzco, 3200 m, Saunders 748 (K). Ayacucho: Huanta, Choimacota valley, 3100 m, Weberbauer 7585 (GH,S). Cajamarca: Hualgayoc, 3400-3500 m, Ferreya 8544 (USM). Cuzco: Urubamba, 3600 m, Vargas 7261 (MO); Urubamba, Puyupatamarca, 3200 m, Vargas 2768 (US). Piura: Huancabamba, La Cruz, Acleto 405 (USM).

BOLIVIA: Cochabamba: Chapare rd, km 110, 3000 m, Steibach 611 (F, GH, MO, NY, S, U, WIS). La Paz: Unduavi, Nordyuangas, 3000-3300 m, Buchtien 68 (G, GH, NY), 2600 (NY), 8919 (K, NY, S), Rusby 58 (NY, US); Larecaja, nr Sorata and Mt Sanguarie, 3200 m, Mandon 1423 (BM, G, GH, K, NY, P, S).

Luzula gigantea is easily recognized as belonging to subg. Anthe-laia by its solitary flowers and wide, large leaves. Within the subgenus it is clearly set apart by its long rachis segments that subdivide the inflorescence into 4-5 subequal nodding parts, one above the other. This feature is also found in the Old World species L. effusa Buchenau which occurs from the eastern Himalayas to China and in the Philippines, Borneo, S. Celebes, and New Guinea. I have examined a few specimens of L. effusa (but not the type), and I believe that it will in the future have to be treated as conspecific with L. gigantea. The long rachis segments of L. gigantea and L. effusa are in contrast to the short ones found in the L. parviflora complex. This complex is circumboreal with extensions into northeastern Asia and southwestern North America reaching

as far south as México and Central America where it is represented by

L. denticulata Liebmann.

2. *Luzula denticulata* Liebmann, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjøbenhavn 46. 1850. Type. México. Veracruz: Vulkanen Orizaba...Vaqueria del Jacal, 3050 m, Sep 1841, Liebmann s.n. (holotype, C; isotypes, C, G, GH, K, P). Fig. 26 A.

Luzula laetevirens Liebmann, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjøbenhavn 46. 1850. Type. México. Veracruz: Vulkanen Orizaba, 2750-3050 m, Sep 1841, Liebmann s.n., (holotype, C; isotypes, C, P).

Luzula latifolia Liebmann, ibid. 47. 1850. Type. México. Oaxaca: Cumbre de Ixtepec, 3050 m, Sep 1842, Liebmann s.n. (holotype, C; isotype, C).

Luzula parviflora (Ehrhart) Desvaux var. *denticulata* (Liebmann)

Buchenau, Bot. Jahrb. Syst. 7: 171. 1885.

Luzula gigantea Desvaux var. *vulcanica* Woodson, Ann. Missouri

Bot. Gard. 26: 278. 1939. Type. Panamá. Chiriquí: Loma Larga to summit, Volcán de Chiriquí, ca. 2500-3380 m, 4-6 Jul 1938, Woodson Jr., Allen & Seibert 1094 (holotype, MO; isotype, GH).

Perennial herb, (15-)25-70(-90) cm high. Rhizome ascending, 1-2 mm diam., often giving rise to ascending runners terminated by a leaf rosette. Culms erect and apically nodding, terete, 0.8-3 mm diam. Basal leaves 3-15 in a rosette; sheaths short; blades erect or more commonly bending away from the culm, linear to narrowly lanceolate, 5-15(-25) x 0.2-1.2 cm, flat, margin hairy. Cauline leaves 3-8 to each culm, resembling basal ones but sheath up to 7 cm long and the blade shorter and erect, upper ones progressively shorter. Inflo-

rescence a terminal loose, much-branched, nodding, anthelately arranged panicle, 5-20 x 3-10 cm; rachis segments very short (less than 1 cm), and not subdividing the inflorescence into subequal parts; flowers solitary on distinct pedicels. Basal bract of inflorescence linear, herbaceous, to 6 cm long. Bracteoles and more distant bracts in the inflorescence linear to lanceolate, membranaceous; margin entire or dissolved into ciliate lobes. Tepals equal or outer ones slightly longer, 1.7-2.5 mm long, light brown to dark, almost black reddish brown, outer ones concave, inner ones flat or slightly concave. Stamens 6, 0.8-1.5 mm long; anthers oblong, 0.4-0.8 mm long, equal to or longer than filaments. Capsule broadly ellipsoidal to suborbicular, short apiculate, trigonous to trilobed, 1.5-1.7 x 1.2-1.7 mm, light green, becoming dark brown and glossy at dehiscence. Seeds ellipsoidal to obliquely oblong, broad apiculate, 1-1.3 x 0.6-0.8 mm, smooth to rugose, reddish brown below a hyaline whitish outer seed coat.

Distribution. From central México to Panamá. Collected at altitudes between 2400 m and 3900 m, but most commonly above 3000 m. Being restricted to the high altitudes, its distribution area is much interrupted.

Representative specimens. MEXICO. Chiapas: NE slope Zontehuist nr summit San Cristóbal de Las Casas, 2850 m, Breedlove 12342 (F); N and W slope of Mt Mozotal below microwave tower along rd from Huixtla to El Porvenir, 3000 m, Breedlove 22754, 40268 (MO). Distrito Federal: Mt Ajusco, 3840 m, Beaman 2806 (GH). México: Sierra de las Cruces, 3650 m, Pringle 4216a (F, GH, NY); Mesón Viejo Temascaltepec, 2930 m, Hinton 1307

(F, GH, MO, NY). Michoacán: Mt Tancitaro, 3200-3700 m, Eggler (1950)44 (MO, WIS), Leavenworth & Hoogstraal 1130a (F), 1139 (F, GH, MO, NY), Hinton 15647 (NY). Oaxaca: Sierra de San Felipe, 3050-3300 m, Smith 932 (A, F, NY), Conzatti & Gonzales 419 (GH), Pringle 5951 (GH); 27 km N of Ixtlán, 2500 m, Roe & Roe 1976 (WIS); Oaxaca-Tuxtepec rd, km 130-140, 3500 m, Carlson 4126 (F). Puebla: Iztaccihuatl above San Juan Tlale and San Juan Tetla, 3800 m, Ern 304 (B); Tesmalaquilla, Sierra Negra, Mt Orizaba, 3200 m, Balls et al. B4475 (K). Veracruz: Pico de Orizaba, 3800 m, Schiede s.n. (B), Galeotti 5764 (G, P), Rose & Hay 5747 (GH).

GUATEMALA. Chimaltenango: Sante Elena, Mt Tecpam, 2400-2700 m, Standley 60998 (F); N side of Mt Fuego, 3550 m, Beaman 4040 (GH); Mt Acatenango above Las Calderas, 2700-2900 m, Standley 61864 (F). El Progreso: Summit Mt Siglo-Calera, 2000-3300 m, Steyermark 43111 (F). Huehuetenango: Sierra de los Cuchumatanes, 3 mi SW of San Mateo Ixtatán, 2900 m, Breedlove 11555 (F). Quezaltenango: Mt Zunil, 3000 m, Steyermark 34923 (F); Mt Santa María above Palojunoy, 3300 m, Standley 67684 (F). Sacatpequez: Mt Agua above Santa María de Jesús, 2250-3000 m, Standley 65098 (F). San Marcos: Mt Tajomulco, 3970 m, Beaman 3179 (GH).

COSTA RICA. Cartago: Mt La Muerte, 3000-3500 m, Webster et al. 12315 (F), Holm & Iltis 474, 485 (A, MO, P), Jiménez 896 (F); Mt Asunción, 3200 m, Lems s.n. (NY); Mt Turrialba, 3175 m, Lent 716 (NY); Mt Las Vueltas, 3300 m, Taylor 4331 (NY); Mt Irazú, 3000-3500 m, Williams & Molina 13928 (F), Davidse & Pohl 1167 (F), Dayton 3142 (F), Brenes s.n. (NY), Hatch 171 (F). San José: Canaan-Los Angeles-Chirripó trail N of Río Talarí, 3200-3400 m, Burger & Leisner 7406 (F, NY).

PANAMA. Chiriquí: E side of Mt Barú, 3000 m, Mori & Bolten 7447 (F, MO), Hammel 2756 (MO); Mt Chiriquí, 3000-4000 m, Davidse & D'Arcy 10245 (MO), Woodson & Schery 432 (MO), Terry 1317 (F).

Luzula denticulata is most easily recognized by its solitary flowers and its inflorescence which is not divided into subequal parts by long rachis segments. All the primary branches of the inflorescence arise in rapid sequence at the end of the culm, and not 5-15 cm apart as in L. gigantea. Of some 90-odd sheets examined, three had the one lower primary branch separated by a long rachis segment. Luzula gigantea always has 4-5 such branches separated by long rachis segments, and only one sheet of over 100 examined were missing these basal parts so that the inflorescence resembles L. denticulata. The two species are geographically strictly separated by the Panamanian Isthmus and L. denticulata has its genealogical affinities in the circumboreal Luzula parviflora complex, which always has short rachis segments, whereas L. gigantea is more closely related to the south-east Asian L. effusa Buchenau. Luzula denticulata was treated as a synonym of L. gigantea by Buchenau (1906) and Hämet-Ahti (1971).

Luzula subg. *Luzula*

Type species. *Luzula campestris* (Linnaeus) A. P. de Candolle.

Luzula sectio *Gymnodes* Grisebach, Spic. fl. rumel. 2: 405. 1845.

Gymnodes Fourreau, Ann. Soc. Linn. Lyon, n.s. 17: 172. 1869.

Luzula subg. *Gymnodes* (Grisebach) Buchenau, Bot. Jahrb. Syst.

12: 77, 113. 1890.

Perennial, caespitose or stoloniferous herbs, 1-100 cm high. Leaf blades apically acute or obtuse and callose tipped. Inflorescence with the flowers congested into round or elongate clusters which are then arranged in anthelae, loose panicles, racemes, or spike like structures.

Distribution. About 50 species covering the range of the genus.

Subg. *Luzula* is most easily recognized by having the flowers congested into clusters or heads, but it is otherwise extremely variable. It includes small 1-4 cm high pulviniform plants in New Zealand and large, up to 1 m high herbs with graciously nodding inflorescences in South America.

3. *Luzula campestris* (Linnaeus) A. P. de Candolle, Fl. franç. 3: 161.

1805.

Fig. 28.

Juncus campestris Linnaeus, Sp. Pl. 1: 329. 1753, pro parte.

Type. Europe. n.v.

Juncodes campestre (Linnaeus) Kuntze, Revis. gen. pl. 3 (2):

320. 1898.

Perennial caespitose herb to 70 cm high. Culms erect. Leaves basal and cauline, apically terminated by an obtuse, callose tip. Inflorescence a few- to many-headed anthela, to twice branched. Stamens 6.

Distribution. Luzula campestris occurs abundantly in the temperate regions of both hemispheres. In the New World it barely reaches into the tropical region in Costa Rica to the north and in southeastern Brazil to the south.

This species is easily recognized by its obtuse, callose-tipped leaves. The inflorescence is characteristic, having the flowers congested into heads, which are arranged in an anthelae, i.e., the more basally originating branches overtop the ones originating more apically. Anthelate inflorescences are common in Juncus, but in Luzula they are found only in the L. campestris complex. Buchenau (1890, 1906) divided L. campestris into 20 varieties, many of which were said to have wide distributions, occurring in two or more continents. Four varieties were listed from North America

Fernald & Wiegand (1913) treated the North American L. campestris as constituting 10 varieties. The temperate South American material of L. campestris was divided into three varieties by Barros (1953). Two of these, var. osteni and var. tristachya, are based on temperate South American types, and var. congesta was considered an introduction from Europe. Luzula ulei is the only name in this complex which is based on a type from the neotropical region. The few Costa Rican specimens agree well with the European/North American L. campestris var. multiflora, according to the North American material so labelled at NY.

Key to the neotropical varieties
of Luzula campestris

- 1. Anthela unbranched; flowerheads elongate. Seeds elongate.
 - 3a. L. campestris var. multiflora.
- 1. Anthela branched, flowerheads round. Seeds subspherical.
 - 3b. L. campestris var. ulei.

3a. Luzula campestris (Linnaeus) A. P. de Candolle var. multiflora
(Ehrhart) Čelakovský, Prodr. fl. Böhmen 1: 85. 1867. Fig. 28 A.

Juncus multiflorus Ehrhart, Calamariae, Gramina et Tripetaloiideae
Linnaei exsiccatae, ca. 1791. Type. Europe. n.v.

Perennial, caespitose herb, to 35 cm high. Rhizome ascending.
Culms erect, smooth or sulcate when dried, 0.7-1.5 mm diam. Basal

leaves several to each culm; sheaths short; blades linear, 5-15 x 0.2-0.4 cm, flat, gradually tapering toward an obtuse callose tip, margin hairy. Cauline leaves 1-2 to each culm, similar to but shorter than basal ones and with longer sheaths (to 2 cm). Inflorescence an unbranched anthela of flower heads, to 5 x 3 cm, branches not spreading, flower heads round or often elongate, 0.8-1.5 x 0.8 cm, 6-12 flowered. Lower inflorescence bracts resembling small cauline leaves, upper ones progressively shorter and membranaceous. Tepals equal, 3.5-4 mm long, lanceolate, acuminate, castaneous. Stamens 6, ca. 2.2 mm long; anthers linear ca. 1.5 mm long, longer than the filaments. Capsule obovoidal, mucronulate, shorter than the tepals. Seeds ellipsoidal, 1-1.4 mm long, with white spongy caruncula occupying up to half the length of the seed.

Distribution. A temperate Eurasian and North American taxon. In North America it is the most widely distributed variety of L. campestris, occurring from Newfoundland to Alaska, south to New Jersey, Pennsylvania, Illinois, Utah, and California (Fernald & Wiegand, 1913). The Costa Rican occurrence reported here is the first for the neotropical region.

Specimens examined. COSTA RICA. Cartago: Mt. Turrialba, upper slopes nr crater rim, 3100 m, 8 Aug 1968, Davidse & Pohl 1182 (MO); along creek in partially wooded pasture, 2800 m, 8 Aug 1968, Davidse & Pohl 1183 (AAU, MO, NY).

Many synonyms of this taxon, nomenclatural and based on European types, are not included above.

FIGURE 28

- 28 A. The distribution of Luzula campestris var. multiflora in the neotropical region. In addition it has a wide distribution in the north temperate regions of both the new and the old world.
- 28 B. The distrubution of Luzula campestris var. ulei in the neotropical region. In addition it occurs southwards in Brasil until Rio Grande do Sul.

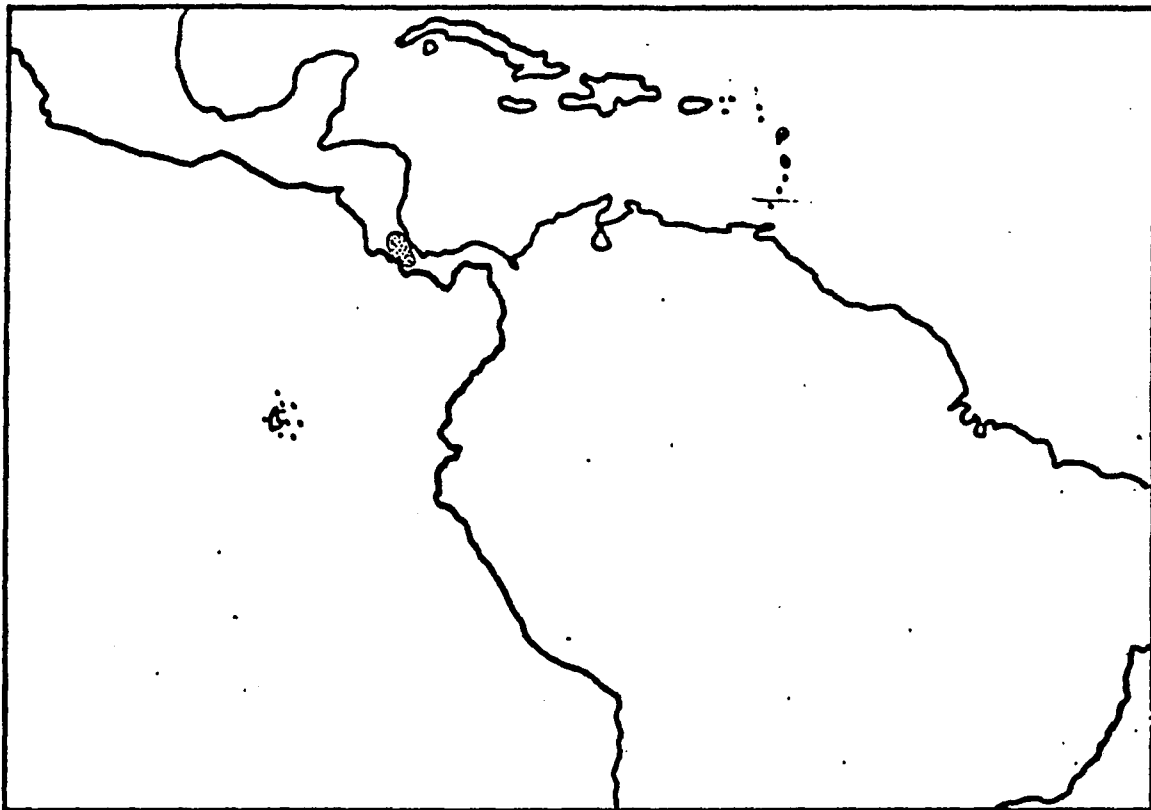


FIGURE 28 A.

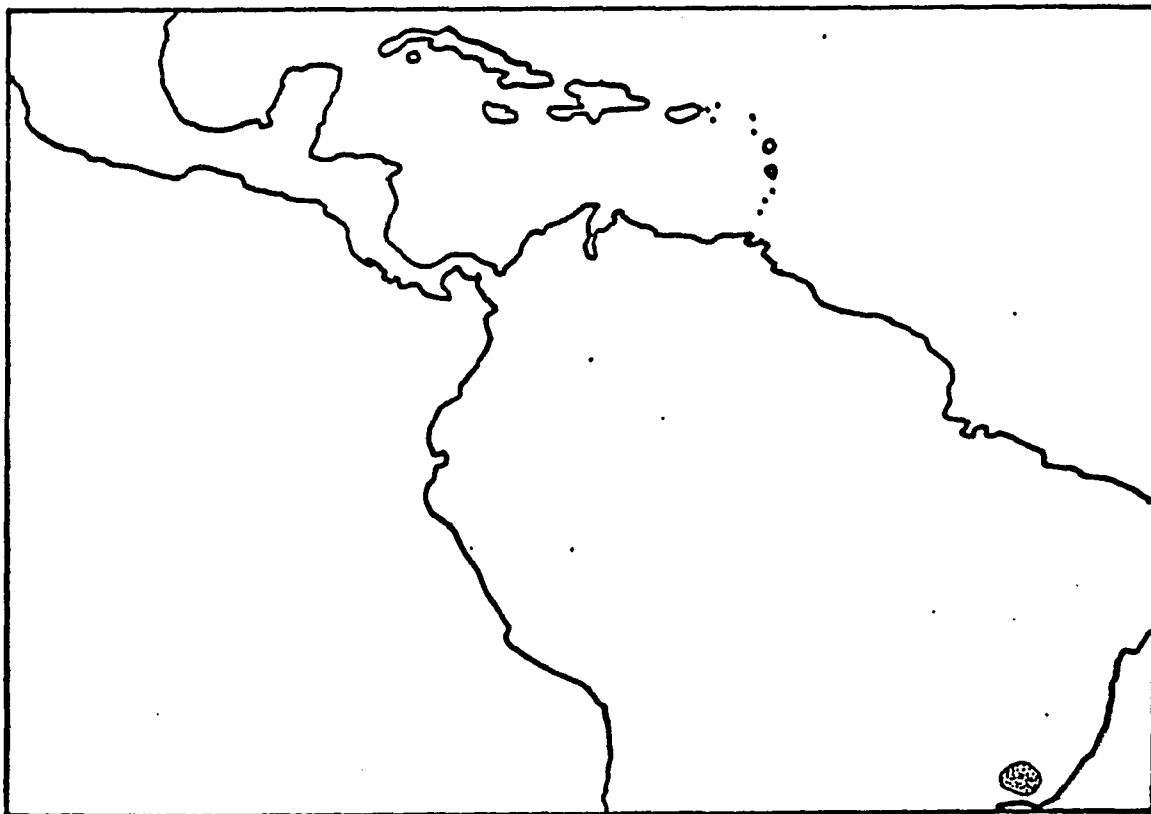


FIGURE 28 B.

3b. *Luzula campestris* (Linnaeus) A. P. de Candolle var. *ulei* (Buchenau)

Barros, *Sellowia* 14: 12. 1962.

Fig. 28 B.

Luzula ulei Buchenau, Bot. Jahrb. Syst. 26: 577. 1899. Type.

Brasil. Rio de Janeiro: Serra do Itatiaia, 2200 m, Feb 1894,

Ule 3505 (lectotype, W; isoelectotype, HBG). Santa Catarina:

Serra Geral, Jan 1891, Ule 1911 (syntypes, P, W).

Perennial, loosely caespitose herb, 30-70 cm high. Culms erect terete, smooth or sulcate when dried, 1-2 mm diam. Basal leaves many; sheaths short; blades linear, 10-25 x 0.5-0.9 cm, flat, gradually tapering towards an obtuse callose tip, margin hairy. Cauline leaves 2-4 to each culm, resembling basal leaves but shorter and with longer sheath (to 4.5 cm). Inflorescence a branched anthela of flower heads, up to 10 x 7 cm, branches spreading, flower heads 5-8 mm diam., 3-8(-12) flowered. Lower inflorescence bracts resembling cauline leaves, but shorter, upper ones progressively shorter and membranaceous. Tepals equal, 1.8(-3) mm long, lanceolate, acute, reddish brown to castaneous basally and dorsally, membranaceous and white to stramineous towards the margin and apex. Stamens 6, 1-2 mm long, slightly shorter than the tepals; anthers linear, 0.7-1.4 mm long, much longer than the filaments. Capsule almost spherical, indistinctly or sometimes distinctly mucronate, 2-2.2 x 2 mm, castaneous. Seeds subspherical, short apiculate, 1.1-1.2 x 0.8-0.9 mm, smooth, dark castaneous.

Distribution. Known only from southeastern Brazil, where it has been collected in the highlands from Paraná to Rio Grande do Sul, at altitudes between 1250 m and 2200 m.

Specimens examined. BRAZIL. Santa Catarina: Campo dos Padres, 1900 m, Reitz 3370, 3428 (S). Rio de Janeiro: Haut de Orguez, Glaziou 6429 (P); Itatiaia, Abrigo Rebouças, Castellanos 6929 (NY): Itatiaia nr source of Rio Preto, Glaziou 9042 (P); Itatiaia, Campo Redondo, Dusén 40 (S). Rio Grande do Sul: Mt Sapucaia nr San Leopoldo, Rambo 37929 (B), 57059 (B, S), 57464 (B); San Francisco de Paula, Cambara, Rambo 37679 (S).

Buchenau (1906), who described this taxon at the species level, stated that it has the habit of Luzula silvatica (Hudson) Gaudin, and that it forms a transition between the subgenera Anthelaea and Luzula (=Gymnodes). The almost spherical seeds were said to be characteristic of the taxon. To me there is no doubt that it is best treated as a variety of L. campestris. The obtuse, callose tipped leaf blades and the anthelate inflorescence clearly reveal this affinity. Luzula campestris (Linnaeus) A. P. de Candolle var. osteni Mattfeld (1921) is a very closely related, maybe not distinct, taxon. It is described from Minas in Uruguay (Type. Osten 15256, S).

4. *Luzula caricina* E. Meyer, *Linnaea* 22: 418. 1849. Type. México.

Oaxaca: 2450 m, 1840, Galeotti 5758 (holotype, W; isotypes, G, K, P, W). The citation of Galeotti 5757 in the protologue is a typographic error. Fig. 29 B.

Luzula interrupta Desvaux, J. Bot. (Desvaux) 1: 163, t.6, f.4.

1808. Type. América calidiora (holotype, P).

Luzula barbata Liebmman, Vidensk. Meddel. Dansk Naturhist. Foren.

Kjøbenhavn 45. 1850. Type. México. Puebla: Chinautla, 2150-2450 m, Liebmann s.n. (lectotype, C; isolectotypes, C, G, GH, K, P, W). Veracruz: Volcán Orizaba, Vaquería del Jacal, 3050 m, Liebmann s.n. (syntype, C).

Juncodes caricinum (E. Meyer) Kuntze, Revis. gen. pl. 2: 724. 1891.

Perennial caespitose herb, 10-60 cm high. Rhizome erect or ascending, sometimes thickened at the base of the culm. Culm erect and usually quite straight, terete, often sulcate when dried, 0.7-2 mm diam. Basal leaves 3-10 to each culm, blade 5-15 x 0.2-0.4 cm, gradually tapering to an obtuse, callose tip, margins hairy, at least when young. Cauline leaves 1-3 to each culm, resembling basal ones but erect and usually shorter. Inflorescence a terminal spike-like erect raceme of flower clusters, 2-5 x 0.5-1 cm, and usually a similar but smaller raceme of flower clusters originating up to 8 cm below the terminal one and inserted on an erect peduncle lifting it up to just below the terminal one; the rachis usually visible between the somewhat distantly inserted flower clusters. Basal inflorescence bracts resembling small cauline leaves, upper ones progressively shorter and membranaceous

with the margins entire or dissolved into ciliate lobes. Tepals lanceolate, acuminate to mucronate, 2-3.5 mm long, stramineous, castaneous or very dark reddish brown, outer ones concave, inner ones flat. Stamens 6, 1.2-2 mm long; anthers linear 0.6-1 mm long, equal to or longer than the filaments. Capsule obovoidal, acute to mucronate, trigonous to 3-lobed, 2-3 x 1.2-1.8 mm. Seeds ellipsoidal 1.5-1.8 x 0.8-1 mm, with conspicuous caruncula, castaneous below a hyaline, finely rugose outer seed coat.

Distribution. From Chihuahua in northern México to Guatemala at altitudes between 2400 m and 3200 m.

Specimens examined. MEXICO. Chiapas: Tenejapa, Paraje Metsab, 2750 m, Ton 948 (NY); Tenejapa, Matsab, 2800 m, Breedlove 15321 (WIS); Rancho Nuevo ca 9 mi SE of San Cristóbal de Las Casas, 2750 m, Breedlove 15106 (WIS). Chihuahua: Sierra Madre, 2750 m, Pringle 1116 (NY); Sierra Mohinora summit, 3100 m, Correll & Gentry 23173 (NY); Mt Mohinora, 8 mi from Guadalupe and Calvo, 2200 m, Nelson 4878 (K). México: Toluca, Pringle 4216 (W, WU); Ojos de Agua, Nevada de Toluca, 3650 m, Balls B4979 (K); 27 km W of Toluca, 2800 m, Mick & Roe 172 (WIS); Mt Ixtaccihuatl SW slope, 3600 m, Cochrane 8561 (WIS); Tres Cruces, Lyonnet 40 (MO); La Venta, 2450 m, Fischer 35218 (MO, NY, P). Morelos: S slope Serjana de Ajusco, 3000 m, Iltis et al. 248 (WIS). Oaxaca: Sierra de San Felipe, 3150 m, Pringle 4853 (MO, NY). Puebla: S slope of Mt Ixtaccihuatl, 3940 m, Beaman 1981 (WIS). Veracruz: Orizaba, 3050-3350 m, Linden 92 (G). State unknown: Teotepec, Mina Gro, 3200 m, Hinton 14452 (NY); La Cima, Lyonnet 43 (NY); "Mexico", Schmitz 816 (W); La Cimienta,

FIGURE 29

29 A. The distribution of Luzula gigantea in the neotropical region.

In addition it occurs in the northernmost parts of Argentina.

29 B. The distribution of Luzula caricina in the neotropical region.

In addition it occurs northwards in México until the state of Chihuahua.

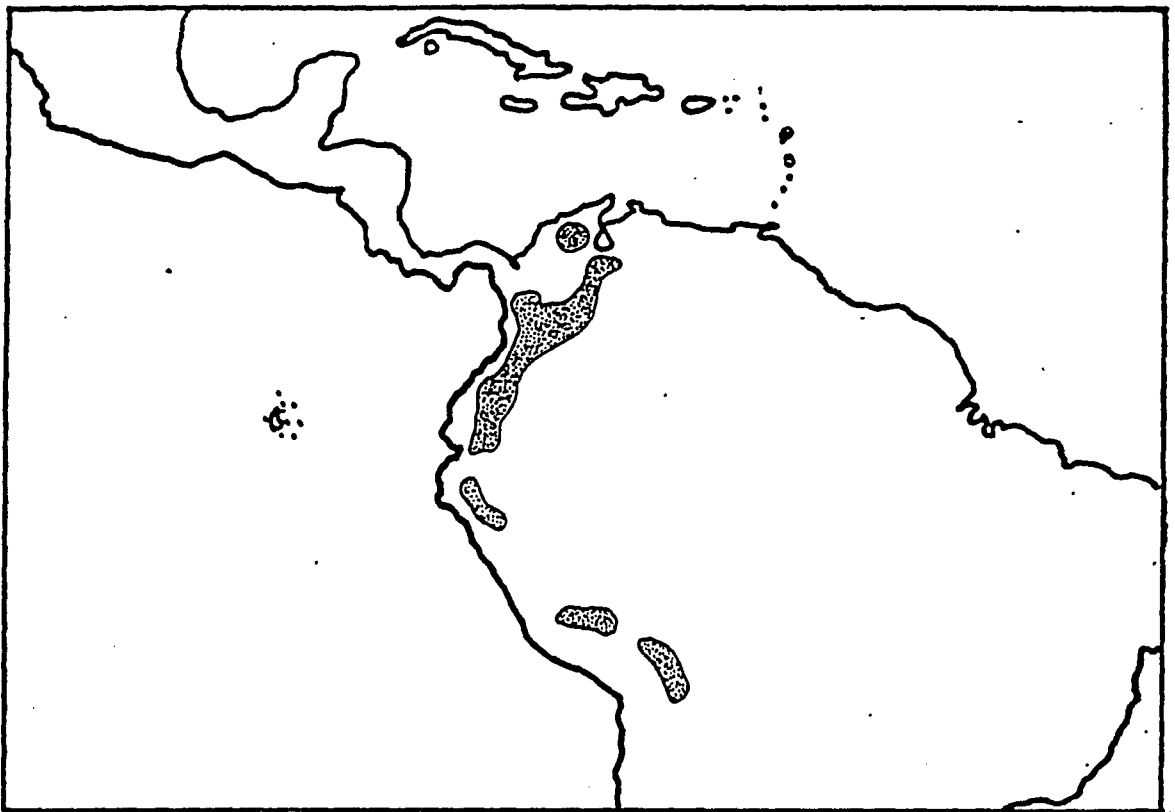


FIGURE 29 A.

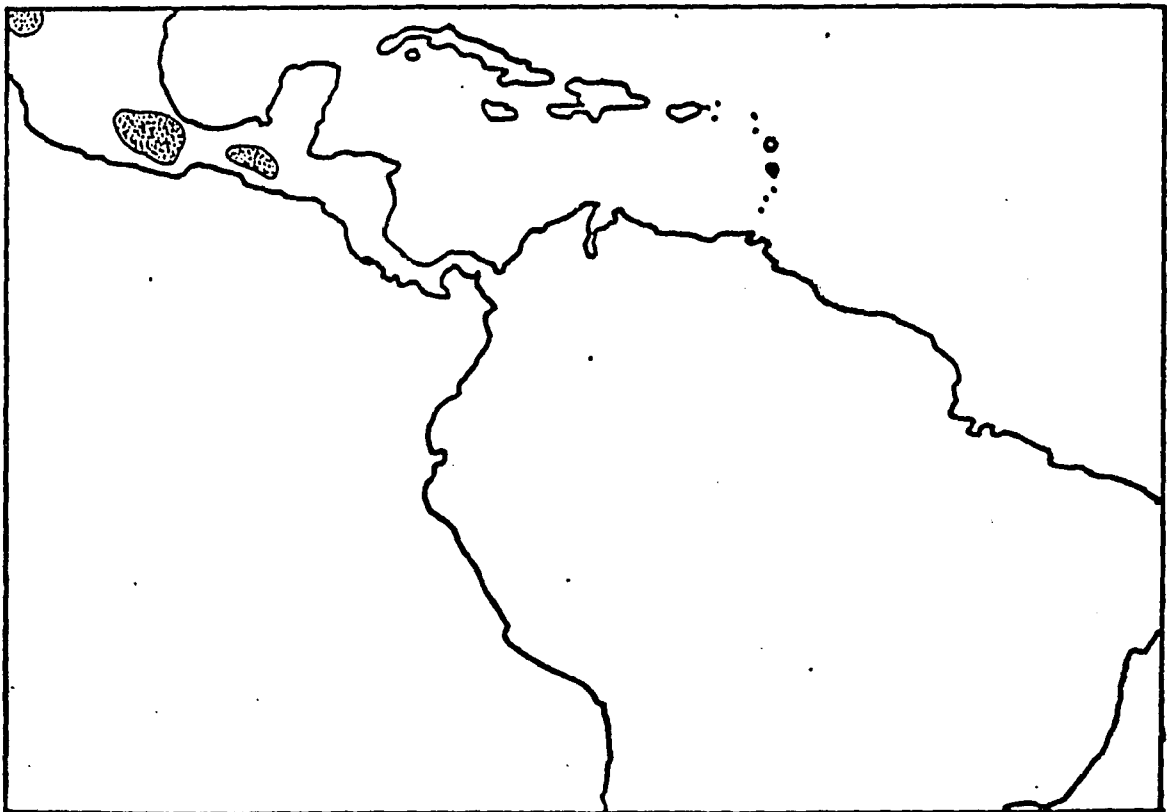


FIGURE 29 B.

Cofre de Perote, 3200 m, Balls B4641 (K); Desierta Vieja Valle de México, Bourgeau 1147 (P); Desierta Vieja, Hahn 1035^{bis} (P).

GUATEMALA: Huehuetenango: Sierra de los Cuchumatanes summit, 3700 m, Steyermark 50215 (NY); .2.5 mi E of San Mateo Ixtatán, Sierra de los Cuchumatanes, 2500 m, Steyermark 49884 (F).

Luzula caricina is most easily recognized by the combination of obtuse, callose-tipped leaf blades, erect spike-like inflorescences with the flower clusters usually somewhat distant so the rachis is visible, and usually very long peduncle of the basal flower cluster. The peduncle of the basal flower cluster is inserted up to eight cm below the terminal part of the inflorescence, but it is erect and lifts the flower cluster up to just below the rest of the inflorescence so that the entire inflorescence often does not appear subdivided. The obtuse callose tipped leaves place L. caricina close to L. campestris which, however, has an inflorescence of round to elongate flower heads in anthelate arrangement.

5. *Luzula ecuadoriensis* Balslev, Fl. Ecuador 11: 11. 1979. Type.

Ecuador. Cotopaxi: Railway station Cotopaxi, 3550 m, 26 May 1939,
Asplund 6494 (holotype, S; isotype, S). Figs. 30, 31 A.

Perennial herb, 50-75 cm high. Rhizome not seen. Culms erect and apically nodding, terete, 1.5-4 mm diam. Basal leaves 3-several in a rosette; sheaths short; blades erect or bending away from the culm, linear, 10-25 x 0.5-1 cm, flat, margin sparsely hairy on young leaves. Cauline leaves resembling basal ones, but sheaths to 7 cm long and blades shorter. Inflorescence a loosely branched panicle of nodding flower clusters, constituting $(1/8-1/3)$ or more of the total plant height, subdivided into 3-6 parts by 2.5-15 cm long rachis segments; flower clusters oblong to ovoidal 1-2.5 x 0.5-1 cm. Basal bracts resembling cauline leaves, to 20 cm long, upper ones progressively smaller. Bracteoles and more distant bracts in the inflorescence linear to lanceolate, membranaceous, with the margins entire or dissolved into ciliate lobes. Tepals unequal, reddish brown, outer ones 2.3-2.6 mm long, inner ones ca. 2.3 mm long. Stamens 3, 0.9-1.2 mm long; anthers oblong, 0.4-0.6 mm long. Capsule broadly obovoidal to suborbicular, trigonous to 3-lobed, 1-1.5 x 1 mm, light brown to dark reddish brown, glossy at dehiscence. Seeds ellipsoidal, broadly apiculate, ca. 1 x 0.5 mm, with polygon pattern, reddish brown below a whitish outer seed coat.

Distribution. So far only collected in Ecuador in the páramos and subpáramos at altitudes between 3300 m and 3800 m. The type locality is now a Pinus radiata plantation in a former bunch grass páramo. On Mt Pichincha I found it on a somewhat protected rocky slopes in an

FIGURE 30

Habit of Luzula ecuadoriensis showing the wide leaves and the much divided inflorescence with the flowers congested into elongate clusters (Drawn from Asplund 6494, S; from Balslev, 1979a).



FIGURE 30

area of bunch grass páramo.

Specimens examined. ECUADOR. Azuay: Angas on W slope of W cordillera due W of Cuenca, 3400 m, Balslev 1509 (NY). Bolívar: Hacienda Talahua, 3300 m, Penland & Summers 567 p.p. (GH). Chimborazo: Hacienda Magna E of Chunchi, Páramo de Cacheaco, 3800 m, Barclay & Juajibioy 8285 (US). Cotopaxi: 0.5 km S of railway station Cotopaxi along railroad, 3600 m, Balslev 1168 (NY); 4 km S of railway station Cotopaxi at rd to Mt Cotopaxi, 3500 m, Balslev 1184 (NY). Pichincha: W slope of Mt Corazón, Asplund 9685 (S). Mt Pichincha above Quito, 3700 m, Balslev AAU-23615 (NY).

Luzula ecuadoriensis is distinct through its paniculate inflorescence with long rachis segments, its flowers in oblong to ovoidal clusters, the more than 2.3 mm long tepals, and the usually large dimensions of the plants. Luzula gigantea is of equal dimensions but has solitary flowers. Luzula excelsa is also large and with a paniculate inflorescence of flower clusters, but its flowers are smaller, the tepals being 1.2-2.2 mm long, and usually stramineous. Like all other species of subg. Luzula this one varies in habit and small specimens may be confused with L. racemosa, in which the flower clusters, however, are sessile on the rachis except for the lowest one.

6. *Luzula excelsa* Buchenau, Abh. Naturwiss. Vereine Bremen 4: 126, t. 4, f. 1-8. 1874. Type. Bolivia. Hab. Prov^a Larecaja. -- Viciniis Sorata, Lancha de Cochipata etc. -- Regio temp., ad 2700-3200 m, Jan-Feb 1860, Mandon 1449 (holotype, n.v.; isotypes, BM, F, G, GH, GOET, K, NY, P, S, US). Fig. 31 B.

Luzula hieronymi Buchenau & Grisebach in Grisebach, Symb. fl.

argent. 318. 1879, also published as Abh. Königl. Ges. Wiss.

Göttingen 24. 1879. Type. Argentina. Tucumán: Cienaga,

10-17 Jan 1874, Hieronymus & Lorentz 735 (syntypes, GOET, F, K,

NY, S), same locality, 10-14 Jan 1874, Lorentz & Hieronymus

610 (syntype, GOET).

Juncodes hieronymi (Buchenau & Grisebach) Kuntze, Revis. gen. pl.

2: 724. 1891.

Juncodes excelsum (Buchenau) Kuntze, ibid.

Luzula hieronymi Buchenau & Grisebach var. pusilla Castillon,

Bol. Mus. Hist. Nat. (Univ. Nac.) Tucumán 7: 19: 1926. Syn-

types. Argentina. Tucumán: Tafí, Real del Derrumbado, 3800 m,

Apr 1926, Schreiter s.n. (Univ. Tuc., n.v.). Tafí, Cerro Muñoz,

3800 m, Jan 1914, Castillon 16422 (LIL, n.v.), 3900 m, Jan 1908,

Lillo 7442 (LIL, n.v.). Cumbres Calchaquies, 4200 m, Jan 1907,

Lillo 5600 (LIL, n.v.), Jan 1915, Castillon s.n., n.v., Jan 1907,

Castillon s.n., n.v.

Luzula hieronymi Buchenau & Grisebach forma bonariensis Barros,

Darwiniana 10: 335. 1953. Syntypes. Argentina. Buenos Aires:

Sierra de la Ventana, 11 Nov 1907, Hicken 76 (probably at SI, n.v.)

Mar del Plata, 6 Jan 1933, Hicken 840 (SI, n.v.), Pigüé, Sierra

de Curumalán, Burkart 4875 (SI, n.v.).

Perennial herb, 40-100 cm high. Rhizome ascending or erect. Culms erect and apically nodding, terete, 1-4 mm diam. Basal leaves 3-20 in a rosette; sheaths short; blades erect in few-leaved plants, linear, 15-20 x 0.5-2 cm, flat, margin hairy on young leaves. Cauline leaves resembling basal ones but sheath to 7 cm long and blades progressively shorter upwards. Inflorescence a loosely branched panicle of nodding flower clusters, constituting 1/3-1/2 of the total plant height, subdivided into 3-6 parts by 5-20 cm long rachis segments; flower clusters cylindrical, ca. 0.5-1.5 x 0.5 cm, flowers usually somewhat distant so the central branchlet is visible. Basal bracts resembling cauline leaves, to 30 cm long, upper ones progressively smaller. Bract-eoles and more distant bracts in the inflorescence linear to lanceolate, membranaceous, margin entire or dissolved into ciliate lobes. Tepals equal or outer ones longer, usually stramineous, sometimes reddish brown, outer ones 1.3-2.5 mm long, inner ones 1.2-2.2 mm long. Stamens 3, ca. 1 mm long; anthers oblong, ca. 0.4 mm long, shorter than the filament. Capsule broadly oblong to obovoidal, trigonous to 3-lobed, ca. 1.5 x 1.2 mm, light to reddish brown, glossy at dehiscence. Seeds ellipsoidal, broadly apiculate, ca. 1 x 0.6 mm, smooth to rugose, reddish brown below a hyaline outer seed coat.

Distribution. In the Andes from Puno in Peru to Tucumán and Catamarca in Argentina. It has been collected between 1600 m and 3500 meters at sunny exposed places, rocky slopes, road banks, etc. in the upper montane forest belt.

FIGURE 31

31 A. The distribution of Luzula ecuadoriensis.

31 B. The distribution of Luzula excelsa in the neotropical region.

In addition it occurs in northern Argentina until Tucumán
and Catamarca.

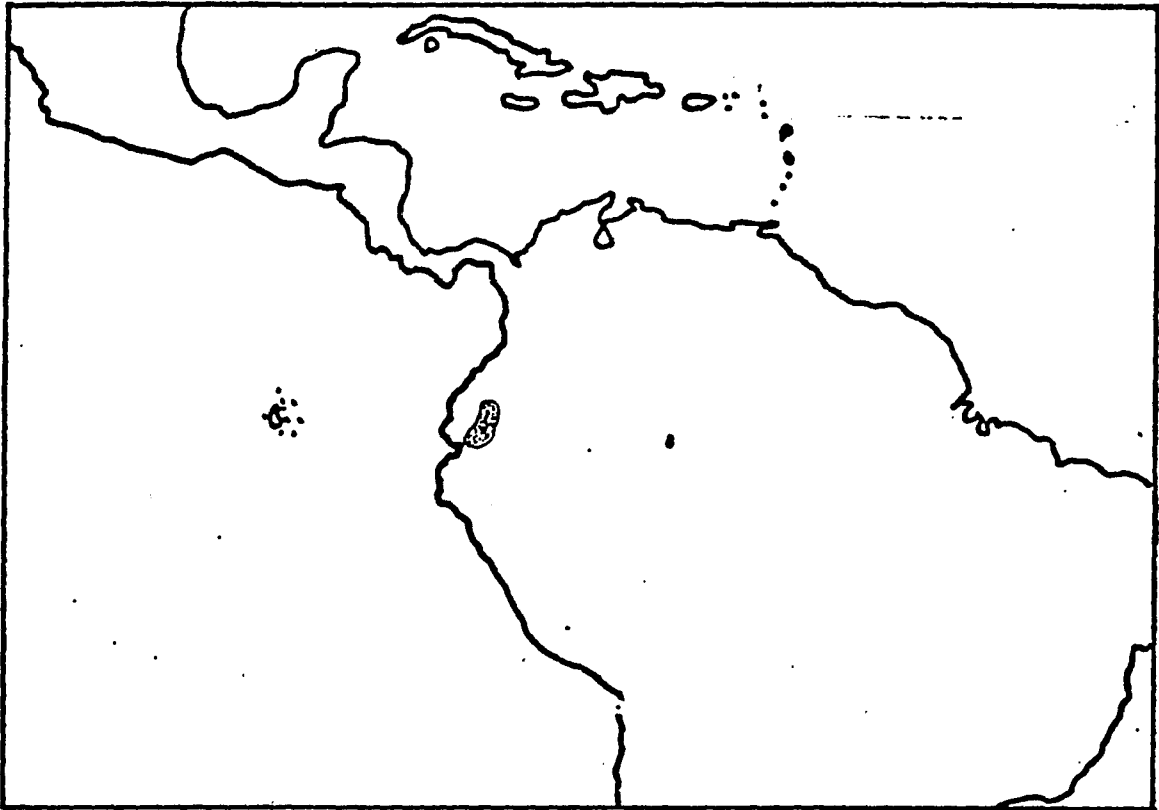


FIGURE 31 A.

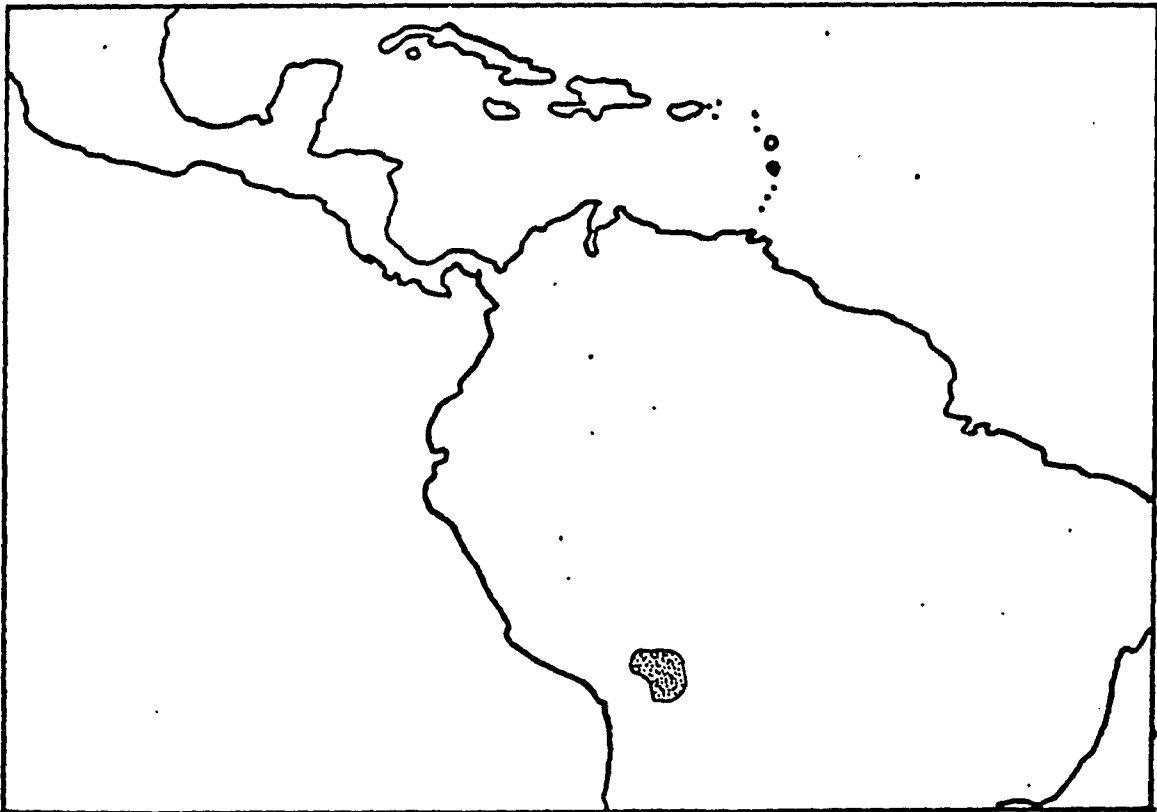


FIGURE 31 B.

Specimens examined. PERU. Puno: Sandia, 1800-1900 m, Ferreyra 16790 (USM).

BOLIVIA. La Paz: Tomina, Weddel 3727 (P); Murillo, Valle de Zongo, 3140 m, Beck 1130, 1130A, 2783 (LPB, NY); Murillo, Pongo de la Cumbre, 3700 m, Beck 4630, 4630A (LPB, NY); La Paz-Coroico rd, km 34, 3550 m, Balslev 1126 (LPB, NY), km 36-37, 3400 m, Balslev 1128 (LPB, NY); Comancho. 2 km S of Ambana, 3500 m, Beck 4172 (LPB, NY); Noryungas, Unduavi, 3100-3300 m, Buchtien 2601 (GH, NY, US), 8920 (HBG), Tate 131 (NY), Eyerdam 25110 (F); Suryungas, San Felipe, Holway 619 (NY); La Paz-Calacoto rd, km 62, 3600 m, Beck 3944 (LPB, NY); Sorata, Holway 551 (GH), Mandon 1447 (P); Calderillo, 3400 m, Fiebrig 2922 (G, K). Without locality: Bang s.n. (NY).

This species is closely related to Luzula ecuatoriensis through the structure of its inflorescence, which is a loose panicle of flower clusters, subdivided by long rachis segments. It is different in having smaller flowers (tepals 1.2-2.2 mm long vs. 2.3-2.6), and stramineous cylindrical flower clusters in which the flowers are somewhat separated so that the central branchlet is visible. These features usually make it easily recognizable, but there are specimens with reddish brown larger flowers, which I suspect are derived from some sort of hybridization with L. racemosa Desvaux. This latter species is less well defined when sympatric with L. excelsa than in areas of allopatry.

7. *Luzula vulcanica* Liebmann, Vidensk. Meddel. Dansk Naturhist. Foren.

Kjøbenhavn 44. 1850. Type. México. Veracruz: Vulkanen Orizaba, 4250 m, Liebmann s.n. (holotype, C; isotypes, C, GH, K, P).
Figs. 32, 33 B.

Luzula ruiz-lealii Barros, Darwiniana 10: 346, Fig. 19. 1953.

Type. Argentina. Mendoza: Tunuyán, valle del alto Tunuyán, 16 Feb 1934, Ruiz Leal 2140 (holotype, LIL-46295, n.v.), see discussion.

Perennial herb, (5-)15-35(-45) cm high. Rhizome erect or ascending, 1-2 mm diam., usually with transverse cracks ca 1 mm apart, producing ascending runners terminated by leaf rosettes. Culm erect, 0.7-2 mm diam., usually with a straight section between basal and apical cauline leaves, sometimes curved, but then often against the nodding direction of the inflorescence. Basal leaves 3-8 to each culm, inner ones erect and more or less appressed to the culm, blade (3-)7-15 x 0.2-0.5 cm, margin hairy when young, later glabrous. Cauline leaves usually 2 to each culm, 1-5(-11) cm long, inserted above the middle of the culm and usually close to the inflorescence, leaving a long leafless straight culm section in mature specimens. Inflorescence a terminal, spike-like raceme of 3-7 flower clusters, 1-4 x 0.5-1.5 cm, constituting less than 1/5 of total plant height, first erect, nodding at maturity, flower clusters 0.5-2 x 0.5-1 cm, sessile or basal one(s) sometimes short pedunculate and separated by a rachis segment about half as long as the cluster itself. Bracts membranaceous, margin dissolved into ciliate lobes, basal one usually about 1 cm long, broadly lanceolate, occasionally to 2 cm long and somewhat herbaceous in large specimens.

FIGURE 32

Habit and detail of Luzula vulcanica (Drawn from Øllgaard & Balslev 9891, AAU; from Balslev. 1979a).

32A. Habit showing the straight culm and the runners.

32B. Flower showing the bracteole with the margin dissolved into ciliate lobes.

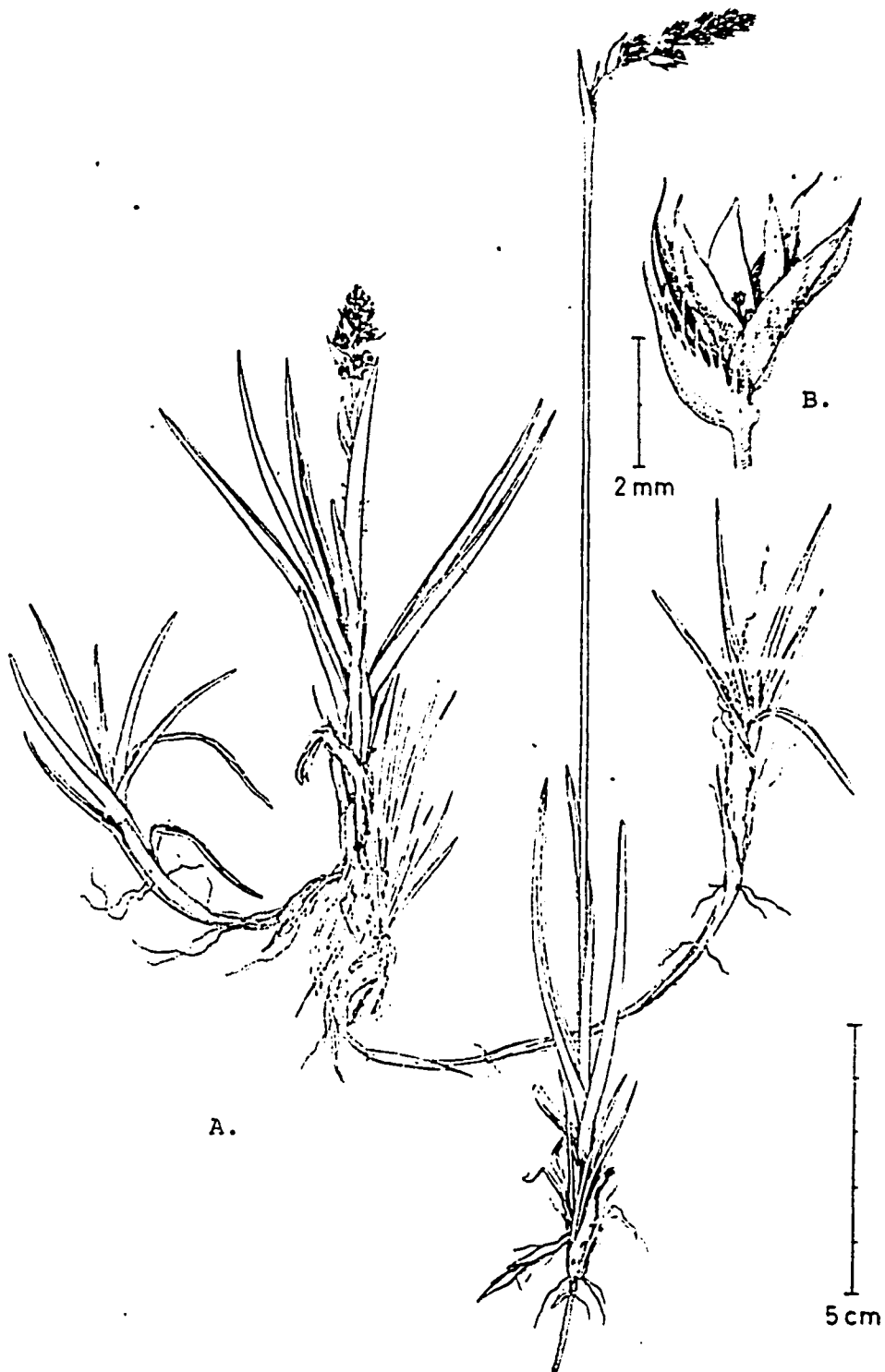


FIGURE 32

Tepals subequal, membranaceous, dark reddish brown in young flowers, outer ones 3-4 mm long, inner ones 2-3.5 mm long. Stamens 3, 1-1.5 mm long; anthers oblong, 0.2-0.6 mm long, shorter than the filaments. Capsule broadly ellipsoidal, basally 3-lobed, apically trigonous, 1.5-2 x 1-1.3 mm, finely rugose, light to reddish brown. Seeds ellipsoidal, apiculate, 1-1.2 x 0.5-0.6 mm, reddish brown below a whitish to light brown, smooth outer seed coat.

Distribution. In the states of Puebla and Veracruz in México and in the Andes from Colombia to Bolivia and in Mendoza in Argentina (the type of L. ruiz-lealii). In México it has been collected at ca. 4300 meters and in the Andes between 3400 m and 4700 m. Occurs most commonly in very wet and boggy places in the páramos, in contrast to the other neotropical Luzulae, which prefer drier habitats.

Specimens examined. MEXICO. Puebla: S side of Mt Ixtaccihuatl 0.5 km NE of summit of Piez, 4300-4350 m, Beaman 2554 (GH).

COLOMBIA. Boyacá: Páramos NW of Belén, Quebrada Minas, 600 m SE of Laguna El Alcohol, 3840 m, Cleef 2046 (U); Sierra Nevada de Cocuy, Alto Valle Lagunillas 1 km N of Laguna Pintada, 3960 m, Cleef 5597 (COL). Caldas: Nevado del Ruíz, 2 km SW of Refugio, 4520 m, Cleef & t'Hart 2418 (NY), Termales-Nevado, 4400 m, Barclay & Juajibioy 6326 (COL, US); Páramo de Quindio, 3700-4300 m, Pennell & Hazen 9858, 9859 (GH, NY, US). Cundinamarca: Páramo de Sumapaz, Chisacá, 3685 m, Cleef & t'Hart 2579 (NY), 3300-4000 m, Barriga 17196 (NY); Cogua-San Cayetano nr Laguna Seca, 3680 m, Cleef 6527A, 6546 (COL). Magdalena: Sierra Nevada de Santa Marta, Río Ancho, Páramo de Macotama, 3770-3840 m, Barclay & Juajibioy 6939 (US).

ECUADOR. Azuay: Molleturo-Quinoas nr Toreador, 3800-3900 m, Steyermark 53100 (NY). Carchi: 28 km N of El Angel, 3400 m, Balslev & Quintana AAU-23896 (AAU, NY). Chimborazo: Mt Chimborazo E slope, 4250 m, Asplund 7794 (S). Cotopaxi: Mt Cotopaxi, 4025 m, Ellenberg 3235 (NY); nr origin of Río Langoa E of Latacunga, Laguna Salayambo Cocha, 3800-4050 m, Øllgaard & Balslev 9891 (AAU). Imbabura: NE slope Mt Cayambe, 4100 m, Cazalet & Pennington 5723 (K, NY, US). Napo: Llanganati, Ainchilibi-Río Portrero E of Romo páramo, 3600-3700 m, Barclay & Juajibioy 9146, 9211 (US); Valle Vicioso E of Mt Cotopaxi, 3600 m, Holm-Nielsen & Balslev 23771, 24038 (AAU, NY). Pichincha: Pifo-Páramo de Guamaní, Balslev AAU-24185 (AAU, NY); NE slope Mt Cayambe, 3600-4000 m, Holm-Nielsen & Balslev 23683, 23684, 23687 (AAU? NY).

PERU. Lima: Ticollo-Rimac valley, 4500 m, Rauh P263 (F); Huarochiri, Lago Aguascocha, Mino Caprichosa above Casapalca, 4780 m, Hutchinson 4254 (US). Puno: Huancane, Occa Pampa, 3125 m, Shepard 62 (GH, NY). Department unknown: Casapalta, 4300 m, Ball s.n. (K); San Antonio de Esquilache, 4700 m, Stafford 1279 (BM, F).

BOLIVIA. La Paz: Larecaja nr Sorata, 4100 m, Mandon 1450 (GH); Gualata, 4200 m, Mandon 1446 (P); Lacatativa, 3600-4500 m, Mandon 1452 (G, K, P); Chacaltaya, Buchtien 9327 (HBG); Murillo, 2 km after take off to Valle Zongo, 4750 m, Beck 1268 (LPB, NY); Los Andes, 42 km NNW of La Paz nr Agencia Palcoco, 4600-4700 m, Beck 4323 (LPB, NY); Aroma, from La Paz 75 km S and 12 km towards Sapahaqui, 4200 m, Beck 6024 (LPB, NY); Lago Zongo S side of Huayna Potosí, 4700 m, Balslev & Beck 1148A (LPB, NY).

This species, originally described from México, is related to L. racemosa Desvaux, with which Buchenau (1906) considered it conspecific.

The differences between these two species are summarized in the following table:

<u>Luzula vulcanica</u>	<u>Luzula racemosa</u>
Runners present.	Runners absent.
Culms straight.	Culms curved.
Lower inflorescence bract broadly lanceolate, membranaceous, about as long as the flower cluster.	Lower inflorescence bract linear, herbaceous, exceeding the flower cluster.
Tepals membranaceous, very dark reddish black when young.	Tepals membranaceous, light reddish brown.

Luzula vulcanica cannot consistently be separated by any one of these features because of ecological modifications, but the combination of features mentioned gives it an appearance by which it is always easy to recognize in the field as well as on herbarium specimens.

Although I have not seen the type of Luzula ruiz-lealii Barros, which is cited as a synonym above, I believe that it belongs here. The description of the protologue, as well as the figure, strongly suggest this.

8. *Luzula racemosa* Desvaux, J. Bot. (Desvaux) 1: 162, t.6, f.3. 1808.

Type. Americâ calidiore, (holotype, P).

Figs. 33 A, 34.

Luzula peruviana Desvaux, J. Bot. (Desvaux) 1: 160. 1808. Type.

Americâ calidiore, (holotype, P).

Luzula humilis Buchenau, Abh. Naturwiss. Vereine Bremen 4: 125.

1874. Type. Bolivia. La Paz: Prov^a Larecaja. - Viciniis

Sorata, in petrosis, nivosis etc. Regio alpina, ad 3700-4200 m,

Jan-Apr 1858, Mandon 1448, (holotype, LUB, n.v.; isotypes, GH, GOET, NY, P).

Luzula boliviensis Buchenau, Abh. Naturwiss. Vereine Bremen 4: 128.

1874. Type. Bolivia. La Paz: Prov^a Larecaja. - Viciniis Sorata;

inter Pongo et Anilaya, in graminosis. - Reg. alpina, 3800 m,

Apr 1858, Mandon 1454, (holotype, LUB, n.v.; isotypes, F, G, GH, NY, P). Most of the labels have 1857 as year of collecting,

rather than 1858 as indicated in the protologue.

Luzula macusaniensis Steudel ex Buchenau, Abh. Naturwiss. Vereine

Bremen 4: 131. 1874. Type. Peru. Macusani, Jun 1854, Lechler

1839 (holotype, P; isotypes, G, GOET, K, P, S).

Juncodes racemosum (Desvaux) Kuntze, Revis. gen. pl. 2: 725. 1891.

Juncodes peruvianum (Desvaux) Kuntze, ibid.

Juncodes boliviense (Buchenau) Kuntze, ibid. 2: 724.

Juncodes macusaniense (Buchenau) Kuntze, ibid.

Luzula racemosa Desvaux var. *humilis* (Buchenau) Fries, Nov. Act.

Reg. Soc. Scient. Uppsala 1 (4): 167. 1905.

Luzula racemosa Desvaux var. *typica* Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 75. 1906.

FIGURE 33

33 A. The distribution of Luzula racemosa in the neotropical region.

In addition it occurs southwards along the Andes.

33 B. The distribution of Luzula vulcanica.

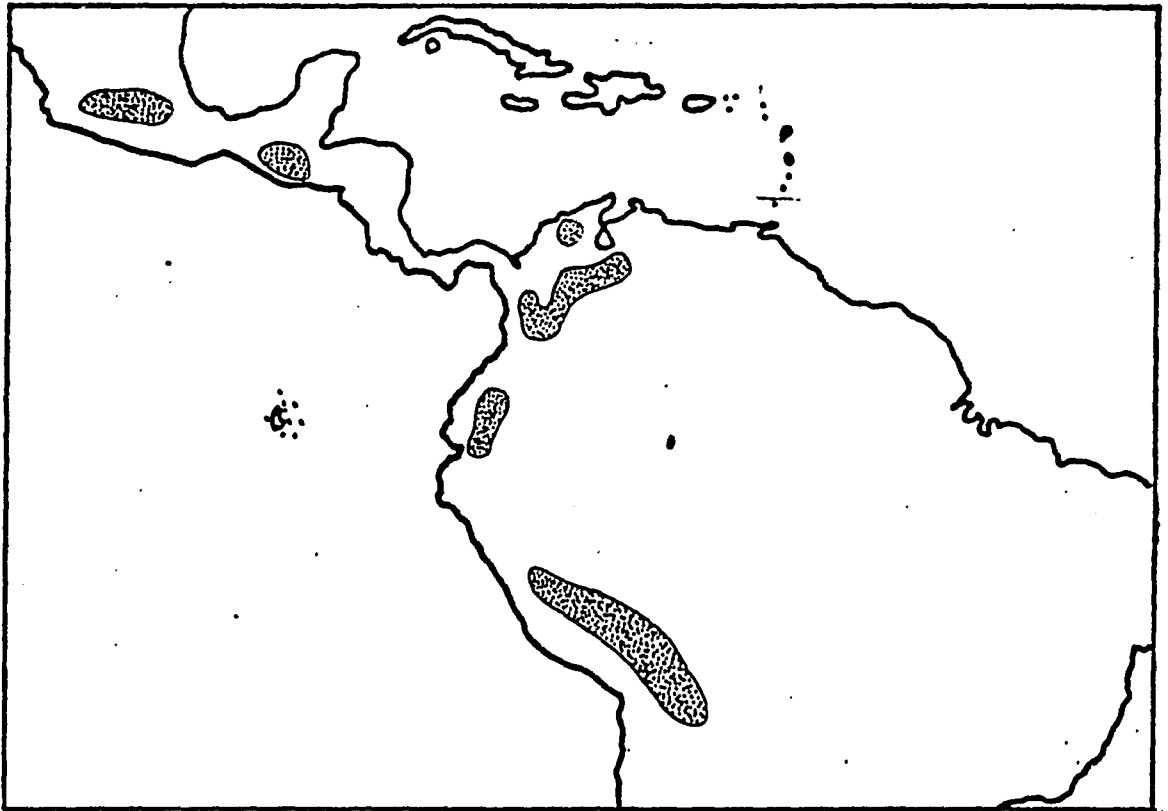


FIGURE 33 A.



FIGURE 33 B.

Perennial, caespitose herb, (5-)10-45 cm high. Rhizome erect or ascending, without runners. Culms erect, straight or more often slightly curved, 0.5-2 mm diam. Basal leaves 5-several to each culm, in loose or sometimes squarrose rosettes; sheaths short; blades apically acute, 5-25 x 0.1-0.5 cm, flat or sometimes thickened and concave. Cauline leaves 0-4 to each culm, to 15 cm long, the sheath occupying $\frac{1}{6}$ - $\frac{1}{3}$ of the length. Leaf margins hairy, especially when young and on cauline leaves. Inflorescence a terminal, erect or nodding, spike like raceme of 3 to several flower clusters, 1-6 x 0.5-2 cm, flower clusters oblong to ovoidal, 0.5-1.5 x 0.3-1 cm, sessile or sometimes short pedunculate, crowded or somewhat spaced along the rachis. Basal inflorescence bract herbaceous, linear, usually much longer than the flower cluster and up to 5 cm long, upper bracts progressively shorter. Tepals unequal, dark reddish brown or whitish membranaceous when old, outer ones 2.5-4 mm, inner ones 2-3.5 mm long. Stamens usually 3 but often 6, 0.6-1.5 mm long; anthers oblong to linear, 0.2-0.5 mm long, usually shorter than the filaments. Capsule broadly ellipsoidal to ovoidal, 3-lobed to trigonous, 1.5-2 x 1-1.5 mm, usually conspicuously shorter than the tepals but sometimes almost as long, reddish brown and dehiscent with the entire valve revolting. Seeds ellipsoidal, apiculate, 0.7-1.1 x 0.4-0.6 mm, brown with a whitish, rugose outer seed coat.

Distribution. In the highlands from central México to Guatemala and along the Andes from Venezuela to Chile and Argentina. Within the neotropical region it has been collected at altitudes between 2900 m and 4700 m, most often above 3500 m. It grows in well-drained, sunny exposed places in grassy openings in the upper montane forest belt and in the páramos above the timberline.

FIGURE 34

Habit and detail of Luzula racemosa, showing the variation which was formerly given taxonomic recognition (From Balslev, 1979a).

34A: Habit of the form formerly called L. peruviana (Drawn from Asplund 7938, US)

34B. Flower of same.

34C. Habit of the form called L. racemosa (Drawn from Bell 78, A).

34D. Flower of same.

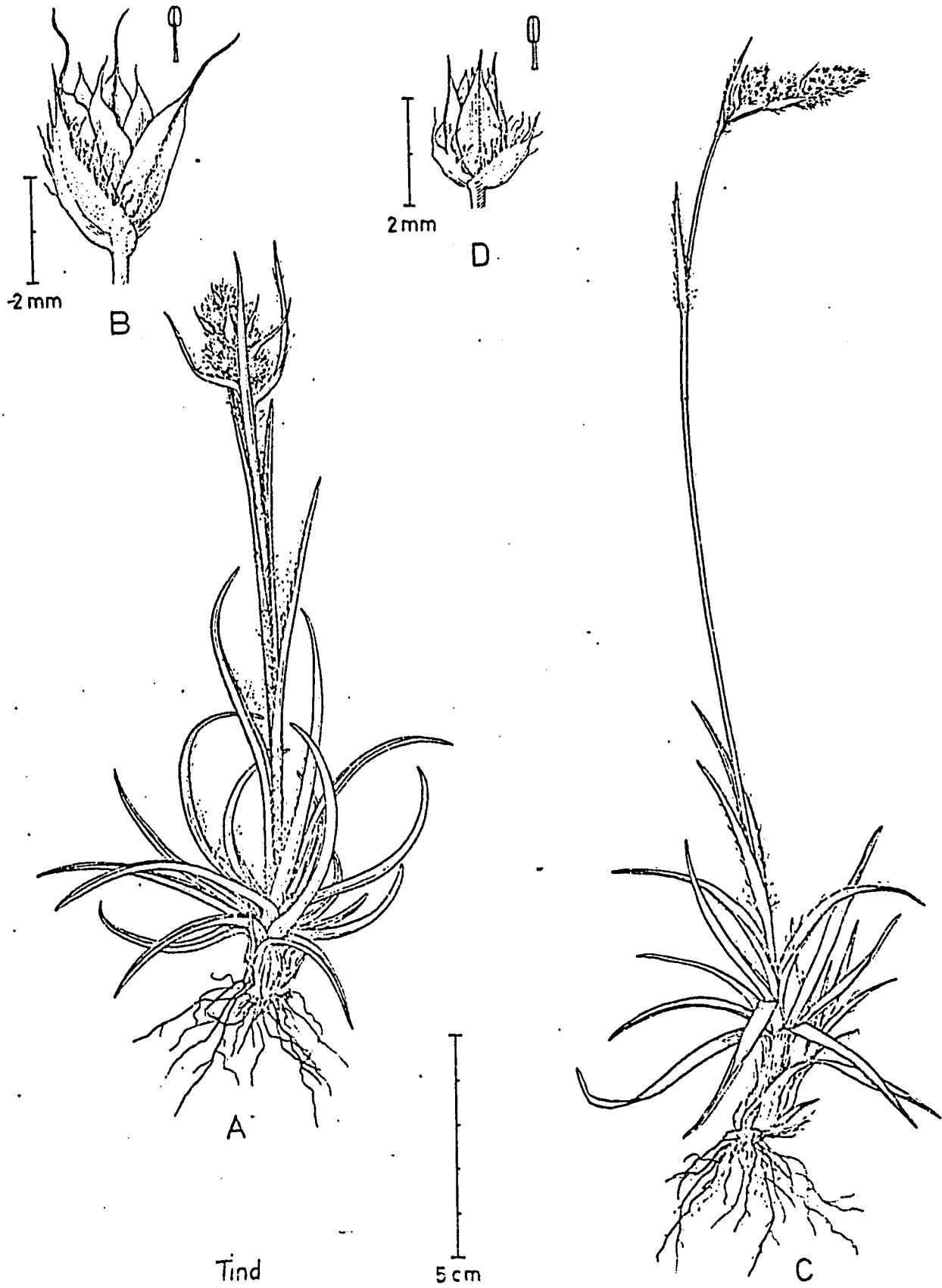


FIGURE 34

Representative specimens. MEXICO. Chiapas: SE side of Mt Tacana, Unio Juarez, 3600 m, Breedlove 29371 (F, MO, NY). Distrito Federal: Ajusco, 3900 m, Lyonnet 263 (MO, NY). Jalisco: Nevado de Colima S of Guzman, 3800 m, Gregory & Eiten 299 (MO, NY). México: Nevado de Toluca inside of crater, Dunn et al. 20415 (MO, NY). Michoacan: Mt Taucitaro, 3500 m, Leavenworth & Hoogstraal 1158 (MO). Tlaxcala: Malinche, 4400-4450 m, Beaman 2225 (NY, WIS). Veracruz: Cofre de Perote summit, 4192 m, Beaman 2148 (NY).

GUATEMALA. Huehuetenango: Aldea San Nicolas, Chiantla, 3130 m, Smith 279 (F). San Marcos: Mt Tajumulco, 4135 m, Beaman 3136 (NY). Totonicapan: Tecum Uman ridge ca 20 km E of Totonicapan, 3340 m, Beaman 4180 (NY).

COLOMBIA. Boyacá: Sierra Nevada del Cocuy, Alto Ritacuva, 4525 m, Barclay & Juajibioy 7342 (NY). Caldas: Páramo de Quindio, 4100-4300 m, Pennell & Hazen 9819 (GH, NY, US). Cundinamarca: Monserrate above Bogotá, 2900-3100 m, Pennell 1990 (GH, NY). Magdalena: Sierra Nevada de Santa Marta S of Picos Reina and Ojeda, 4200-4300 m, Cuatrecasas & Castañeda 24580 (US). Norte de Santander: Páramo de Santurban, 4030 m, St. John 20777 (NY). Santander: Páramo de las Vegas, 3700-3800 m, Killip & Smith 15639 (GH, NY). Tolima: Páramo de Ruíz, 3800-4300 m, Pennell 3028 (NY).

VENEZUELA. Mérida: Alto de Pinango between Las Corales and La Lagunita, 3500 m, Steyermark 55835 (F); Laguna Mucubají nr Los Aparaderos and San Rafael 35 km NE of Mérida, 3800 m, Maguire 39421 (NY); Páramo Muncuchies below Aguila pass, 4118 m, Walter & Walter 299 (B).

ECUADOR. Azuay: Angas on W slope of W cordillera, due W of Cuenca, 3400 m, Balslev 1492 (NY). Bolívar: E slope of Mt Chimborazo, 3500 m,

Barclay & Juaibioy 8163B (US). Cañar: Panamerican Highway at highest point between Cañar and Biblian, 3500 m, Balslev 1207 (NY). Carchi: Tulcán-El Angel rd, km 30, nr El Voladero, 3500 m, Harling & Andersson 12122 (GB). Chimborazo: Mt Chimborazo, 4500 m, Rimbach 120 (GH, US). Cotopaxi: S of Cotopaxi railroad station at rd to Mt Cotopaxi, 3500 m, Balslev 1183 (NY). Imbabura: Laguna Mojanda W of Otavalo, 3700 m, Balslev & Quintana AAU-24111 (NY). Napo: Laguna Micacocha SW slope of Mt Antisana, 3900-4100 m, Øllgaard & Balslev 8916 (AAU). Pichincha: Páramo de Guamaní, W slope along Quito-Baeza rd, 3800-4100 m, Balslev 1618 (AAU, NY). Tungurahua: Panamerican Highway 10 km S of Mocha, 3500 m, Harling et al. 6937 (GB).

PERU. Apurimac: Abancay, Ampay, 3800 m, Vargas 1070 (GH). Ayacucho: Huanta, Mt Razuhuillca, 4500 m, Weberbauer 7493 (F, US). Cuzco: Paruro, Hacienda Araypallpa, 3800 m, Vargas 544 (F). Huancavelica: Tayacaja S of Surcubamba, 4200 m, Weberbauer 6475 (F, GH). Junín: Mt La Juntay nr Huancayo, 4700 m, Killip & Smith 22066 (GH, NY, US). Lima: Nr Antaicocha, Cerro Colorado E of Canta, 4000-4200 m, Pennell 14677 (F, GH, NY, S). Puno: Chuquikambilla, 3850-3900 m, Pennell 13383 (F, GH, NY).

BOLIVIA. La Paz: Omasuyo, Penas rd, km 47 via Mina Fabulosa, 4500 m, Beck 2894 (LPB, NY); Loysa, Caxata 7 km towards Quime, 4540 m, Beck 4349 (NY); La Paz-Coroico rd, km 35, 3500 m, Balslev 1131 (LPB, NY); Sorata-Achacachi rd, km 28, 3850 m, Balslev 1105 (LPB, NY); Lago Zongo on S side of Huayna Potosí, 4700 m, Balslev & Beck 1148 (LPB, NY); Valle de Zongo on S side of Huayna Potosí, 4650 m, Balslev & Beck 1142 (LPB, NY). Potosí: Chayanta, Ocuri 7 km towards Ravelo-Sucre, 3950 m, Beck 6188 (LPB, NY).

In an earlier publication (Balslev, 1979), I recognized three species (L. racemosa, L. peruviana, and L. chilensis) within L. racemosa as here defined. In the latest monograph of the genus (Buchenau, 1906) this material was referred to four species in two different groups (9 and 10).

Examination of a large amount of material, covering the area from México to Bolivia, has convinced me that, even if several genetically different lines may be represented in the material, it is impossible at present to consistently distinguish any taxa therein. If present, the genetically-caused morphological differences are quite subtle, and they are obscured by much larger differences caused by ecological modifications. The characters used by Buchenau (1906) to separate the species, such as the number of stamens (3 or 6), inflorescence erect or nodding, inflorescence lobate or interrupted, etc. have proven useless. The characters I used (Balslev, 1979) to separate three species in Ecuador also break down when a larger sample of material is examined. The fact that some specimens are intermediate between L. racemosa and the otherwise distinct L. excelsa, further complicates the picture, and suggests that hybridization may be responsible for some of the morphological expressions, which to us appear as taxonomic problems.

6. *Juncus* Linnaeus, Sp. Pl. 1: 325. 1753; Engelmann, Trans. Acad. Sci. St. Louis 2: 424-458. 1866; *ibid* 2: 459-499. 1868; Buchenau, Bot. Jahrb. Syst. 12: 167-461. 1890; Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 98-266. 1906; Barros, Darwiniana 10: 358-460. 1953. Type species. *Juncus acutus* Linnaeus.

Cephaloxys Desvaux, J. Bot. (Desvaux) 1: 321. 1809. Type species.

Cephaloxys flabellata Desvaux (= *Juncus repens* Michaux)

Caespitose annual or rhizomatous perennial, glabrous herbs. Culms usually erect, rarely procumbent or ascending. Leaves alternate, scale-like on the rhizomes, cataphyllous (i.e. with reduced blade) and/or blade bearing basal on the culm, and bracteous in the inflorescence. Sheaths open, usually conspicuously auriculate at the junction to the blade. Blade linear with varying cross section: flat with raised margins and slightly channeled above, canaliculate, round to elliptical, or completely flat. Inflorescence compound and often decompound, cymose or racemose, often anthelate. Inflorescence bracts resembling blade bearing leaves, scale-like or membranaceous, lower one often conspicuously larger, diminishing in size upwards. Flowers subtended by two membranaceous, subtriangular bracteoles, situated immediately below the flower and clasping it (species 4-10) or without such bracteoles (species 1-4 and 17-37). Flowers bisexual. Tepals equal or unequal, lanceolate, entire, persisting, light green when young, turning pale brown, reddish brown or dark brown, margin membranaceous or conform. Stamens 3 or 6; filaments filiform or flat, sometimes widened at the base; anthers linear or oblong,

obtuse. Ovary sessile. Style short, filiform. Stigmas 3, filiform, twining, covered with sticky papillae Capsule 1-locular, 3-septate, or 3-locular. Seeds many, ellipsoidal, oblong to ovoidal, smooth, rugose or sometimes with reticulate pattern, brown or yellowish to reddish brown.

The name Juncus is derived from the Latin verb 'jungo' which means to join or unite, probably referring to the ancient use of these plants to bind things together.

Distribution. A cosmopolitan genus of about 220 species, most of which occur in the north temperate region, but with some proliferation in the south temperate region. In the tropics the genus is totally absent in the lowlands but present at higher altitudes, usually above 2000 meters altitude. Tropical South and Central America with 45 species is richest among the tropical regions, followed by tropical Africa with seven and tropical Asia with four species. Fig. 35 A.

Taxonomic History of Juncus

Since Linnaeus' Species Plantarum (1753) the name Juncus has been stable in the botanical literature, including an ever-increasing number of species, some of which have gradually been removed to segregate genera. Of 15 Juncus species mentioned by Linnaeus (1753) three now belong in Luzula. Rostkovius' monograph of Juncus (1801) included 52 species, 13 of which have been transferred into Luzula (A. P. de Candolle, 1805), Prionium (Meyer, 1832), Rostkovia and Marsippospermum (Desvaux, 1809).

Laharpe (1827) treated 78 species of Juncus, Kunth (1841) 105, Buchenau (1890, 1906) 176 and 207 respectively. Since Buchenau's work the genus has only been treated regionally. A number of new species have been described, parts of the genus have been revised to reduce the number of species, but no current published and firmly based estimate of the number of Juncus species has appeared.

FIGURE 35

35 A. The distribution of the genus Juncus in the neotropical region.

In addition the genus has a wide distribution in the temperate regions of both the southern and the northern hemispheres.

35 B. The distribution of Juncus acutus subsp. leopoldii in the neotropical region. In addition it occurs in South Africa, temperate South America, southwestern North America and the Atlantic islands.

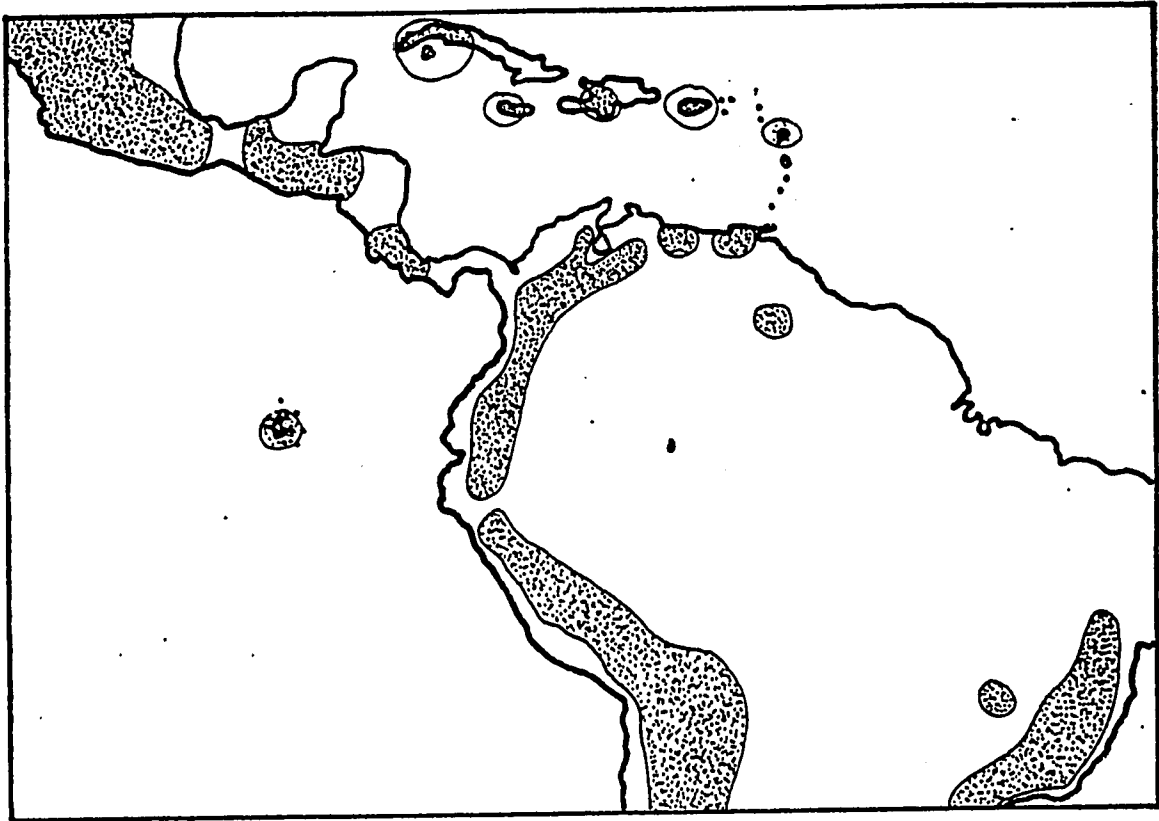


FIGURE 35 A.

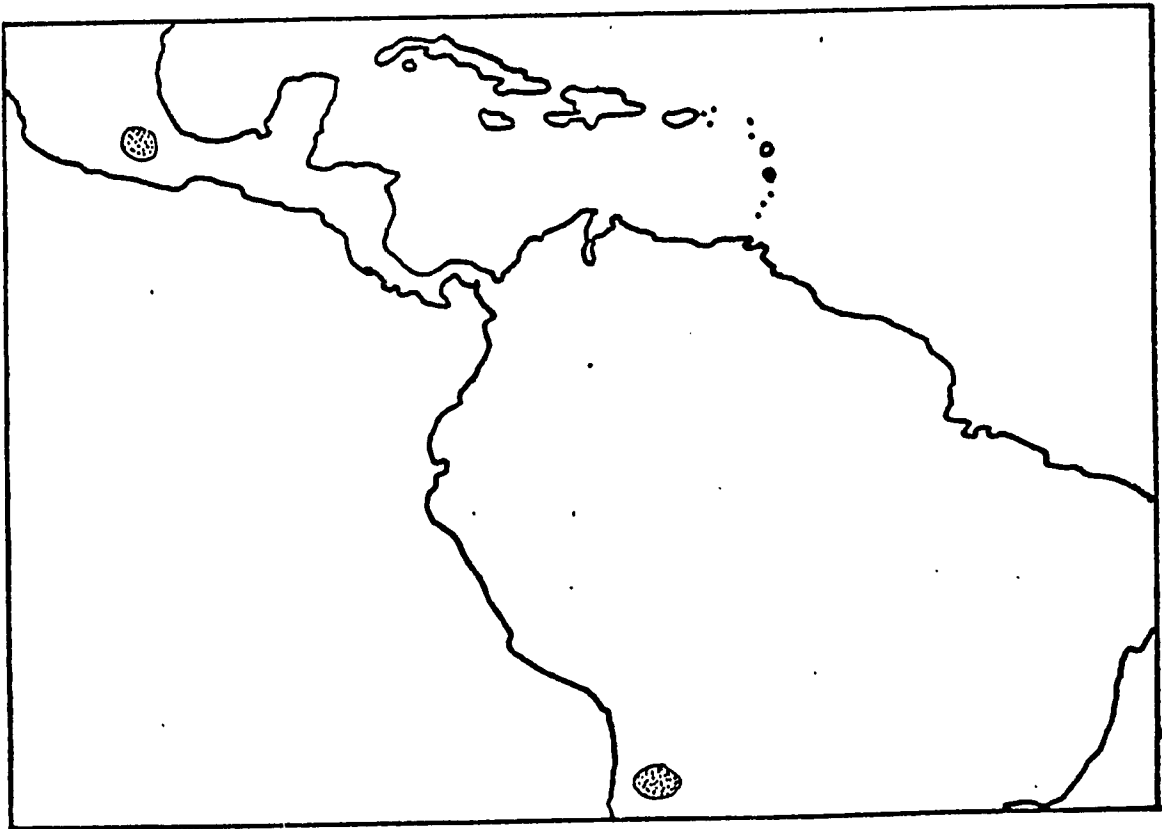


FIGURE 35 B.

Key to the subgenera of Juncus occurring in the
neotropical region

1. Entire plant heavily sclerified and rigid, more than 60 cm tall.
Culms and leaf blades terete and solid; vascular bundles spread throughout the cross section. Leaves and inflorescence bracts terminating in hard pointed apices. Sheaths of basal leaves thick and somewhat swollen. Juncus.
1. Plants not heavily sclerified, 2-200 cm tall. Culms terete or laterally compressed with vascular bundles in a ring along the periphery; leaf blades flat, canaliculate, or terete, when terete then hollow with transverse septa and the vascular bundles restricted to a ring along the periphery. Leaves and inflorescence bract acute, but not terminating in hard pointed apices. Leaf sheaths not swollen.
2. Each flower clasped by two bracteoles inserted on the pedicel just below the tepals in addition to the bract supporting the pedicel. Inflorescence compound cymose, with the parts often consisting of repeatedly one-sided or two-sided cymes branching in one plane (drepania or rhipidia).
3. Leaves with well developed blade, linear, flat or canaliculate. Inflorescence terminal on the culm; lower inflorescence bract similar to cauline leaves. Poiophylli.
3. Leaves with rudimentary needle-like blade only, present as basally sheathing cataphylls. Inflorescence pseudolateral; lower inflorescence bract appearing as a continuation of the culm Genuini.

2. Flowers without clasping bracteoles, supported only by the bract supporting the pedicel. Inflorescence compound- racemose, usually with the flowers congested into several heads in anthelate arrangement.
4. Leaves dorsiventrally flattened, i.e. with the flat side towards the culm. Graminifolii.
4. Leaves terete or laterally flattened, i.e., with the edge towards the culm.
5. Leaves terete, hollow and septate by cross partitions usually appearing externally as nodules. Septati.
5. Leaves laterally flattened, sword like, ensiform, equitant as in Iris, sometimes somewhat hollow and incompletely cross septate. Ensifolii.

Juncus subg. Juncus

Type species. Juncus acutus Linnaeus.

Juncus subg. Juncus section Maritimi Engelman, Trans. Acad. Sci.

St. Louis 2: 433. 1866.

Juncustrum Fourreau, Ann. Soc. Linn. Lyon, n.s. 17: 172. 1869.

Juncus subg. Thalassici Buchenau, Abh. Naturwiss. Vereine Bremen

4: 406, 418. 1875.

Juncus sectio Pungentes Coutinho, Bol. Soc. Brot. 8: 96. 1890.

Juncus sectio Juncastrum (Fourreau) Post & Kuntze, Lex. gen. phan.

303. 1903.

Juncus subg. Thalassii Buchenau in Engler, Pflanzenreich IV, 36

(Heft 25): 100. 1906.

Juncus sectio Acuti Rouy, Fl. fr. 229. 1912.

Juncus sectio Maritimi Rouy, Fl. fr. 230. 1912.

Juncus sectio Thalassii (Buchenau) Vierhapper in Engler & Prantl,

Nat. Pflanzenfam. 2 ed., 15a: 216. 1930.

Juncus subg. Juncastrum (Fourreau) Krechetovic & Goncharov,

Fl. URSS 3: 543. 1935.

Perennial herbs to 230 cm high. Rhizome densely branching and the entire plant caespitose, or the rhizome creeping and the culms arising somewhat distantly. Culms erect, terete, very rigid and sclerenchymatous with fine longitudinal ridges. Leaves all basal with prominent, somewhat swollen reddish brown sheaths and terete, rigid, apically hard pointed blades which are not hollow and do not have transverse septa.

Inflorescence compound racemose, paniculate, many flowered with irregular alternation of long shoots and short shoots, varying from loose to congested in overall appearance. Flowers without bracteoles in addition to the bract supporting the pedicel.

Distribution. Subg. Juncus has five species in the New World and a similar number in the Old World, some occurring in both. All appear to be confined to saline soils in tidal swamps and inland deserts, etc. In the New World the subgenus is conspicuously disjunct, occurring in the north and south subtropical regions, from which it barely reaches into the tropical region. The north-south disjunction in the New World proceeds below the subgeneric level, as two of the species (J. acutus and J. maritimus) have populations in both hemispheres.

This subgenus is most easily recognized by its vegetative appearance because of the very rigid and hard sclerenchymatous culms and leaves. The apices of leaves and bracts are hard-pointed like spines, and the sheaths are thicker, somewhat swollen, larger and more prominent than in the other subgenera. For the more technical distinguishing features one has to observe the absence of two bracteoles clasping each flower, and the terete leaf blades which are not hollow, but which have the vascular bundles spread throughout the cross section. Blades with round cross section are found also in subg. Septati. There they are hollow, have transverse septa, and the vascular bundles lie in one ring along the periphery.

Key to the neotropical species of

Juncus subg. Juncus

1. Capsule triseptate, obviously longer than the tepals, spherical to broadly ellipsoidal. Anthers reddish brown. Rhizome densely branching, not creeping. 1. J. acutus.
1. Capsule trilocular, about as long as the tepals, ellipsoidal to narrowly ellipsoidal. Anthers yellow. Rhizome horizontal creeping.
 2. Seeds inserted on swollen spongy placentas. Inflorescence branches thin, flexuose, the ultimate ones ca. 0.2 mm diam. 2. J. roemerianus.
 2. Seeds inserted on not swollen placentas. Inflorescence branches rigid, the ultimate ones more than 0.2 mm diam. 3. J. maritimus.

1. *Juncus acutus* Linnaeus subsp. *leopoldii* (Parlatore) Snogerup, Bot.

Not. 131: 187. 1978.

Fig. 35 B.

Juncus leopoldii Parlatore, Giorn. Bot. Ital. 2: 324-325. 1845.

Type. South Africa. Cape of Good Hope, Ecklon & Zeyer s.n.

(syntype, n.v.), same locality, Drege s.n. (syntype, n.v.).

Juncus macrocarpus Nees, Linnaea 20: 243. 1847. Type. South

Africa. Cape of Good Hope, Ecklon & Zeyer s.n., n.v.

Juncus acutus Linnaeus var. *leopoldii* (Parlatore) Buchenau, Abh.

Naturwiss. Vereine Bremen 4: 421. 1875.

Juncus acutus Linnaeus var. *sphaerocarpus* Engelmann in Wheeler,

Rep. U.S. Geogr. Surv. west of 100th meridian 6 (Botany): 376.

1878. Type. USA. California: Santa Barbara, near the seacost,

Rothrock 102 (holotype, probably at US, n.v.; isotype, NY).

Juncus robustus Watson, Proc. Amer. Acad. Arts 14: 302. 1879.

Basionym. *Juncus acutus* Linnaeus var. *sphaerocarpus* Engelmann.

Juncus acutus Linnaeus var. *sphaerocarpus* Engelmann forma *xanthosus*

Jepson, Fl. Calif. 1: 249. 1921. Type. USA. California:

Thousand Palms Cañon, NW of Indio, Jepson 6041 (holotype, probably at JEPS, n.v.).

Perennial densely caespitose herb, 50-150 cm high. Rhizome densely branching and producing shoots in axils of blade bearing leaves, the base of the plant therefore thickened. Culms rigidly erect, terete, 2-5 mm diam., longitudinally striate, heavily sclerified, pith parenchymatous with vascular bundles spread throughout. Leaves 40-120 cm long, 5-7 to each culm, all basal; sheaths 5-30 cm long, with narrow membrana-

naceous margin gradually tapering upwards and terminating into a narrow, few centimeters long adaxial groove; blades terete, rigid with hard spine like apices, pith parenchymatous with vascular bundles spread throughout. Inflorescence compound paniculate, congested and only 3 x 3 cm or more lax and up to 20 x 10 cm, the branching alternating between short shoots and long shoots so the inflorescence often becomes subdivided, flowers clustered together in glomerules of 2-4 flowers each and clasped by the bracts supporting the pedicel, but without bracteoles inserted on the pedicel. Lower inflorescence bract half as long as or equalling the inflorescence, more rarely longer, rigidly erect with a wide sheath and a terete, spine like pointed blade. Tepals ca. 2 mm long, outer ones acute to obtuse with scarious margins terminating in two small auricles, V-shaped in cross section, inner ones mucronate to obtuse with large scarious white auricles, U-shaped in cross section. Stamens 6, 1.5-2 mm long, equal to or slightly longer than the tepals; filaments short and widened at the base; anthers several times as long as filaments, reddish brown. Style ca. 0.5 mm long. Stigmas 1 mm long. Capsule about twice as long as tepals, obovoidal to almost globular, shortly mucronate, round in cross section, 3.5-4 x 3-3.5 mm, light to dark brown, 3-septate. Seeds varying and irregularly shaped, usually somewhat curved, 0.9-1.1 x 0.3-0.4 mm, with transparent extensions of the outer seed coat at both ends.

Distribution. Juncus acutus subsp. leopoldii occurs in South Africa, South America, southwestern North America and the Atlantic Islands. It differs from the mostly Mediterranean subsp. acutus in having obovoidal, blunt, usually dark brown to chestnut colored capsules (Snogerup, 1978). The North American populations, traditio-

nally referred to as Juncus acutus var. sphaerocarpus, occur along the Californian coast from San Luis Obispo county southwards to Isla Cedros of Baja California and inland to the Colorado desert and Arizona. There is a disjunct occurrence in Puebla in México. The South American populations occur in the Andean salt deserts from Atacama in northern Chile, southwards to Mendoza and Río Negro in Argentina, and also in the coastal salt marshes on the east coast from Florianopolis in Santa Catarina, Brasil, southwards to Bahia Blanca in Argentina. The neotropical occurrences therefore include no more than the 'inner edges' of a temperate north-south disjunction.

Specimens examined. MEXICO. Puebla: W of Río Salado on and around Petlanco, 1000-1500 m, Smith et al. 3675 (G, GH, MO, NY).

CHILE. Antofagasta: San Ramon Quebrada N of Taltal, Johnston 5126 (GH, K). Apart from these, many specimens from North and South America outside of the tropical region have been examined and annotated.

2. *Juncus roemerianus* Scheele, *Linnaea* 22: 348. 1849. Type. USA.

Texas: Mustang Island at Galveston, Römer s.n., n.v. Fig. 36 A.

Perennial stout herb, 90-230 cm high. Rhizome horizontal creeping, 5-7 mm diam., densely covered with brown scales, internodes 1-5 cm long. Culms rigidly erect, terete, 1-4 mm diam., longitudinally striate, heavily sclerified, pith parenchymatous, with vascular bundles spread throughout. Cataphylls 2-3, similar to leaf sheaths, to 15 cm long. Blade bearing leaves all basal, 1-4 to each culm and often overtopping it; sheaths 5-15 cm long, margins thin, gradually tapering upwards; blades terete, rigid with hard spine-like apices, pith parenchymatous with vascular bundles spread throughout. Inflorescence compound paniculate, congested and only 3 x 3 cm, or more lax and up to 15 x 15 cm, the branching alternating between short shoots and long shoots, flowers clustered together in glomerules of 2-8 flowers each and clasped by the bract supporting the pedicel but without bracteoles inserted on the pedicel. Lower inflorescence bract 3-30 cm long, usually overtopping the inflorescence, rigidly erect with a wide sheath and a terete spine-like pointed blade. Flowers gynodioecious. Tepals of perfect flowers ca. 4 mm long and of pistillate flowers ca. 3 mm long, outer ones broadly lanceolate, obtuse to acute, inner ones shorter with scarious margined apex. Stamens in perfect flowers 6, anthers 1.5-2.5 mm long, ca. 5 times as long as filaments; stamens of pistillate flowers reduced to a short staminode. Stigmas in perfect flowers yellow to light brown, in pistillate flowers red and exceeding the tepals. Capsule in perfect flowers to 5 mm long, equal to or shorter than the tepals, subglobose, obtuse, mucronate, in pistillate flowers ca. 5.5 mm long and exceeding the tepals. Seeds in

perfect flowers 0.3-0.6 mm long, obovoidal, acute, tailed, finely reticulate, yellow to brown, in pistillate flowers 0.4-0.6 mm long, light to dark brown.

Distribution. Along the east coast of North America from Delaware southwards to Florida and eastwards to Texas. Also on the Bahama Islands and probably reaching the tropical region in Haiti on the Island of Hispaniola (see below).

Specimens examined. HAITI. Gde Caimite, Nan Sables, slightly moist places. 25 Aug 1927, Ekman 8963 (NY).

Juncus roemerianus was recently the subject of a detailed autecological study by Eleuterius (1974a, 1974b, 1975, 1976a, 1976b, 1978, etc.). He described two plant types with different floral morphology in this species. One is hermaphroditic bearing perfect flowers, and the other is female bearing imperfect pistillate flowers. Both types are found in tidal marshes, where by means of the vigorous rhizome they may dominate several acres or more. This species has not previously been reported from the Bahama Islands, but it is represented by several collections from those islands in the herbarium at NY. The above cited specimen from Haiti is sterile and does not have a rhizome, so a sure identification is not possible on morphological grounds. Certainly, however, it belongs to subg. Juncus, and from the distribution of the five New World species of that subgenus it is most likely that the specimen represents Juncus roemerianus.

FIGURE 36

36 A. The distribution of Juncus roemerianus in the neotropical region.

In addition it occurs along the North American east coast.

36 B. The distribution of Juncus maritimus in the neotropical region.

In addition it is widely distributed in western Europe and scattered in the southern hemisphere.

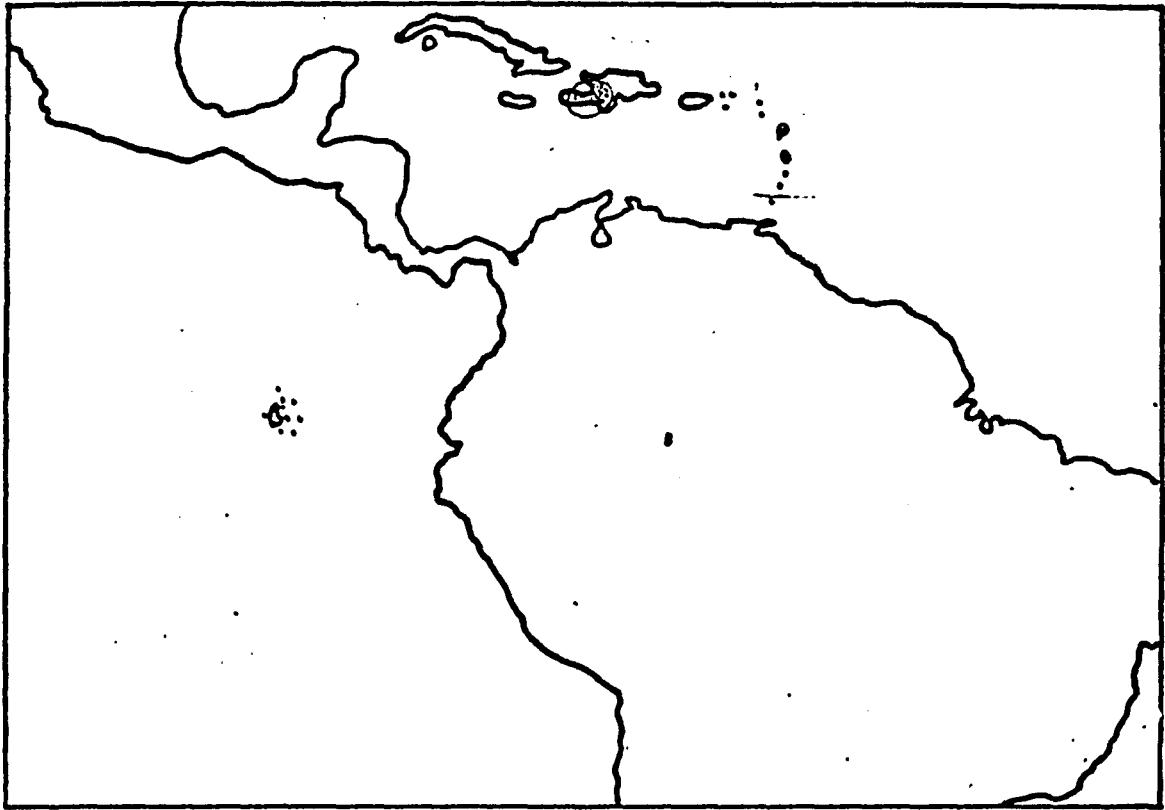


FIGURE 36 A.

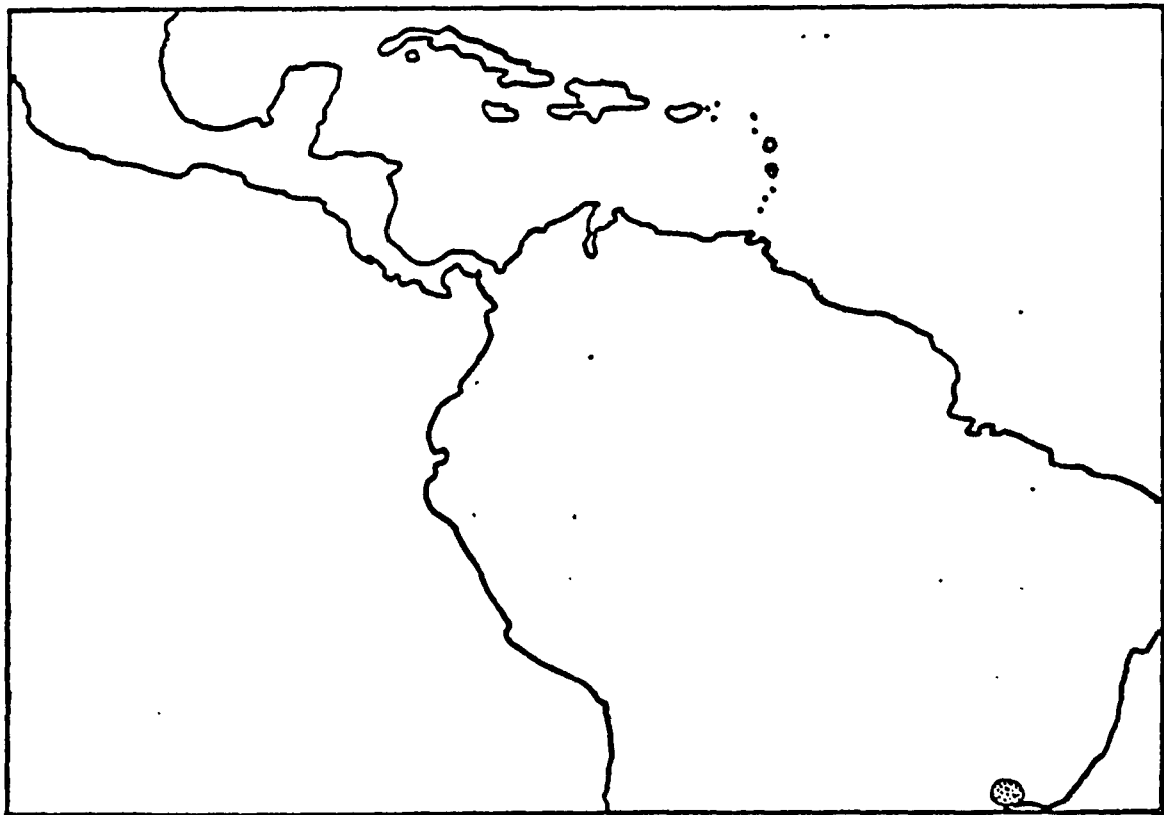


FIGURE 36 B.

3. *Juncus maritimus* Lamarck, Encycl. 3: 264. 1879. Type. Europe.

Angleterre, en France, &c. aux lieux maritimes & marecageaux,

(holotype, P).

Fig. 36 B.

Perennial stout herb, 50-200 cm high. Rhizome horizontal creeping, 5-8 mm diam., densely covered with brown scales, internodes 2-4 cm long. Culms rigid, erect, 2-8 mm diam., longitudinally striate, heavily sclerified, pith parenchymatous with vascular bundles spread throughout. Blade bearing leaves all basal, 1-4 to each culm; sheaths 5-15 cm long, swollen, reddish brown; blade terete, rigid with hard pointed apex, pith parenchymatous with vascular bundles spread throughout. Inflorescence compound paniculate, 5-25 x 5-25 cm, the branching alternating between short shoots and long shoots and the inflorescence thereby sometimes + subdivided, flowers in clusters of 2-8 flowers each. Lower inflorescence bract shorter than the inflorescence or much longer to 40 cm, with terete striate blade terminated in a hard pointed apex. Tepals lanceolate 2.5-3.5 mm long, stramineous to reddish brown, outer ones mucronate with a whitish papery margin towards the apex, inner ones obtuse with scarious tip or acute without scarious tip. Stamens 6, ca. 1.5 mm long, much shorter than the tepals; filaments short, widened at the base; anthers 3-4 times as long as the filaments, brown to yellow. Style 0.5-1 mm long. Stigmas ca. 0.5 mm long. Capsule as long as the tepals, ellipsoidal, acute, shortly mucronate, trigonous, ca. 3 x 1 mm, brown, trilocular. Seeds 0.9-1.1 x 0.3-0.4 mm, ellipsoidal, with the outer seed coat extended into long hyaline appendages, inner seed coat reddish brown.

Distribution. Occurs in the entire Mediterranean region, north to Sweden, and eastwards to India. Scattered occurrences are found in the Azores, Canary Islands, Africa, Australia, New Zealand, Coney Island on the North American eastcoast near New York, Bermuda, and the east coast of South America at São Paulo in Brazil and at Montevideo in Uruguay.

Specimens examined. BRAZIL. São Paulo: Santos, Mosén 3502 (P, S).

This Brazilian collection is incomplete, lacking leaves and rhizome. It is much larger and more robust than any other collection I have seen of Juncus maritimus. The culm is 8 mm in diameter, the inflorescence bract is ca. 40 cm long, the inflorescence is 25 x 25 cm, and has about a thousand glomerules, each of 4-8 flowers.

Juncus subg. *Poiophylli* Buchenau, Abh. Naturwiss. Vereine Bremen

4: 406. 1875. Type species. *Juncus bufonius* Linnaeus.

Juncus sectio *Tenageia* Dumortier, Fl. belg. 142. 1827.

Juncus subg. *Tenageia* (Dumortier) Kuntze in Post & Kuntze, Lex.
gen. phan. 303. 1904.

Juncus sectio *Poiophylli* (Buchenau) Vierhapper in Engler & Prantl,
Nat. Pflanzenfam. 2 ed., 15a: 215. 1930.

Juncus subg. *Pseudo-Tenageia* Krechetovich & Goncharov, Fl.

URSS 3: 527. 1935. Type species. *Juncus compressus* Jacquin.

Perennial or annual herbs to 60 cm high. Rhizome absent, short creeping with the culms arising in dense rows, or densely branched with the culms arising clustered. Culms erect, terete or slightly compressed, ridged or smooth. Leaves all basal in perennial neotropical species, and also cauline in annual species; blade narrowly linear with the cross section varying from flat and smooth to terete and longitudinally ridged, but constant within a given species, never hollow and septate. Inflorescence compound cymose, varying from lax with the flowers widely separated to congested or capitate, composed of few to several unilateral cymes (drepania), each with few to 10 or more flowers. Pedicels originating in the axil of a floral bract in addition to which two bracteoles are inserted just below the flower which they clasp.

Subg. *Poiophylli* comprises about 25 species and occurs on all continents. Most species of this subgenus occur in temperate North America, where it probably originated. It includes weedy and aggressive

species such as J. bufonius and J. tenuis, widespread amphiatlantic species such as J. compressus Jacquin and J. gerardi Loiseleur, species with restricted distributions but with sporadic occurrences in remote areas such as J. imbricatus and J. capillaceus, and a few endemic species such as J. plebejus R. Brown. In general the species seem to be easily dispersed over long distances, which has created a good deal of taxonomic confusion since peripheral populations have often been described as new taxa.

Subg. Poiophylli is distinct through the combination of two features. One is the structure of the inflorescence which is composed of unilateral cymes (drepania) with the flowers clasped by two bracteoles (often called prophylls), and the other is the presence of leaves with well developed blades. It is most closely related to subg. Genuini in which the inflorescence structure is basically similar, but the lower bract is always developed into a culm-like extension so the inflorescence appears lateral, and the leaf blades are reduced to a needle-like rudiment. Krechetovich & Goncharov (1935) and Snogerup (1971, 1980) separated the perennial species as subg. Pseudo-Tenageia.

Key to the neotropical species of

Juncus subg. Poiophylli

1. Annuals without rhizome. Inflorescence occupying half or more of total plant height. Auricles absent. 4. J. bufonius.
1. Perennials with rhizome. Inflorescence occupying 1/4 or less of total plant height. Auricles present at the junction of the sheath to the blade.
 2. Rhizome densely branching, not horizontally creeping, without filamentous cover of splitting leaf bases, the culms arising in tufts. 5. J. tenuis.
 2. Rhizome horizontally creeping, covered with a filamentous layer of splitting leaf bases and cataphylls, the culms arising in dense rows.
 3. Leaf blades flat in cross section. 7. J. arequipensis.
 3. Leaves terete or angled in cross section.
 4. Capsule equal to or longer than the tepals 6. J. imbricatus.
 4. Capsule shorter than the tepals.
 5. Culms and leaves slender and delicate, less than 0.7 mm diam. 8. J. capillaceus.
 5. Culms and leaves thicker and rigid, more than 0.7 mm diam. 9. J. uruguensis.

FIGURE 37

Habit of Juncus imbricatus, J. tenuis, J. capillaceus and J. bufonius, all of subg. Poiophylli (From Balslev, 1979a).

37A. Juncus imbricatus (Drawn from Asplund 6996, S).

37B. Flower of same, showing two bracteoles clasping the flower.

37C. Juncus tenuis var. tenuis (Drawn from Asplund 6997, US).

37D. Juncus capillaceus, showing the sometimes long culm-like lower bract of the inflorescence (Drawn from Rose 23073, GH).

37E. Juncus capillaceus, showing more compact specimen (Drawn from Asplund 16151, US).

37F. Juncus bufonius, showing large specimen (Drawn from Holm-Nielsen & Jeppesen 1537, NY)

37G. Juncus bufonius, showing small specimen (Drawn from Holm-Nielsen & Jeppesen 1168, AAU)



4. *Juncus bufonius* Linnaeus, Sp. Pl. 1: 328. 1753. Type. Europe.

Van Royen s.n. (lectotype, L, n.v., designated by Cope & Stace, 1978, who also cited several paratypes at L). Figs. 37 F-G, 38 A.

Juncus prolifer Humboldt, Bonpland & Kunth, Nov. gen. sp. 1: 236.

1816. Type. Colombia. Tolima: Andium Quinduensium prope El Paso de Machin, alt. 1030 hex, Humboldt & Bonpland s.n. (lectotype, P; isoelectotype, B). The sheet at P is a mixed collection of four plants of which the three on the right side are here designated as lectotype.

Juncus inaequalis Willdenow ex E. Meyer, Synops. Luz. 33. 1823, nom. in syn. A herbarium name attached to Humboldt and Bonpland's duplicate of J. prolifer in the Willdenow herbarium at B.

Juncus bufonius Linnaeus var. pumilio Grisebach, Symb. fl. argent.

316. 1879, also published as Abh. Königl. Ges. Wiss. Göttingen 24: 316. 1879. Syntypes. Argentina. in reg. Puna, Hieronimus & Lorentz 139, n.v. (see Buchenau, 1879, p. 178); Cangrejas (Puna) Jujuy, May 1873, Lorentz & Hieronymus 826 (GOET).

Annual caespitose herb, 5-40 cm high. Rhizome absent. Culms erect, procumbent or ascending, terete, smooth, 0.5-1.5 mm diam., sometimes producing leafy shoots in leaf axils on procumbent stems. Cataphylls absent or rarely one to each culm and then inconspicuous, membranaceous, 7-12 mm long. Blade bearing leaves 1-5 basal and 1-3 cauline to each culm, 4-15 cm long; sheaths 0.5-3 cm long, with membranaceous margin which is not extended into auricles; blade flat with raised margins,

slightly channeled above, 0.5-1.5 mm wide. Inflorescence usually occupying more than half of the total plant height, lax, compound, consisting of several unilateral cymes (drepania) with the flowers inserted individually and removed from one another, or rarely 2-4 flowers clustered together, individual drepania up to 10 cm long. Lower inflorescence bract herbaceous, resembling cauline leaves, up to 10(-15) cm long, upper bracts progressively shorter, the ultimate ones to 5 mm long and membranaceous. Each flower clasped by two 1.5-2.5 mm long bracteoles. Tepals unequal, lanceolate, acuminate, light green with membranaceous margins, turning brown at fruit ripening, outer ones 4-6 (-7) mm long, inner ones 3.5-5(-6) mm long. Stamens 6, 1.3-2.2(-2.6) mm long; anthers linear or oblong, 0.3-1(-1.5) mm long. Capsule ellipsoidal, trigonous, truncate and mucronate, 3-3.5(-4) x 1.5-2 mm, with persisting 0.1-0.3 mm long style, reddish brown at maturity, dehiscing apically, 3-locular. Seeds oblong, apiculate, 0.4-0.6 x 0.2-0.3 mm, smooth to slightly rugose, yellowish brown.

Distribution. Juncus bufonius is a weedy cosmopolitan species most common in the north temperate region, but also found in the cool highlands of all tropics. It also occurs in all major south temperate areas. Adamson (1950) believed it to be introduced to South Africa, and Cheeseman (1925) considered it as introduced to New Zealand during the colonization. In the neotropical region it is a weedy species, most often found on open and exposed soils along roads, ditches, etc. It shows the usual altitudinal pattern of the genus, occurring at higher altitudes (up to 4000 meters) near the equator, and lower down at higher latitudes.

Its altitudinal amplitude is wider than most other Juncaceae, and it has been collected as low as 1000 meters in Ecuador and 350 meters in Peru.

Representative specimens. MEXICO. Chiapas: Tenejapa, Paraje Matsab, 2600 m, Ton 964 (NY). México: Temascaltepec, Los Hornos, 2600 m, Hinton 3702 (MO, NY, US). San Luis Potosí: San Luis Potosí, Schaffner 211 (NY).

GUATEMALA. Quezaltenango: Santa Elena, 2400-2700 m, Skutch 424 (US).

COSTA RICA. Alajuela: Mt Poás between La Lecheria and hotel, 2100-2600 m, Standley 34608 (US). Cartago: Cordillera de Talamanca, Ojo de Agua, 3000 m, Williams et al. 28272 (MO, NY). San José: Las Nubes, 1500-1900 m, Standley 38433 (US).

JAMAICA. St. Andrew: Hardwar Gap, 1200 m, Nichols 103 (F, GH, MO, NY).

GUADELOUPE. Bains Jaunes, 900 m, Rodriguez 4800 (P), Stehle W669 (P).

COLOMBIA. Boyacá: Sierra Nevada del Cocuy, 3500 m, Grubb et al. 791 (K). Caldas: Páramo de Las Letras, 3700 m, Barclay & Juajibioy 6266 (US). Cundinamarca: Zipaquira, 2600 m, Pennell 2557 (F, GH, MO, NY). Tolima: Quindio highway between Cajamarca and divide, 2438 m, Killip & Varela 34538 (F, GH, MO, NY, P, US). Norte de Santander: Mutiscua-Pamplona, 2700-3400 m, Killip & Smith 19698 (NY).

VENEZUELA. Distrito Federal: Colonia Tovar, Fendler 1570 (G, GH, GOET, K, NY). Táchira: Pata de Judio 25-28 km S of San Vicente de la Revancha, 2900-3000 m, Steyermark et al. 101220 (NY).

ECUADOR. Azuay: Panamerican Highway 33 km S of Cuenca, 3000 m, Balslev 1437 (NY). Cañar: El Triunfu-Cañar rd nr Rodeo, 1800 m, Balslev 1192 (NY). Carchi: Tulcán-El Angel rd 34 km S of Las Juntas, 3550 m, Balslev & Quintana 892 (NY). Cotopaxi: Pilaló, 2400 m, Holm-Nielsen & Jeppesen 1537 (AAU, NY, S). Imbabura: Laguna Mojanda W of Otavalo, 2700 m, Balslev & Quintana AAU-24129 (AAU, NY). Loja: Loja-Malacatos rd, km 13-15, 2100-2200 m, Balslev 1310 (NY). Napo: Papallacta-Quito rd, km 4, 3400-3600 m, Holm-Nielsen et al. 6779 (AAU, S). Pichincha: N slopes of Mt Paschoa S of Quito, 3000-3500 m, Balslev 1827 (NY). Tungurahua: Cunchibamba N of Ambato, 2600 m, Acosta-Solis 5864 (F, US). Zamora-Chinchipe: Loja-Zamora rd, km 15-16, 2700-2800 m, Balslev 1247 (NY).

PERU. Ancash: Carhuas, Cordillera Blanca, Río Marcará valley, Vicos, 2960 m, Hutchinson & Wright 4287 (F, USM). Cajamarca: Contumaza, Jeton Guzmanga, 2000 m, Sagastegui et al. 6357 (NY). Cuzco: Anta, Laguna Huipa, 18 km NW of Cuzco, 3600 m, Iltis et al. 862 (WIS). Huancavelica: Tayacaja, Hacienda Toeas between Colcabamba and Paucartambo, 3000-3100 m, Tovar 1933 (US). Huanuco: Huanuco, Carpish, 2850 m, Asplund 12885 (US). La Libertad: Trujillo, Barraza, Río Moche, Lopez Miranda & Sagastegui 7993 (F, NY). Lima: Lomas Atocongo, 32 km S of Lima, 350 m, Cerrate 2731 (US, USM).

BOLIVIA. Cochabamba: Chapare rd, km 104, 3100 m, Steinbach 578 (F, GH, MO, NY, WIS). La Paz: La Paz-Coroico rd, km 36-37, 3400 m, Balslev 1127 (LPB, NY); Laguna Jacha Kkota ca. 8 km straight S of La Paz, 3750 m, Balslev 1137 (LPB, NY). Santa Cruz: St. Comarapa-Valle Grande rd, km 254, 2750 m, Steinbach 254 (F, GH, MO, NY, U, WIS).

Morphologically Juncus bufonius is very variable. In western Europe and in the Middle East it has been treated as an aggregate of several closely related micro-species (Cope & Stace, 1978; Van Loenhoud & Sterk, 1976; Snogerup, 1971, 1980; Krechetovich & Goncharov, 1935). No less than 60 names of specific and subspecific rank applying to the aggregate have been published. Fernald (1904) suggested that the J. bufonius aggregate had two species in North America, J. bufonius Linnaeus and J. sphaerocarpus Nees, and that the former had two varieties, var. halophilus Buchenau & Fernald and var. congestus Wahl. Hermann (1975) treated the aggregate as one species with three varieties: J. bufonius var. bufonius, var. halophilus and var. occidentalis F. J. Hermann. The latter had been called J. sphaerocarpus in North America. From South America only two names relating to this species have been published. Juncus prolifer is based on a large specimen from Colombia, whereas J. bufonius var. pumilio is based on a depauperate specimen from northern Argentina. Both probably represent ecological modifications. Barros (1953) referred some specimens to J. bufonius var. genuinus Coutinho and var. condensatus Coutinho, both of which are names based on European types, and he also referred some material to J. bufonius var. halophilus, which is based on a North American type. The neotropical material examined for the present study certainly exhibits wide morphological variation. The extremes easily encompass larger differences than those used for taxonomic distinctions in other areas. However, I have not been able to discern discrete morphological units or any geographically correlated variation in the material, which, accordingly, is treated as one variable species.

FIGURE 38

38 A. The distribution of Juncus bufonius in the neotropical region.

In addition it is widely distributed in temperate areas of both the northern and southern hemispheres.

38 B. The distribution of Juncus tenuis var. tenuis in the neotropical

region. In addition it is widely distributed in temperate North America, and introduced to western Europe.

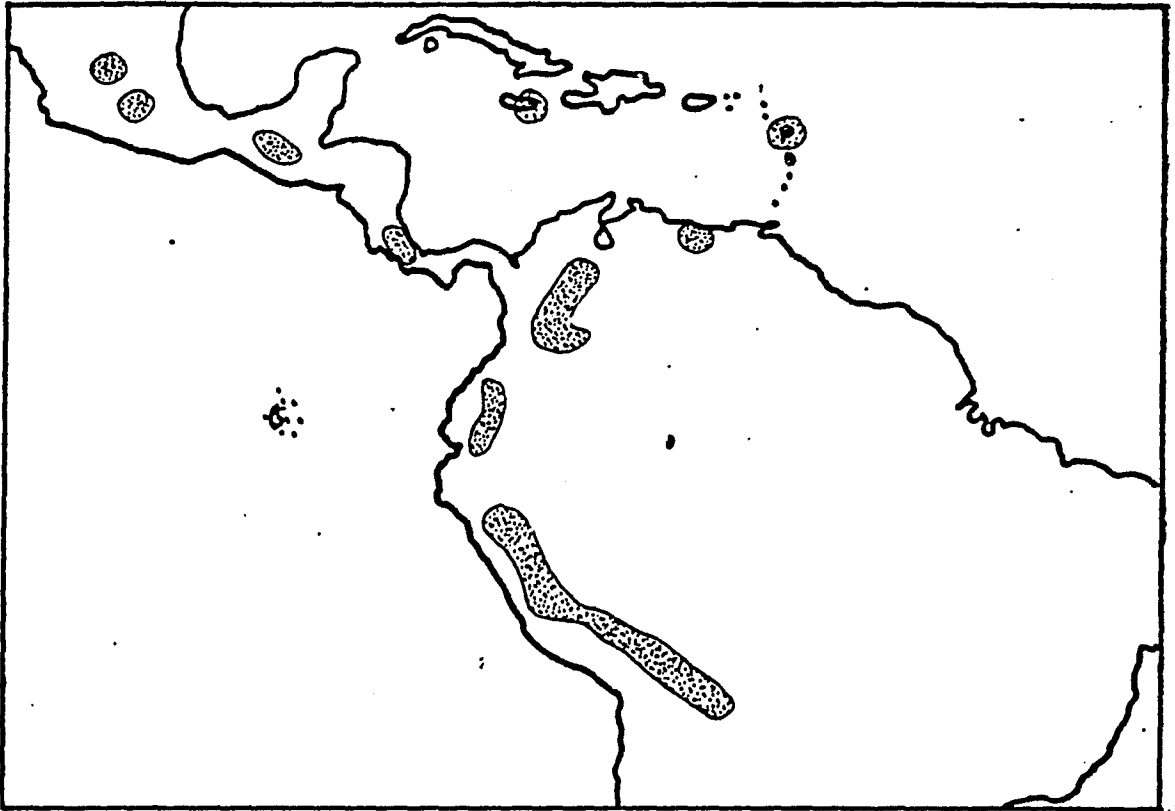


FIGURE 38 A.

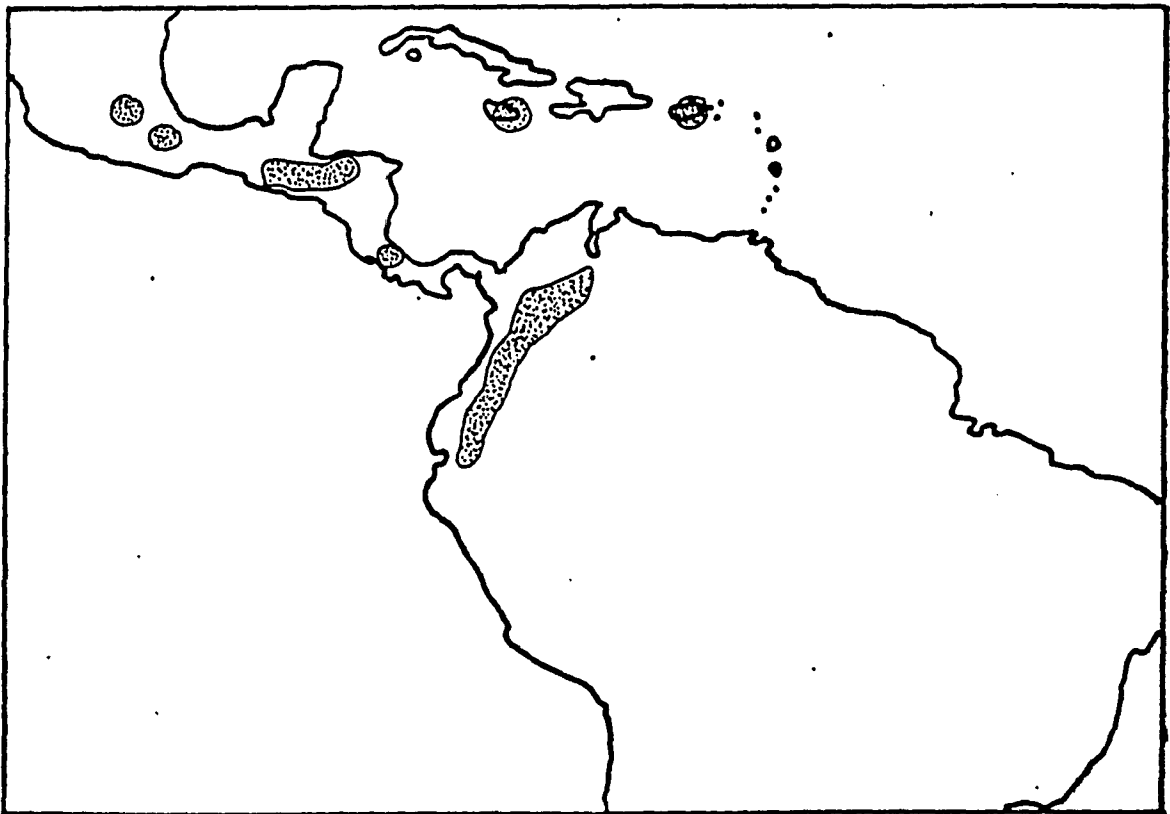


FIGURE 38 B.

5. *Juncus tenuis* Willdenow in Linnaeus, Sp. Pl. 4 ed., 2: 214. 1799.

Type. USA. America boreali, collector unknown (4 syntypes at B).

Perennial caespitose herb, 15-70 cm high. Rhizome densely branching, 1.5-2 mm diam. Culms erect, terete, smooth or longitudinally ridged, 0.8-1.5 mm diam. Cataphylls 0-3 per culm, inconspicuous, to 5 cm long, margin membranaceous, rudimentary blade needle like, to 15 mm long. Blade bearing leaves all basal, erect, $1/3$ as long as to equaling the culm; sheaths 1.5-9 cm long, with membranaceous margin terminating in two scarious or cartilaginous auricles; blade linear, flat or terete and canaliculate in cross section, 0.5-1.5 mm wide. Inflorescence terminal on the culm, occupying less than $1/4$ of total plant height, compound-cymose, consisting of several unilateral cymes (drepania), varying in degree of congestion. Lower inflorescence bract resembling basal leaves, herbaceous, 2-20 cm long, upper ones progressively shorter, ultimate ones membranaceous to 5 mm long. Bracteoles two to each flower, 1.5-2 mm long. Tepals unequal, lanceolate, acute to acuminate, first green with distinct membranaceous margin, turning brown to stramineous, outer ones 3.5-5 mm long, concave, inner ones 3-4.5 mm long, flat. Stamens 6, 1.3-1.8 mm long; anthers linear to oblong, 0.4-0.8 mm long. Capsule ellipsoidal, acute to obtuse, apiculate, 2.5-3.5 x 2-2.5 mm, light brown at maturity, 3-septate. Seeds ellipsoidal, apiculate, often curved, 0.4-0.6 x 0.2-0.3 mm, smooth to slightly rugose, yellowish brown.

Distribution. Widespread and common in temperate North America. Introduced to western Europe in the 19th century, where it is now widespread and still spreading. Scattered introductions are found in Japan, the Azores and New Zealand. In the neotropical region this species is found throughout the highlands. Juncus tenuis belongs to a North American species complex in need of revision. Wiegand (1900) clarified some problems, but his study is now outdated. The morphological variation and discontinuities found among the neotropical populations of this species indicate that they are the result of several introductions and/or migrations from temperate North America. A satisfactory solution of the taxonomy of the neotropical material will therefore depend on revision of the entire species complex in North America. I am here presenting a provisional treatment. None of the characters mentioned in the key to the three varieties are completely constant, but there is good correlation between them. By using more than one character, the large majority of specimens should key out. I have correspondingly preferred to treat these three taxa as varieties of one species, even if var. dichotomus has usually been treated as a separate species, and var. platycaulos merely as a synonym of J. tenuis.

Juncus interior Wiegand (type from Illinois, USA), has been reported from northern México, but is so similar to the taxa accepted here, that it, if included, would probably have to be treated as a synonym under one of them, or at most as a variety.

Key to the neotropical varieties of

Juncus tenuis

1. Blades flat or channeled with even thickness over the cross-section, adaxial surface with a band of hyaline cells occupying at least $3/4$ of the width. Auricles at the junction of the sheath to the blade membranaceous, white and scarious, often elongate and longer than wide. Inflorescence + lax and irregular, flowers in several loose few flowered clusters, with visible branch segments in between.

5a. J. tenuis var. tenuis.

1. Blades terete, angled or channeled in cross-section, when channeled then thicker in the central part of the cross section, adaxial surface with a band of hyaline cells occupying less than $1/3$ of the width or lacking. Auricles firm and cartilaginous, rounded and shorter than wide. Inflorescence lax or congested.
2. Inflorescence congested and + capitate. Blades channeled, terete or angled, with narrow but visible adaxial band of hyaline cells. Culms smooth or slightly longitudinally ridged

5b. J. tenuis var. platycaulos.

2. Inflorescence not capitate, the flowers at least in part inserted regularly and equidistantly in unilateral cymes. Blades terete or angled, adaxial band of hyaline cells narrow or lacking. Culms longitudinally ridged.

5c. J. tenuis var. dichotomus.

5a. *Juncus tenuis* Willdenow var. *tenuis*.

Figs. 37 C, 38 B.

Juncus macer S. F. Gray, Nat. arr. Brit. pl. 2: 164. 1821.

Type. S. F. Gray's herbarium and types are unknown.

Perennial caespitose herb to 60 cm high. Rhizome densely branching. Culms smooth or sometimes slightly longitudinally ridged. Auricles 0.5-1.5 mm long, usually longer than wide, rounded, thin scarious. Leaf blade flat, adaxial side with band of hyaline cells occupying 3/4 or more of the width, only the margins with dense, chlorophyll filled cells. Inflorescence composed of several few-flowered, unilateral cymes, the branching irregular and the inflorescence is not equally dense throughout, i.e. relatively long, flower-free branch segments alternate with more clustered sections. Lower inflorescence bract similar to basal leaves, upper ones gradually shorter. Tepals recurving apically towards maturity. Capsule shorter than the tepals when mature, thin walled, the valves not recurved along the seams and the capsule therefore not 3-keeled.

Distribution. This is the common variety of *J. tenuis* found throughout temperate North America, and it is the one introduced to Japan, New Zealand and Europe where it has been given many different names of which *J. macer* is the most commonly used. In the neotropical region it occurs throughout the Méxican and Central American highlands, on Jamaica and Puerto Rico and in the Andes from Venezuela to Ecuador

and again in Argentina. It is weedy and typically anthropochorous, commonly found at altitudes between 1000 m and 3300 m, along roads and in places where the soil is disturbed and wet from seeping water. In Ecuador it is found in high rainfall areas indicating that the seeds will not survive prolonged periods of drought. The dispersal is facilitated by the outer seed coat which, when wet, swells up to a sticky gelatinous cover that adheres to passers-by.

Representative specimens. MEXICO. México: Temascaltepec-Toluca rd, km 15, 2800 m, Marcks 1132b (WIS). Oaxaca: Sierra Juarez 27 km N of Ixtlan, 2500 m, Roe 1942 (NY, WIS).

GUATEMALA. Baja Verapaz: Santa Rosa, 1500 m, Türkheim 1295 (K). Huehuetenango: Sierra Cuchumatanes between Paquix and Llanos San Miguel, 3300 m, Molina 21240 (NY). Sololá: Above lake Atitlan, 3-5 km W of Panajachel, 2100 m, Williams 25368 (NY).

HONDURAS. Intibuca: Marcala rd, km 10-13, El Huise, 1600 m, Molina 13847 (NY). Morazan: Jutiapa ca. 7 km NE of Tegucicalpa, 1600 m, Davidse & Pohl 2112 (MO, NY). Ocotepeque: El Moral on Cordillera Merendon, 1600 m, Molina 22257 (NY).

EL SALVADOR. Chalatenango: Se slope of Los Esesmiles, 2160-2250 m, Tucker 1192 (NY). Sta. Ana: Hacienda Montecristo, 2200 m, Rohweder 915 (HBG).

COSTA RICA. Cartago: Nr La Sierra ca. 25 km S of Cartago, 2000 m, Williams 28179 (NY). San José: Cordillera Talamanca above San Isidro, 3000 m, Godfrey 66672 (MO).

JAMAICA. Blue Mountains Peak, 2250 m, Harris 12497 (GH, MO, NY).

PUERTO RICO. Caribbean National Forest, Toro Negro Division, highway 143 at foot of Cerro de Punta, 1000 m, Luteyn & Lebrón-Luteyn 5146 (NY). Toro Negro Mountains, Gonzalez s.n. (NY). Cerro de Punton, Woodbury s.n. (NY).

COLOMBIA. Antioquia. Bello, 1500-1800 m, Archer 182 (US).
Caldas: Salento, 2100-2500 m, Pennell 8879 (GH, K, NY, US). Cauca:
Above Carpenteria, E slope of W cordillera, 2500 m, Alston 8227 (NY).
Cundinamarca: SW of Las Cruces, Bogotá, 2600-2700 m, Pennell 2166
(NY, US). Norte de Santander: Sarare, 1300 m, Cuatrecasas et al. 12115
(F). Valle: Carrizales, N of Las Brisas, 2200 m, Cuatrecasas 22543
(F, US).

VENEZUELA. Táchira: Above Betania at base of Páramo de Tamá, 2285-2430 m, Steyermark 57274 (F, NY).

ECUADOR. Azuay: From Soldados E along the rd until Hacienda San Vicente, W of Cuenca, 3200-3300 m, Balslev 1540 (NY). Loja: Loja-Malacatos rd, km 13-15, 2100-2200 m, Balslev 1317 (NY). Napo: Cordillera de Huancamayos on Tena-Baeza rd, 2000 m, Balslev 1604 (NY). Pichincha: Lloa valley W of Quito, 15 km below Lloa, 2200 m, Balslev 1924 (NY). Tungurahua: Hacienda Agoyan 10 km E of Baños, 1600 m, Holm-Nielsen & Jeppesen 260 (AAU, F, S). Zamora-Chinchipe: Zamora-Loja rd, km 1, 1200 m, Balslev 1270 (NY).

5b. *Juncus tenuis* Willdenow var. *platycaulos* (Humboldt, Bonpland & Kunth) Buchenau, Bot. Jahrb. Syst. 12: 194. 1890. Fig. 39 A.

Juncus platycaulos Humboldt, Bonpland & Kunth, Nov. gen. sp.

1: 236. 1816. Type. Colombia. Tolima/Quindio: in declivitate montis Quindio inter Ibagué et La Palmilla, alt. 80-950 hex, Humboldt & Bonpland s.n. (holotype, P; isotypes, B, MO fragment).

Juncus coarctatus Willdenow ex Sprengel, Syst. veg. 2: 109.

1825. Type. The duplicate of *J. platycaulos* H.B.K. that Humboldt sent to Willdenow in Berlin (holotype, B; isotype, P, MO fragment).

Juncus andreanus Weatherby, Contr. Gray Herb. 81: 84. 1928.

Type. Colombia. Cundinamarca: Facatativa, 2680 m, 16 Jun 1875, André 624 (holotype, GH; isotypes, F, K, NY, P, S).

Juncus pallidus Willdenow, herbarium name. Original collection.

America meridionalis, Humboldt s.n. (B).

Perennial caespitose herb, to 70 cm high. Rhizome densely branching. Culms usually smooth, sometimes slightly longitudinally ridged. Auricles ca. 0.5 mm long, wider than long, rounded, cartilaginous. Leaf blade terete or channeled, when channeled the central part of the cross-section is thicker than the edges, adaxial side with narrow band of hyaline cells occupying less than 1/3 of the width. Inflorescence composed of several few- to many-flowered unilateral cymes, congested into one + dense head. Lower inflorescence bract usually

filiform, flexuose, obviously longer than the upper ones. Tepals not or only slightly recurving. Capsule thin walled, usually clearly shorter than the tepals when mature, valves not recurved along the seams and the capsule therefore not 3-keeled.

Distribution. Scattered in the Central American highlands, in the Andes from Venezuela to Ecuador and apparently somewhat disjunctly in central Peru, but maybe undercollected in northern Peru. Grows in wet places, along streams, lakes and roads and in meadows and grass lands. In South America it has been collected at altitudes between 2600 m and 3600 m, which is, on the average, higher than that of var. tenuis.

Specimens examined. MEXICO. México: 26 km W of Toluca, 2500 m, Iltis & Cochrane 205 (WIS); Baños de Netzahualcoyotl 7 km E of Tezcoco, 2500 m, Koch 76186 (WIS). Oaxaca: Sierra Juarez 27 km N of Ixtlan, 2500 m, Roe 1970 (NY, WIS). San Luis Potosí: Sierra de Alvarez, Alvarez, 2200-2400 m, Pennell 17886 (NY).

GUATEMALA. Huehuetenango: Río Chixoy ca. 10 km SW of Huehuetenango, 1800 m, Williams et al. 22532 (NY).

EL SALVADOR. Santa Ana: Montaña, Montecriste, 2000 m, Molina 12553 (NY).

COLOMBIA. Boyacá: Nr Sata, 2800 m, Alston 7394 (F p.p., NY, US); Sierra Nevada del Cocuy, Río San Paulino-Finca Ritacuva, 3650 m, Barclay & Juajibioy 7320 (US); Tunja, 2820 m, Ballesteros & Villamizar 3 (COL). Cundinamarca: Bogotá, 2640 m, André 1369 (K); SW of Las Cruces,

2600-2700 m, Pennell 2167 (NY p.p.); Zipaquira, 2600 m, Pennell 2558 (GH, MO, NY, US); Bogotá, Idinoel 6 (NY). Santander: E slope of Páramo de Las Coloradas above La Baja, 3900 m, Killip & Smith 18483 (GH, NY, US). Valle: Río Bugalagrande, Loma de Barragan, 2750-2660 m, Cuatrecasas 20644 (F, US).

VENEZUELA. Mérida: Apartaderos-Valera rd, km 25, 3000 m, Breteler 4147 (NY, U).

ECUADOR. Pichincha: Cayambe-Olmedo rd, km 7, 2900 m, Holm-Nielsen & Balslev 23635 (AAU, NY). Zamora-Chinchipe: Loja-Zamora rd, km 15-16, 2700-2800 m, Balslev 1251 (NY).

PERU. Junín: Mito, 2750 m, MacBride & Featherstone 1451 (F, GH, K, S, US).

FIGURE 39

- 39 A. The distribution of Juncus tenuis var. platycaulos.
- 39 B. The distribution of Juncus tenuis var. dichotomus in the
neotropical region. In addition it occurs in temperate
North and South America.

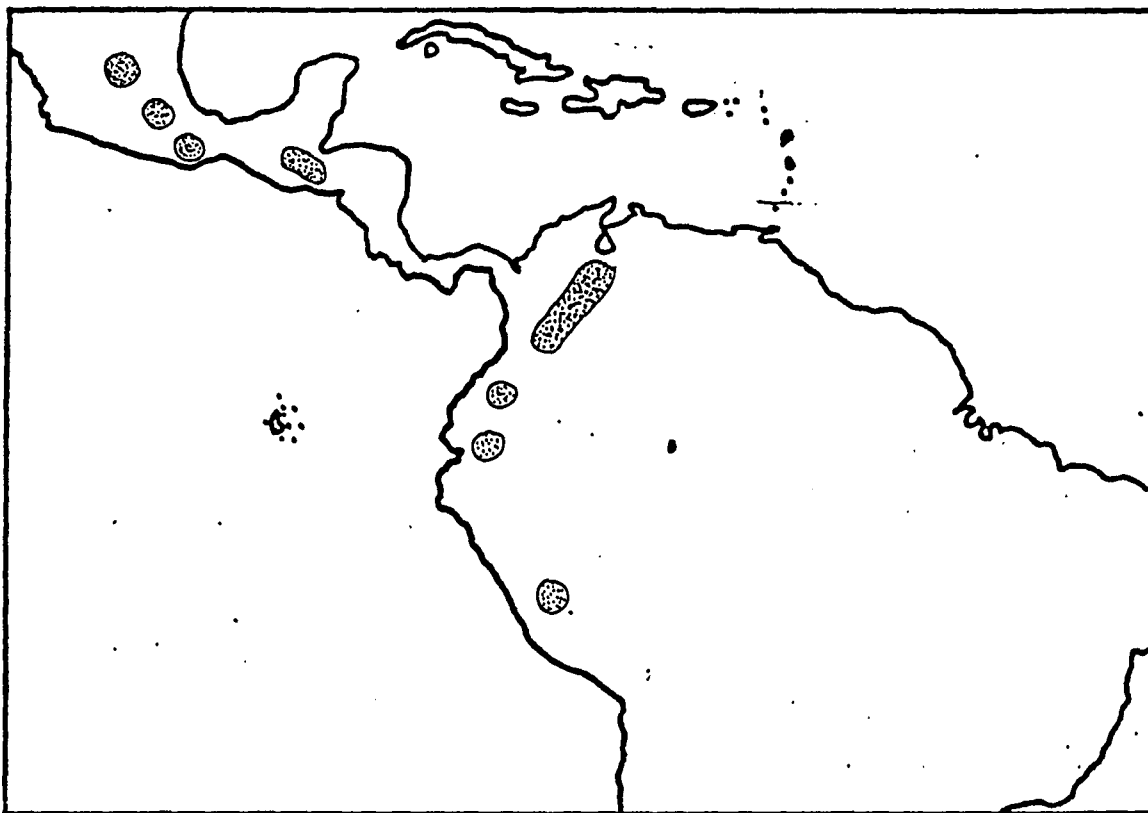


FIGURE 39 A.



FIGURE 39 B.

5c. *Juncus tenuis* Willdenow var. *dichotomus* (Elliot) Wood,

Classbook of Botany 726. 1861.

Fig. 39 B.

Juncus dichotomus Elliot, Sketch bot. S. Carolina 1: 406. 1817.

Type. USA. South Carolina or Georgia: location and collector unknown. The Juncaceae are missing from the Elliot herbarium at CHARL and NY, where Elliot's types are otherwise to be found.

Juncus cognatus Kunth, Enum. pl. 3: 349. 1841. Syntypes. Uruguay.

Montevideo, 1821/1822, Sellow s.n. (MO, the B specimen cited in the protologue extinct); Brazil. Insula St. Catharina, Gaudichaud s.n. (P, 4 sheets). México. Haenke s.n., n.v.. México.

Ialapa, Schiede s.n. (MO).

Juncus tenuis Willdenow var. *unicornis* E. Meyer, Linnaea 3: 371.

1828. Syntypes. Brazil. Chamisso s.n. (LE, n.v.). México.

Haenke s.n., n.v.

Perennial caespitose herb, 10-70(-90) cm high. Rhizome densely branching. Culms longitudinally ridged. Auricles ca. 0.5 mm long, wider than long, rounded, cartilaginous. Leaf blade terete or channeled, when channeled the central part of the cross-section is thicker than the edges, adaxial side with or without narrow band of hyaline cells occupying less than 1/3 of the width. Inflorescence composed of several unilateral cymes with the flowers, at least in part, regularly inserted at equal distance from one another. Lower inflorescence bract varying, shorter or longer than the inflorescence, usually conspicuously longer than the upper bracts. Tepals straight or only slightly recurved.

Capsule shorter to longer than the tepals at maturity, thick walled, valves recurved along the seam and the capsule therefore with three low ridges or slightly 3-keeled.

Distribution. Occurs in eastern North America from Massachusetts to Oklahoma and Texas. In the neotropical region it occurs on Jamaica, through the Mexican highlands and again in Bolivia and southeastern Brazil, reaching into Uruguay and the province of Buenos Aires in Argentina. Grows in wet places along streams and roads, in bogs, etc., at altitudes from sea level in Uruguay up to 1000 m in southeastern Brazil and 2500 m in Bolivia. In México it has been collected at altitudes from 1900 m to 2700 m.

Specimens examined. MEXICO. Chiapas: Pueblo nuevo Solistahuacan, 2000 m, Ton 2915 (NY, WIS); Tenejapa, San Cristobal Las Casas rd, 2150 m, Breedlove 10881 (W); Paraje Matsab, 2750 m, Ton 946 (NY), 1294 (WIS). México: Valle de México nr San Augustin, Schaffner 530 (MO). Michoacán: Morelia, Cerros San Miguel, 2200 m, Arséne s.n. (NY), 5306 (P). Oaxaca: Oaxaca-Valle rd, 20 km E of Iztlan, Llano de Las Flores, 2870 m, Beaman 3729 (W). San Luis Potosí: San Miguelita, Schaffner 555 (K).

HONDURAS: Morazan: Quebrada El Chorruto, Mt Hule, 20 km S of Teguicalpa, 1500 m, Molina 18499 (G).

EL SALVADOR. Chalatenango: E slope of Los Esesmiles, 2130-2160 m, Tucker 1022 (G).

COSTA RICA. Cascajal, Lankester 227 (K).

JAMAICA. Hardware Gap, 1250 m, Harris 10905 (F, NY), 11842

(F, GH, MO, NY). St. Andrew, Cold Spring Gap, 1300 m, Harris 11421 (F, GH, NY), 12494 (GH, MO, NY); Newcastle, 1200 m, Patrick 229 (NY), Adams 5733 (MO); Newcastle-Hardware Gap, 1150 m, Stearn 41 (GH); St. Thomas, nr summit of East Blue Mountain Peak, 2250 m, Stearn 130 (GH).

BRAZIL. Minas Gerais: Serro de Espinhaço, Pico de Itacolomí ca. 3 km S of Ouro Preto, 1650 m, Irwin et al. 29580 (NY). Paraná: Serrinha, Dusén 15172 (G); Matinhos-Paranagua, Dombrowski 1634 (K); Curitiba, Clayton 4217 (K). Rio de Janeiro: Alto do Serra-Meio do Serra, 400-800 m, Smith 1568 (F, S). São Paulo: Ypanema, Loefgren 12425 (B); Juru-Mirim, Loefgren & Edwall 12419 (NY); Rio Pinheiros 7 km from center of São Paulo, Skvortzov 13 (K).

BOLIVIA. Cochabamba: Tocona, 2900 m, Steinbach 8709 (G, GH, K, MO, NY, S). Department unknown: Villamontes, 450 m, Troll 429 (B); Tarigia, Fries 1268 (P); Bermeju (?), 1800 m, Fiebrig 1212 (U).

PARAGUAY. Pirayu, Balansa 392a (G); Imbitimi, Balansa 392b (P); Villa Rica, Balansa 392 (P).

6. Juncus imbricatus Laharpe, Essai monogr. jonc. 61. 1825, also published in Mem. Soc. Hist. Nat. Paris 3: 149. 1827. Type. Argentina. Buenos-Ayres, Commerson s.n. (syntype, n.v.). Chile. Concepción, M. Lesson s.n. (syntype, K). Figs. 37 A-B, 40 A.

Juncus chamissonis Kunth, Enum. pl. 3: 348. 1841. Type.

Chile. Chamisso s.n. (syntype, MO fragment, P, W). Uruguay.

Montevideo, Sellow s.n. (syntype, W).

Juncus spanianthus Steudel, Syn. pl. glum. 2: 306. 1855. Type.

Chile. Aconcagua, Bertero 348 (holotype, n.v.; isotype, G, MO, P).

Juncus collinus Steudel, *ibid.* Type. Chile. Juan Fernandez,

Bertero 1469 (holotype, P; isotypes, G, P, K). The citation of Bertero 1496 in the protologue is a typographical error.

Juncus multiflorus Bertero ex Steudel, *ibid.* Bertero's herbarium name on the type of J. collinus (see above).

Juncus lechleri Steudel, *ibid.* Type. Chile. Lechler 339 (holotype, P; isotypes, G, GOET, K, P, W). Some of the isotype material belongs to J. capillaceus Lamarck.

Juncus urvillei Steudel, *ibid.* Type. Chile. Concepción, Urville s.n., n.v.

Juncus capillaceus Lamarck var. chilensis Buchenau, Abh. Naturwiss.

Vereine Bremen 6: 377. 1879. Basionym. Juncus imbricatus Laharpe.

Juncus imbricatus Laharpe var. chamissonis (Kunth) Buchenau in Engler, Pflanzenreich IV, 36 (Heft 25): 122. 1906.

Juncus imbricatus Laharpe var. lechleri (Steudel) Buchenau, *ibid.*

Juncus pringlei Fernald, Proc. Amer. Acad. Arts 14: 416. 1910.

Type. México. Oaxaca: Cuesta de San Juan del Estado, 7000',

21 Aug 1894, Pringle 5818 (holotype, GH).

Perennial caespitose herb, (15-)20-45 cm high. Rhizome creeping, 2-3 mm diam., covered with a filamentous dark brown layer of remaining sclerenchyma strands from splitting up cataphylls and leaf bases, internodes very short and the culms arising in densely crowded rows. Culms erect, canaliculate, 0.5-1.5(-1.8) mm diam. Cataphylls 3-4 to each culm, to 5 cm long, dark brown or upper ones sometimes yellowish brown or light green, with a rudimentary blade to 5 mm long. Blade bearing leaves all basal, 1-2 to each culm, 10-35 cm long; sheaths 1.5-6 cm long with membranaceous margins terminating in two 0.3-0.5 mm long auricles; blades filiform, 0.6-1 mm diam., canaliculate and obtuse-angled, with an adaxial groove basally. Inflorescence terminal, compound, 1-30 flowered, consisting of (1-)2-4 clustered unilateral cymes (drepania). Lower inflorescence bract resembling a basal leaf, herbaceous, to 8 cm long and exceeding the inflorescence, or shorter than the inflorescence and needle like, upper bracts progressively shorter, the ultimate ones membranaceous, to 3 mm long. Each flower clasped by two 1.5-2 mm long bracteoles. Tepals unequal, lanceolate, midrib green, turning brown, margins reddish brown, membranaceous at fruit ripening, outer ones 3.5-5 mm long, inner ones 3-4 mm long. Stamens 6, 1.7-2.1 mm long; anthers linear, 0.8-1 mm long. Capsule ellipsoidal, apically obtuse to truncate, trigonous with somewhat concave sides, (3.5-)4-5 x 1.8-2.5 mm, reddish brown, glossy at maturity, thick walled and not showing impressions of the contained seeds, 3-septate. Seeds broadly ovoidal, asymmetrical, slightly

apiculate, 0.4-0.6 x 0.2-0.3 mm, rugose, brown.

Distribution. A mainly South American species occurring in the Andes from Colombia to northern Argentina, in Concepción in Chile, and in eastern South America in Corrientes in Argentina, in Uruguay, and in the highlands south of Buenos Aires. It also occurs in México, in the Cape Province of South Africa (Adamson, 1950, under the name J. chamissonis), in Australia (Beadle et al., 1972), and in Portugal (Snogerup, 1980), where it presumably is recently introduced since the plants are ruderal there. In the Andes of Ecuador, Peru and Bolivia, where I have seen the species, it is typically a weed at roadsides and in abandoned fields at altitudes from 2500 m to 3800 m. Together with J. capillaceus it is remarkable in the genus, being relatively xeric, often growing and flowering in hard, completely dried out soil. In Argentina and Uruguay it occurs at much lower altitudes and even at sea level, but I do not have any information about its ecology there.

Representative specimens. MEXICO. Hidalgo: Hacienda Tetlapayac 12 km E of Apam, 2600 m, West F-28 (WIS); W slope of Mt Maziahua above Rancho Ojo de Agua, 2600 m, West I-5 (WIS).

COLOMBIA. Cundinamarca: Guasca, 2300-2700 m, Ariste-Joseph A141 (US), A364 (US). Valle: Río Bugalagrande, Loma de Barragan, 2700 m, Cuatrecasas 20674 (F, US).

ECUADOR. Azuay: 2-4 km W of Sayausí (W of Cuenca), 2900 m, Balslev 1566 (NY). Cañar: Pimo-Santa Rosa, Acosta Solis 21335 (US). Chimborazo: Panamerican Highway 10 km N of Riobamba, 3050 m, Balslev 1047 (NY). Imbabura: Panamerican Highway at Otavalo, 2500 m, Balslev

957 (NY). Loja: Santiago W of Panamerican Highway ca. 40 km N of Loja, 2400 m, Balslev 1362 (NY). Pichincha: Roadside at power station nr Tumbaco E of Quito, 2600 m, Balslev 1166 (NY). Tungurahua: Pilahüin, 3300 m, Acosta Solis 9218 (US).

PERU. Ancash: Bolognesi, Matarragara NE of Chiquian, 3550 m, Cerrate 37 (US, USM). Apurimac: Chincheros, 2930 m, West 3685 (GH, MO). Cajamarca: Contumaza, Cazcabamba, 3050 m, Sagastegui 9019 (F). Cuzco: . Calca, Hacienda Paucartiva, 2950 m, Keel K-434A (NY). Huancavelica: Tayacaja, Hacienda Huari, 3600-4200 m, Salaverry 39 (US). Junín: Jauja-La Oroya rd, km 5 NW of Parco, 3400 m, Balslev 1082 (NY). La Libertad: Huamachuco, Munmalca, Hacienda Cochabamba, 3200 m, Lopes Miranda 1468 (NY, US). Puno: Cerros de Puno, 3800-3900 m, Tovar 3501 (USM).

BOLIVIA. Chuquisaca: Tomina, Pomabamba, Weddell 3815 (P). Cochabamba: Mizque 3 km S of Vilavila, 2700 m, Eyerdam 25037 (F, G). La Paz: Sorata-Achacachi rd, km 21, 3500 m, Balslev 1098 (LPB, NY); Laguna Jacha Kkota ca. 8 km straight S of La Paz, 3750 m, Balslev (LPB, NY).

Juncus imbricatus is most closely related to J. capillaceus, with which it shares the feature of a brush like cover of splitting leaf sheaths and cataphylls on the creeping rhizome. The two species are similar in several other respects, but are always distinct through the larger dimensions of J. imbricatus in both vegetative and reproductive structures, especially the size of the capsule (3.5-5 mm long vs. 2.3-2.6 mm long). It is remarkable that these two species are sympatric throughout their areas, including South Africa and Australia, where they are introduced.

FIGURE 40

40 A. The distribution of Juncus imbricatus in the neotropical region.

In addition it occurs in temperate South America, and is
introduced to Europe and Australia.

40 B. The distribution of Juncus arequipensis.

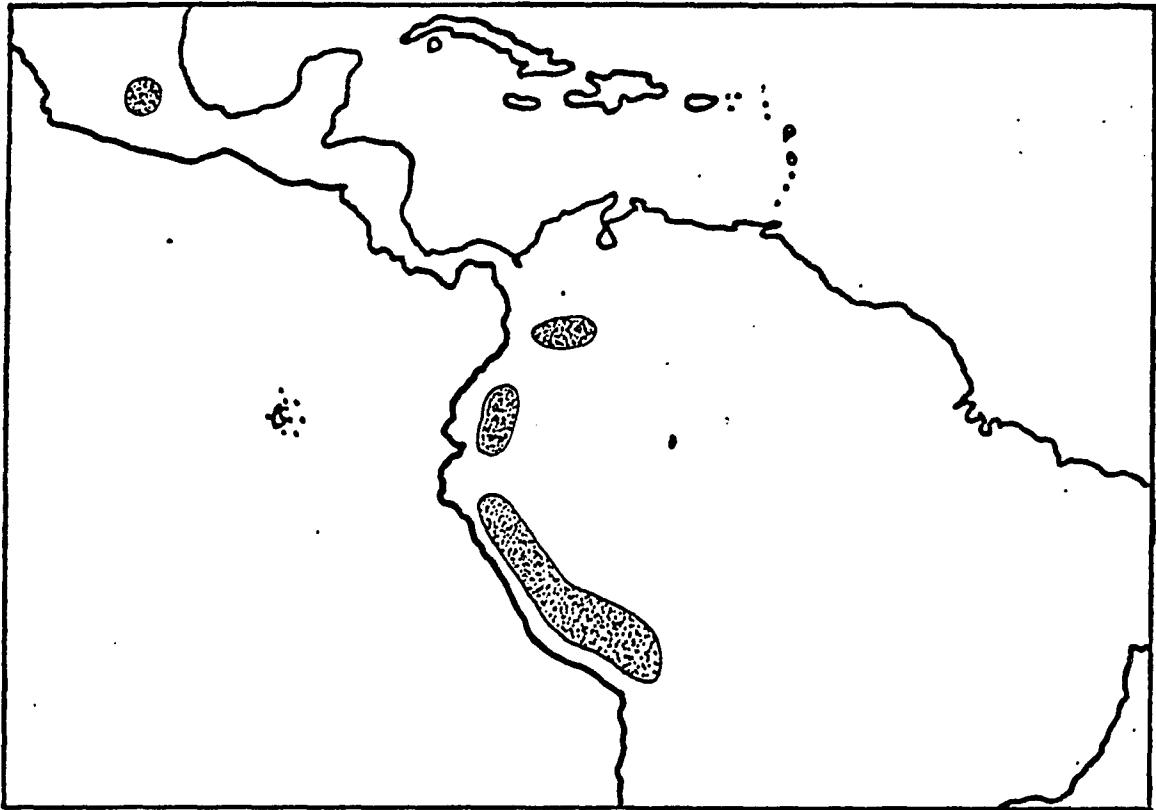


FIGURE 40 A.

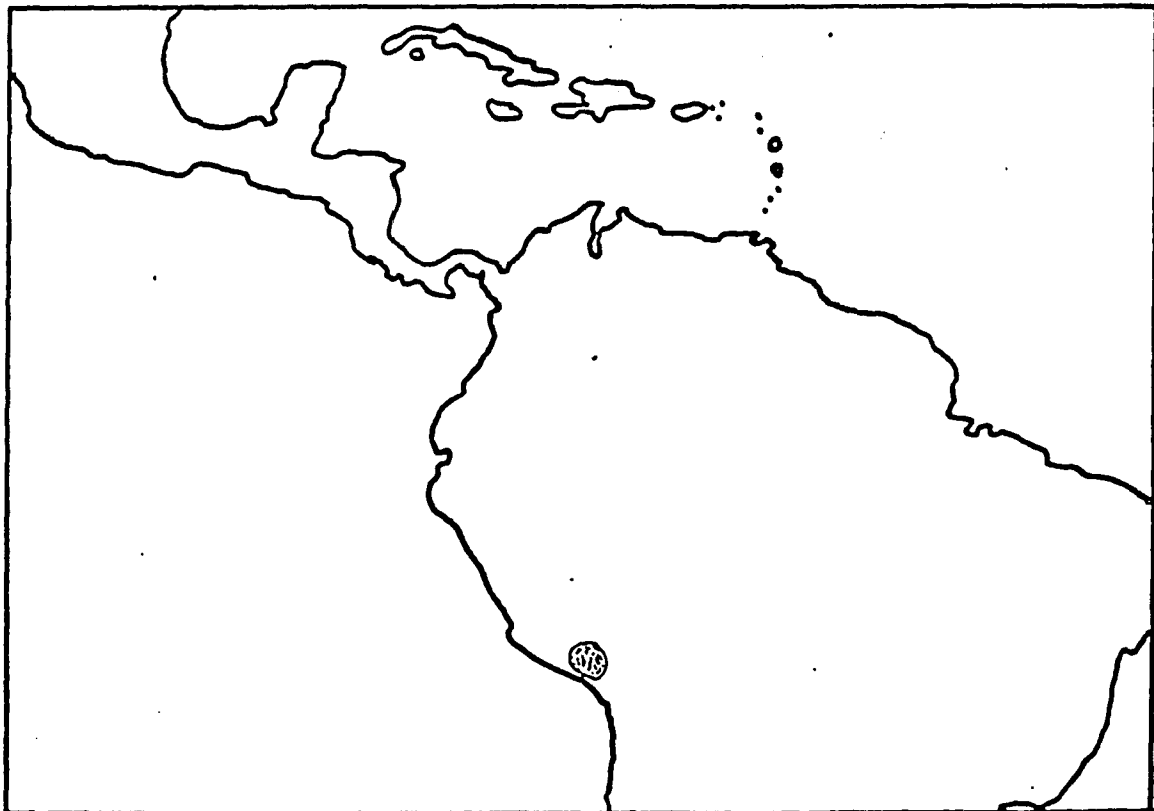


FIGURE 40 B.

7. *Juncus arequipensis* Balslev, sp. nov. Type. Peru. Arequipa: Islay, Mollandu, 7 km NE of Matarani, 850 m, 9 Aug 1974, E. Lopes T. 015 (holotype, MO). Fig. 40 B.

Perennial caespitose herb, 15-20 cm high. Rhizome horizontal, creeping, 1.5-2 mm diam., covered by a brushy, filamentous cover of persisting sclerenchyma strands from degraded leaf bases and cataphylls, internodes very short and the culms arising in densely crowded rows. Culms erect, terete, smooth or longitudinally ridged, 0.6-1.1 mm diam. Leaves 2-3 to each culm, all basal, 5-15 cm long, mostly not overtopping the inflorescence; sheaths 1.5-2 cm long with membranaceous margins terminating in two 0.2-0.5 mm long auricles which are scarious or slightly cartilaginous towards the center; blades linear, flat, 0.8-1.3 mm wide with an adaxial band of hyaline epidermal cells occupying the width of the blade except for the 0.1 mm wide margin. Inflorescence terminal 1.5-3 x 1-2 cm, consisting of 1-5 up to 4-flowered unilateral cymes (drepania). Lower inflorescence bract resembling a basal leaf, herbaceous, 1.5-2.5 cm long, shorter or longer than the inflorescence, upper bracts much smaller, scale like or membranaceous. Each flower clasped by two obtuse ca. 2 mm long membranaceous bracteoles. Tepals unequal, lanceolate, acuminate, stramineous, with membranaceous margin, outer ones 5-6 mm long, concave, inner ones 4.5-5 mm long, flat or slightly concave. Stamens 6, ca. 2 mm long; filaments filiform; anthers linear, ca. 0.8 mm long. Capsule ellipsoidal, acute to obtuse, round to slightly trigonous in cross section, 3.5-4 x 1.5-2.5 mm, ca. 1/5 shorter than the tepals, yellowish brown, unilocular to slightly trisepate. Seeds ellipsoidal, apiculate, 0.3-0.4 x ca. 0.2 mm

rugose, castaneous.

Distribution. So far known only from the type collection, which was made in loma vegetation.

This new species is closely related to Juncus imbricatus and J. capillaceus with which it shares the peculiar feature of a brushy and filamentous cover of sclerenchyma strands that remain on the creeping rhizome when the leaf bases and cataphylls degrade. It differs from Juncus capillaceus in being more robust and larger in both vegetative and reproductive parts. It differs from J. imbricatus in having (1) flat leaf blades with an obvious broad band of enlarged hyaline epidermal cells occupying almost the entire adaxial surface instead of terete or angular blades with only a narrow band of hyaline cells, (2) scarious auricles instead of cartilaginous, (3) the capsule much shorter than the tepals instead of much longer, and (4) tepals 5-6 mm long instead of 4-5 mm long.

8. *Juncus capillaceus* Lamarck, Encycl. 3: 266. 1789. Type. Uruguay.

Montevideo, Commerson s.n. (holotype, P; isotypes, B, MO, P, W).
Figs. 37 D-E, 41 A.

Juncus tenuifolius Steudel, Syn. pl. glum. 2: 306. 1855. Type.

Chile. Bertero 1062 (holotype, P; isotypes, MO, P).

Juncus capillaceus Lamarck var. *montevidensis* Buchenau, Abh.

Naturwiss. Vereine Bremen 6: 377. 1879. Basionym. *Juncus*
capillaceus Lamarck.

Perennial caespitose herb, (5-)10-30 cm high. Rhizome creeping, 1.5-2 mm diam., covered with a filamentous dark brown layer of remaining sclerenchyma strands from splitting up leaf bases and cataphylls, internodes very short and the culms arising in densely crowded rows. Culms erect canaliculate, 0.4-0.7 mm diam. Cataphylls 1-3 to each culm, to 1.5 cm long, yellowish brown, with a rudimentary blade to 5 mm long. Blade bearing leaves all basal. 1-2 to each culm, 5-20 cm long; sheaths 0.7-1.7 cm long with the margins terminating in two 0.3 mm long, rounded auricles; blade filiform, 0.3-0.6 mm diam., obtuse-angled with an adaxial groove basally. Inflorescence terminal or pseudolateral; compound 2-10-flowered, consisting of 2-3 short unilateral cymes (drepania). Lower inflorescence bract 1.5-5 cm long, appearing as a continuation of the culm and exceeding the inflorescence, upper bracts progressively shorter, the ultimate ones membranaceous, to 3 mm long. Each flower clasped by two 1 mm long bracteoles. Tepals unequal, lanceolate, light green with membranaceous margin, turning brown to stramineous at fruit ripening, outer ones 2.3-3 mm long, inner ones 2-2.5 mm long. Stamens 6, 1.1-1.3 mm long; anthers oblong, 0.3-0.4 mm long. Capsule ellipsoidal to oblong, apiculate or often becoming

truncate towards dehiscence, trigonous with concave sides, 2.3-2.6 x 1.2-1.6 mm, brown, glossy at maturity, thin walled and often with impressions of the contained seeds, 3-septate. Seeds ovoidal, asymmetrical, slightly apiculate, 0.4-0.6 x 0.3-0.4 mm, finely patterned by narrow, transversally arranged polygons, brown.

Distribution. At high altitudes, usually above 2700 m, along the Andes from Venezuela to Ecuador and Bolivia. Rare in Peru. At low elevations, down to sea level, in Concepción in Chile and again along the east coast of South America from Rio de Janeiro in Brazil to Buenos Aires in Argentina. Occurrences in South Africa (Adamson, 1950) and in Australia (Beadle et al., 1972) presumably represent recent introductions since the plants are ruderal there. In the northern Andes it is ecologically similar to J. imbricatus, growing and flowering on dry hard soil, and the two species are often seen together. It is found in small clumps along roads or in old grass fields. Morphologically similar and sympatric with J. imbricatus.

Specimens examined. COLOMBIA. Cundinamarca: Bogotá-Usme rd, ca. km 5, 2800 m, Galen Smith & Idrobo 1342 (GH, US); Salto de Tequendama, 2400 m, McKee 10414 (COL, P, US); Bogotá, Pérez-Arbeláez 3204 (COL, GH, US). Norte de Santander: Between Mutiscua and Pamplona, 2700-3400 m, Killip & Smith 19687 (GH, NY, US). Valle: Bugalagrande, Loma de Barragan, 2700 m, Cuatrecasas 20697 (F, US).

VENEZUELA. Mérida. Páramo de La Negra between Bailaderos and La Grita, 2745-3045 m, Steyermark 57071 (F, NY).

ECUADOR. Azuay: Cumbe, 3000 m, Harling 798 (NY, S). Carchi: Tulcán, 3000 m, Acosta Solis 13214 (US); Páramo El Angel, 3500 m, Asplund 7110 (S, US). Cotopaxi: Panamerican Highway + 6 km N of Lasso, 3400 m, Sparre 15830 (S); 2 km from Panamerican Highway along turn-off to Parque Nacional Cotopaxi, Balslev 1190 (NY). Loja: Nr Tablon de Oña, Rose 23073 (GH, NY). Pichincha: Mt Ilaló, 2700 m, Acosta Solis 14040 (US); Mt Pichincha above Quito, 3000-3100 m, Asplund 16151 (F, G, K, NY, S, US), Balslev AAU-24181 (AAU, NY); Quito, 2800-2900 m, Acosta Solis 10027 (F, US); Cayambe-Olmedo rd, km 7, 2900 m, Holm-Nielsen & Balslev 23638 (AAU, NY); Panamerican Highway 10 km N of Cayambe, 3000 m, Balslev & Quintana 962 (NY). Tungurahua: Mochapate, 3000 m, Acosta Solis 21262 (US). PERU. Above Sunchubamba and Chicamatal, 3200-3750 m, Ellenberg 1699 (U), 1870 (U).

BRAZIL. Rio de Janeiro: Rio de Janeiro, Anderson s.n. (S).

BOLIVIA. Cochabamba: Vacas, 3600 m, Cárdenas 775 (US); Chapare, San Benito, 3300 m, Steinbach 9532^{bis} (GH); Chapare, Jucacorral, 2350 m, Steinbach 9542 (GH). Department unknown: Valle de Montepunco, 2800 m, Adolfo 237g (US).

The typespecimens , both holotypes and isotypes, of Juncus tenuifolius are intermediate between J. capillaceus and J. imbricatus, and the name is placed under synonymy of J. capillaceus rather than J. imbricatus for convenience only.

FIGURE 41

- 41 A. The distribution of Juncus capillaceus in the neotropical region.
In addition it occurs in temperate South America, and is introduced to South Africa and Australia.
- 41 B. The distribution of Juncus uruguensis in the neotropical region.
The main area of the species is in Uruguay, and the neotropical record is based on a single collection from Bolivia.

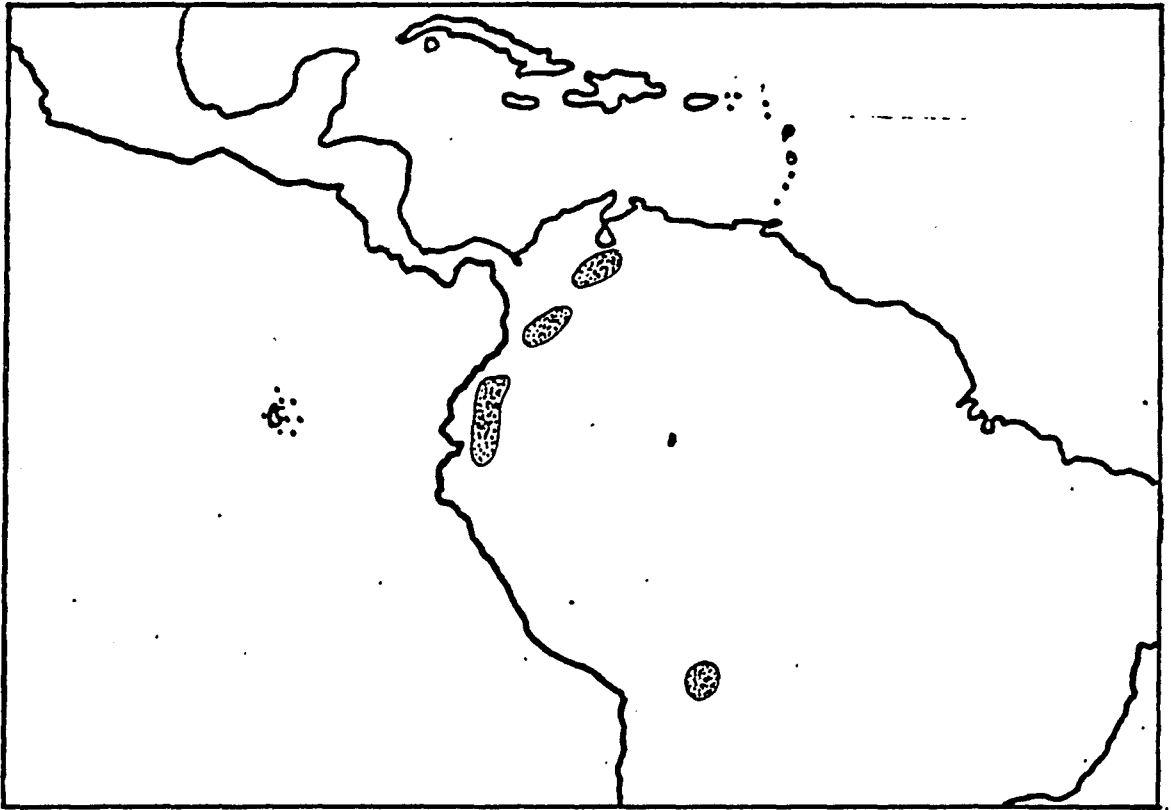


FIGURE 41 A.

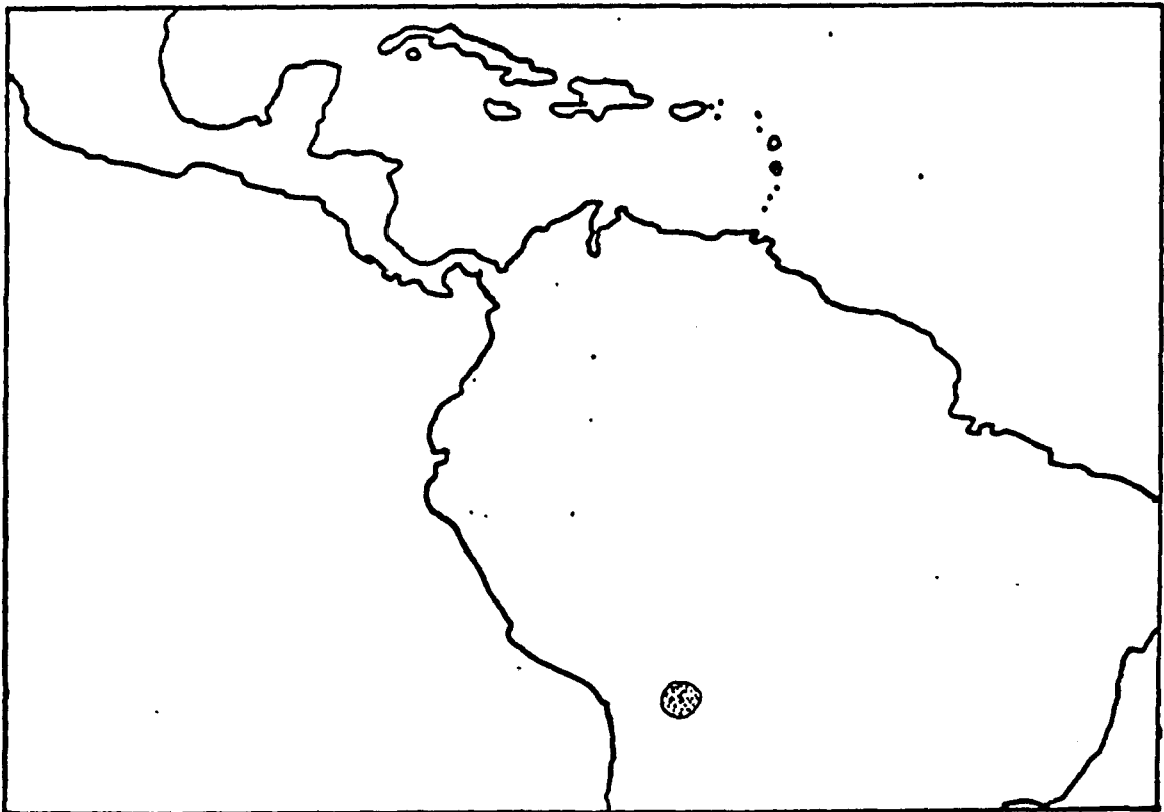


FIGURE 41 B.

9. *Juncus uruguensis* Grisebach, Symb. fl. argent. 317. 1879, also published as Abh. Königl. Ges. Wiss. Göttingen 24 (1). 1879. Type. Uruguay. in campis pr. Concepción del Uruguay, Lorentz 1126 (GOET) is probably the holotype, though no particular specimen was cited in the protologue. Fig. 41 B.

Perennial caespitose herb, 20-60 cm high. Rhizome 1-3 mm diam., densely branching and giving rise to small clumps of culms or creeping with short internodes and the culms arising in densely crowded rows. Culms arising from small bulbous thickenings covered with brown to castaneous scales, erect, with 10-25 longitudinal ridges, 1-2.5 mm diam., straight, stiff. Cataphylls 0-2 to each culm, to 7 cm long with a rudimentary needle like blade to 5 mm long. Blade bearing leaves all basal, 1-2 to each culm, erect, 10-25 cm long or usually half or less as long as the culm; sheaths 3-8(-11) cm long with membranaceous margins terminating in two 0.5-1 mm long auricles; blade filiform 0.7-2 mm diam., with the adaxial surface reduced and therefore round or elliptical in cross section, longitudinally ridged or striate. Inflorescence terminal, compound, 1.5-4(-7) x 1.5-3 cm, (15-)30-100-flowered, consisting of several unilateral, clustered cymes (drempania). Lower inflorescence bract 1.5-4.5 cm long, usually shorter than or equalling the inflorescence, but occasionally longer, with well developed sheath and short pointed lamina, sometimes drawn out into a hairlike point; upper bracts progressively shorter, the ultimate ones membranaceous, to 2 mm long. Each flower clasped by two 1.5-2 mm long bracteoles. Tepals unequal, lanceolate, first green, turning bright castaneous, outer ones 4-5 mm long, strongly concave, margins thin membranaceous, central part

thick and extending into a mucronate tip, inner ones 3.5-4.2 mm long, flat, membranaceous towards the margin, acute. Stamens 3, 1.5-2.5 mm long; anthers linear, 0.8-1.5 mm long, always longer than the flat and basally widened filaments. Capsule ellipsoidal, obtuse to truncate, sometimes widening before dehiscence, basally trigonous to trilobed in cross section, apically 3-keeled before dehiscence, 3.5-4 x 1.5-2 mm, castaneous, glossy, thick walled, 3-locular or sometimes with a free central columella through disintegration of the papery thin partitions between the loculi. Seeds ellipsoidal, apiculate, 0.3-0.4 x 0.15-0.2 mm, rugose or ridged, brown.

Distribution. Mainly in the provinces of Entre Rios in Uruguay and Buenos Aires in Argentina, and disjunctly in Bolivia. The single Bolivian specimen agrees in all morphological details with material from the main area of the species. It was collected at 1200 m altitude in red clay soil among stones along the road. I have no information available about the habitat of the species in its main area of distribution.

Specimens examined. BOLIVIA. Cochabamba: Chapare, ca. 32 km NE of Chimore, 1200 m, Eyerdam 24997 (F, G, K).

This species was referred to subg. Genuini by Buchenau (1890, 1906) and Barros (1953). The lower bract is, however, never culm-like, and blade bearing leaves are always present. Therefore, it obviously belongs in subg. Poiophylli, and therein it is most closely related to, and probably derived, from J. imbricatus.

Juncus subg. *Genuini* Buchenau, Abh. Naturwiss. Vereine Bremen 4: 406.

1875. Type species. *Juncus glaucus* Ehrhart (= *J. inflexus* Linnaeus)

Juncus sectio *Juncotypus* Dumortier, Fl. belg. 142. 1827.

Juncus section *Genuini* (Buchenau) Vierhapper in Engler & Prantl, Nat. Pflanzenfam. 2 ed., 15a: 215. 1930.

Juncus subg. *Juncotypus* (Dumortier) Krechetovic & Goncharov, Fl. URSS 3: 546. 1935.

Perennial herbs to 200 cm high. Rhizome horizontal, either creeping with short internodes, the culms arising in dense rows, and the entire plant densely caespitose, or creeping with conspicuous internodes, the culms arising spaced, and the entire plant forming loose stands. Culms erect, terete, smooth or with fine longitudinal ridges. Leaves present only as cataphylls sheathing the culms basally, i.e. blade bearing leaves absent. Inflorescence appearing lateral because of the culm-like extension created by the lower inflorescence bract, compound of few to several one- or two-sided cymes (drepani and rhipidia); entire inflorescence varying from somewhat lax to congested and densely capitulate. Pedicels originating in the axil of a floral bract in addition to which two bracteoles are inserted just below the flower which they clasp.

Distribution. About 25 species on all continents except Antarctica. Several species with restricted distributions occur in Australia, whereas the north temperate region harbors often widespread species such as *Juncus effusus*, *J. conglomeratus* and *J. inflexus*.

The neotropical species constitute a mixture of widespread north temperate elements (J. effusus and J. conglomeratus), varieties of circumboreal species (J. arcticus var. mexicanus, var. montanus and var. andicola), Australian/New Zealand element (J. procerus), North American elements (J. patens and J. aemulans) and South American elements (J. ramboi subsp. colombianus).

Subg. Genuini is distinct through the combination of (1) the pseudolateral, cymose inflorescence with each flower clasped by two bracteoles (often called prophylls), and (2) the absence of blade-bearing leaves. It is most closely related to subg. Poiophylli which has a basically similar inflorescence (compound cymose with two bracteoles clasping each flower). In subg. Poiophylli, however, the lower bract of the inflorescence is not developed into a culm-like extension, and the inflorescence therefore does not appear lateral. Subg. Poiophylli furthermore always has blade bearing leaves.

Key to the neotropical species of

Juncus subg. Genuini

1. Pith parenchymatous.	16. <u>J. ramboi</u> subsp. <u>colombianus</u> .
1. Pith aerenchymatous.	
2. Culms smooth, not ridged or striate by longitudinal subepidermal sclerenchyma strands.	15. <u>J. arcticus</u> .
2. Culms ridged or striate by longitudinal subepidermal sclerenchyma strands.	

3. Pith interrupted. Cataphylls not densely sheathing the culm.
Lower inflorescence bract less than 1/10 of total plant height.

14. J. procerus.

3. Pith continuous. Cataphylls densely sheathing the culm.
Lower inflorescence bract usually more than 1/7 of total
plant height.

4. Capsule subglobose, shorter than the tepals and spreading
them. Stamens 6.

13. J. patens.

4. Capsule ellipsoidal to obovoidal, apically obtuse or emar-
ginate, shorter than or equalling the tepals, not spread-
ing them. Stamens 3.

5. Culms with 12-30 ridges below the inflorescence.

12. J. conglomeratus.

5. Culms with 40-60 ridges or striae below the inflores-
cence.

6. Culms thin, less than 1.7 mm in diam. Tepals
castaneous, 2-3.5 mm long.

11. J. aemulans.

6. Culms usually thicker, 1.5-6 mm in diam. Tepals
stramineous or castaneous, if castaneous then
more than 3.5 mm long.

10. J. effusus.

FIGURE 42

Habit of Juncus effusus, J. procerus and J. arcticus, all from subg. Genuini (From Balslev, 1979a).

42A. Juncus effusus (Drawn from Prescott 694, NY).

42B. Juncus procerus (Drawn from Asplund 17758, S).

42C. Juncus arcticus var. andicola (Drawn from Asplund 8455, S).

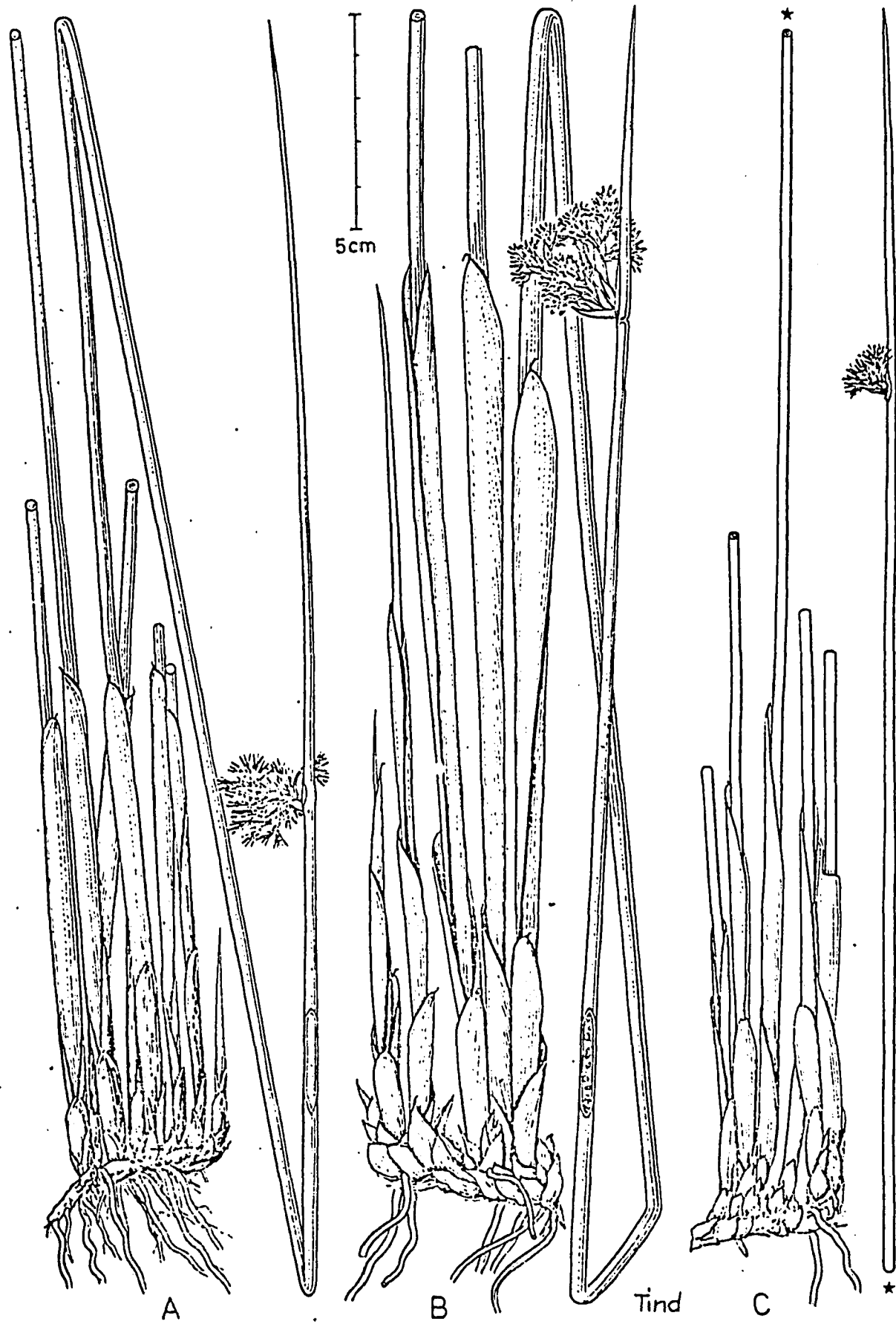


FIGURE 42

10. *Juncus effusus* Linnaeus, Sp. Pl. 1: 326. 1753; Fernald & Wiegand,

Rhodora 12: 81-93. 1910; Hämet -Ahti, Ann. Bot. Fenn. 17:

183-191. 1980. Type. Europe, n.v. Figs. 19, 42 A, 43 A.

Juncus bogotensis Humboldt, Bonpland & Kunth, Nov. gen. sp. 1: 235.

1816. Type. Colombia. Cundinamarca: in alta planitie Bogotensi

prope Tenjo, Coto et Sabana, Humboldt & Bonpland s.n. (holotype,

P; isotypes, B, P). The sheets are annotated "Sta Fe" (=Bogotá).

Perennial densely caespitose herb, 50-100 cm high. Rhizome creeping, 2-5 mm diam., covered with dark reddish brown scales, internodes very short and the culms arising in densely crowded rows. Culms erect, terete, 1.5-6 mm diam., externally striate by 40-60 longitudinal, sub-epidermal sclerenchyma strands running parallel to the vascular bundles, pith continuous, aerenchymatous of asteriform cells. Cataphylls 3-5 to each culm, to 30 cm long, with rudimentary blade to 5 mm long, usually densely sheathing, dark castaneous basally, changing to light brown or stramineous upwards. Blade bearing leaves absent. Inflorescence pseudolateral, many flowered, loosely branching and up to 10 x 20 cm, but usually smaller and sometimes congested, capitate and only 1.5 x 1.5 cm, sometimes + subdivided, compound cymose, consisting of several congested cymes, the ultimate ones being unilateral cympania. Lower inflorescence bract appearing as a continuation of the culm, (10-)15-45 cm long and usually constituting 1/5 or more of total plant height (rarely only 1/10 in Costa Rican plants), smoothly jointed to the culm, sheath narrow, upper bracts scale like or membranaceous. Each flower clasped by two 0.7-2 mm long bracteoles. Tepals unequal, lanceolate 2-5 mm long, stramineous to castaneous, outer ones concave slightly

longer than the flat inner ones. Stamens 3, 1-2 mm long; anthers linear or oblong, 0.3-1 mm long, shorter than or equalling the filaments. Capsule ellipsoidal to obovoidal, obtuse, trigonous to 3-lobed, 1.5-5 x 1-2.5 mm, stramineous to castaneous, 3-septate. Seeds ovoidal, asymmetrical, short apiculate, 0.4-0.6 x 0.2-0.3 mm, rugose, yellow to brown.

Distribution. A cosmopolitan species, most common in the north temperate region, but frequent at higher elevations in the tropics and scattered in the south temperate region. Weimarck (1946) shows the total distribution. In the neotropical region Juncus effusus occurs on the Antillean Islands of Hispaniola and Guadeloupe, through the Mexican and Central American highlands southward to Costa Rica, in the Andes from Venezuela to northern Peru, in Bolivia and Tucumán in Argentina, and also in the southeastern Brazilian highlands. It grows in pastures, along roads and ditches and other places under human influence. Around equator it is found above 2000 m altitude, but often lower towards the north and the south.

Representative specimens. MEXICO. Chiapas: Amatenango del Valle, 1750 m, Breedlove 14617 (NY). México: México-Queretaro rd, 2 km W of Chautitlan, 2250 m, Hidalgo 12 (NY, US, WIS). Michoacán: Río del Salto-La Polvilla, ca. 18 mi E of Morelia, 2200-2450 m, King & Soderstrom 5121 (NY). Oaxaca: Zempoatepetl nr Ayutla, Camp 2749 (NY). Vera Cruz: Ixhuatlancillo nr Orizaba, Bourgeau 2592 (P).

GUATEMALA. Alta Verapaz: Río Frío between Tactic and Santa Cruz, 1460 m, Molina & Molina 12215 (NY). Quiché: S of Chiche Castenango,

1850 m, Standley 62420 (NY).

HONDURAS. Intibucá: Huise river, 9 km E of La Esperanza, 1600 m, Molina 25566 (MO, NY). Morazán: Mt La Tigra SW of San Juancito, 1800-2100 m, Molina et al. 17016 (NY). Ocotepeque: Belén Gualcho, 1500-2000 m, Rubio 053 (MO).

EL SALVADOR. Los Esesmilas, 2150 m, Tucker 1161 (NY).

COSTA RICA. Cartago: Interamerican Highway, 1 km S of Ojo de Agua, Solomon 2517 (MO). Hereida: Mt Barba between Ríos Las Vueltas and Nuevo, 2000 m, Burger & Baker 9454 (MO, NY). San José: Ca. 3 km NW of Cascajal nr union of Ríos Cascajal and Bajo Maquina, 1750 m, Taylor 11329 (MO, NY).

HAITI. Massif de la Salle, Crete-a-Piquantes, Port-au-Prince, Morne Malanga, 1300 m, Ekman 9511 (GH, K).

GUADELOUPE. Massif de la Soufriere, Bains Jaunes, 900 m, Sastre 2836 (P), 6843 (P).

COLOMBIA. Antioquia: Santa Rosa de Osos, 86 km NE of Medellín, 2500 m, Callejas 976 (JAUM). Boyacá: Socha in Río Chicamocha valley, 2700 m, Fosberg 22227 (F, GH, US). Caldas. Río Quíndio, Salento, 1500-1600 m, Killip & Hazen 8955 (GH, NY, US). Cauca: Calaguaca, Coconuco, 2500-2800 m, Pennell 7126 (GH, NY, US). Cundinamarca: Salto de Tequendama, 2400 m, McKee 10412 (COL, P, US). Huila: Balsillas, 2000-2100 m, Rusby & Pennell 738 (NY), 771 (F, GH, MO, NY, US). Nariño: Río Tescual above Córdoba, 2850 m, Ewan 16297 (US). Norte de Santander: Matorrales en Chichera between Fáramo de Fontibon and Pamplona, 2580 m, Cuatrecasas et al. 12250 (GH, U, US). Putumayo: Valle de Sibundoy, 2200 m, Bristol 403 (COL, GH). Santander: Río Surata valley above Surata, 2000-2300 m, Killip & Smith 16709 (GH, NY, S, US). Tolima: Toche, 2300 m, von Snei-

derm 3054 (A, GH, MO, S).

VENEZUELA. Distrito Federal: Between Colonia Tovar and La Rosita, El Limón, 1700 m, Rojas 1428 (F). Mérida: Río Cajas, Curran 2132 (NY). Miranda: Pico de Naiguatá above Los Chorros, 2200-2765 m, Steiermark 63010 (F, NY). Táchira: NNE slopes of Pata de Judío, 2100-3500 m, Luteyn et al. 5955 (NY). Zulia: Sierra de Perija, Serranía de Valledupar, Río Guasare, 2700-3300 m, Tillet 747-1008 (NY).

ECUADOR. Azuay: Cuenca-Loja rd, km 82, 3000 m, Balslev 1238 (NY). Carchi: Tulcán-Julio Andrade rd, 13 km S of Las Juntas, 3000 m, Balslev 803 (NY), 827 (NY). Loja: Yangana-Zumba rd, km 15-20, N slopes of Cordillera de Sabanilla, 2550 m, Balslev 1274 (NY). Pichincha: S of Quito towards Tambillo, 2900 m, Asplund 7025 (G, S, US). Zamora-Chinchi: Loja-Zamora rd, km 15-16, 2700-2800 m, Balslev 1253 (NY), km 17-18, 2500-2650 m, Luteyn et al. 6602 (NY).

PERU. Amazonas: Chachapoyas, Mathews s.n. (GH). Cajamarca: Cutervo-Socota, 2500 m, Lopez et al. 6724 (NY); Cutervo, La Colmena-Llama, 2750 m, Sandeman 4176 (K).

BRAZIL. Minas Gerais: Vicoso, Barroso rd, Corrêga de São Domingo, 700 m, Mexia 5374 (F, MO, NY). São Paulo: Campos do Jordão, Leite 3643 (A, GH).

BOLIVIA. Without locality: Bang 2410 (F, GH, K, MO, NY, US).

Eastern Asiatic material of Juncus effusus is often treated as a separate variety, var. decipiens Buchenau (Buchenau, 1890, 1906; Kao & Devol, 1978), or as a separate species, Juncus decipiens (Buchenau) Nakai (Nakai, 1928; Satake, 1938). European material of J. effusus was not divided further in the recent treatment for Flora Europaea (Snogerup, 1980). The North American material was divided into nine varieties by

Fernald & Wiegand (1910), a varying number of which have been accepted in later floras (e.g. Gleason & Cronquist, 1963; Hitchcock et al., 1969). Barros (1953, 1962) divided the temperate South American material into two varieties, var. effusus and var. compactus Lejeune & Cortois, both based on European types, and some material of J. effusus was misidentified as J. leersii Marsson, which is a synonym of the distinct J. conglomeratus Linnaeus.

The Méxican and Central American material commonly has lax inflorescences with many stramineous small flowers with the tepals as short as 2 mm. This is probably the same as J. effusus subsp. solutus (Fernald & Wiegand), Hämeth-Ahti (Hämeth-Ahti, 1980). Some specimens from Costa Rica and Guatemala have the lower inflorescence bract as short as 10 cm and constituting only 1/10 of the total plant height. The north Andean material commonly has a congested or almost capitate inflorescence of rather long (3-3.5 mm) dark reddish brown flowers, and it always has a long lower inflorescence bract that constitutes 1/5 or more of the total plant height. This north Andean material has been called J. bogotensis in many herbaria. The material from southeastern Brazil has small stramineous flowers like the Central American plants. The neotropical material thus exhibits quite different extremes but the transitions are gradual, and in my opinion it is best treated as belonging to one variable species.

Uses. At Cobán in Guatemala and Dota in Costa Rica the culms are used for weaving mats (Standley, 1937; Standley & Steyermark, 1952).

FIGURE 43

43 A. The distribution of Juncus effusus in the neotropical region.

In addition it is widely distributed in the north temperate region, and scattered in the south temperate and tropical regions (see also Fig. 19).

43 B. The distribution of Juncus aemulans.

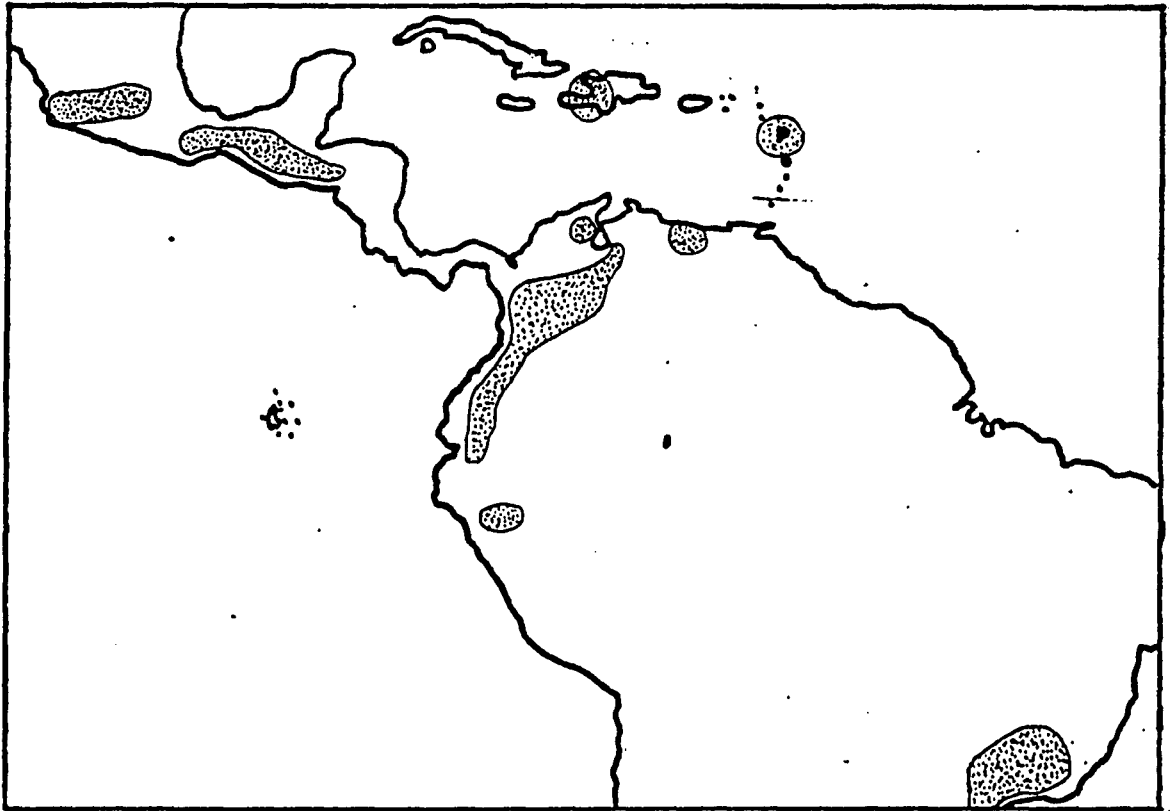


FIGURE 43 A.

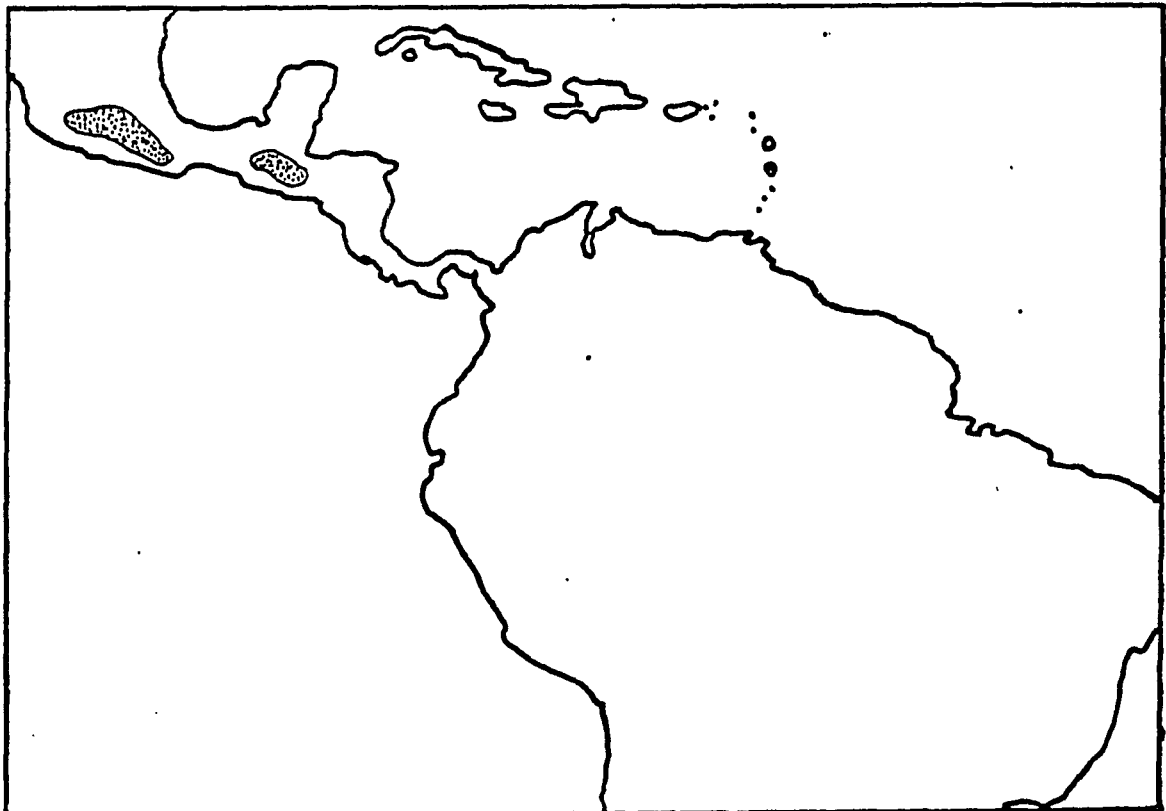


FIGURE 43 B.

11. *Juncus aemulans* Liebmann, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjøbenhavn 38. 1850. Type. México. Cerro León nr Perote, 2150 m, Jul 1841, Liebmann s.n. (holotype, C; isotypes, C, K, MO fragment, P). Fig. 43 B.

Juncus effusus Linnaeus var. *aemulans* (Liebmann) Buchenau
in Engler, Pflanzenreich IV, 36 (Heft 25): 136. 1906.

Perennial densely caespitose herb, 50-110 cm high. Rhizome creeping, 2-4 mm diam., densely covered with acute, brown scales, internodes very short and the culms arising in clumps or in short rows, densely crowded. Culms erect, terete, 0.7-1.7 mm diam., longitudinally striate by subepidermal sclerenchyma strands, pith continuous, aerenchymatous of asteriform cells. Cataphylls usually 3 to each culm, densely sheathing, to 14 cm long, with an up to 5 mm long needle like rudimentary blade, basally castaneous, stramineous to pale green upwards. Blade bearing leaves absent. Inflorescence pseudolateral, many-flowered, usually lax, compound cymose, composed of many-sided cymes and in the ultimate parts unilateral drepania. Lower inflorescence bract appearing as a continuation of the culm, 10-17 cm long, usually constituting 1/7 or more of the total plant height, smoothly jointed to the culm, upper bracts membranaceous, progressively shorter upwards, the ultimate ones to 4 mm long. Each flower clasped by two acuminate, 0.8-1 mm long bracteoles. Tepals unequal, lanceolate, acuminate, castaneous, green along the midrib when young, outer ones 2-3.5 mm long, concave, inner ones slightly shorter, flat. Stamens 3, 1.2-1.5 mm long; filaments filiform; anthers oblong to linear, 0.5-0.7 mm long, yellow. Capsule

obovoidal, trigonous to trilobed, ca. 2 x 1 mm, brown, 3-septate.

Seeds not seen.

Distribution. From Central México to Guatemala, at altitudes between 2300 m and 2800 m.

Specimens examined. MEXICO. Chiapas: Tenejapa, Achlum, 2800 m, Ton 2360 (NY, WIS). México: 3 km E of San Rafael, Tlalmanalco, 2750-2900 m, Cisnero 1645 (WIS); Tepexpan, Valle de México, 2300 m, Matuda 19141 (NY). Oaxaca: Highway 179 Oaxaca-Pochutla, ca. 15 mi S of Miahuatlan, 2200 m, Croat 46199 (MO, NY).

GUATEMALA. Totonicapan: Sierra Madre Mts nr Polagua, 20-25 km N of Cristóbal, 2800 m, Williams et al. 22666 (NY, WIS).

Juncus aemulans is closely related to J. effusus, from which it is distinguished by the combination of short (2-3.5 mm long), dark castaneous tepals, and the slender (0.7-1.7 mm diam.) culms. It is closest to the Pacific North American J. effusus L. var. gracilis Hooker (sensu Hitchcock et al., 1969).

12. *Juncus conglomeratus* Linnaeus, Sp. Pl. 1: 326. 1753. Type.

Europe. Van Royen s.n. (lectotype, L, selected by Snogerup, 1971).
Fig. 44 A.

Juncus communis E. Meyer var. conglomeratus (Linnaeus) E. Meyer,
Junci Generis Monogr. Specimen 20. 1819.

Juncus subuliflorus Drejer, Fl. excurs. hafn. 127. 1838; Dandy,
Watsonia 7: 169. 1969. Type. Denmark. Furesøen, 1834, Lieb-
mann s.n. (syntype, C); same loc., Drejer s.n. (syntype, C).

Juncus leersii Marsson, Fl. Neu-Vorpommern u. Rügen 451. 1869.
Type. n.v.

Juncus effusus Linnaeus var. conglomeratus (Linnaeus) Engelmann
in A. Gray, Manual 5 ed., 537. 1867.

Similar to Juncus effusus in habit, but the culms with only 12-30
conspicuous ridges below the inflorescence, the lower inflorescence
bract with a wide sheath, the inflorescence usually in one or sometimes
more (e.g., our specimen) compact cluster(s), tepals 2-4 mm, stamens
1-2.5 mm long, anthers 0.4-0.7 mm, usually shorter than the filament,
and capsule usually emarginate, mucronate, about equalling the tepals.

Distribution. Juncus conglomeratus occurs most commonly in
Europe from the British Isles to the Volga River in the USSR, and less
commonly further eastward into the Peoples Republic of China. In
northern Africa it grows from Morocco to Tunis, and in North America
it is infrequent along the northeastern coast from Newfoundland to
New Jersey. Wienstedt (1937) mentioned it as occurring in Brazil

FIGURE 44

44 A. The distribution of Juncus conglomeratus in the neotropical region.

In addition it is widely distributed in western Europe, and scattered on the North American east coast.

44 B. The distribution of Juncus procerus in the neotropical region.

In addition it occurs in Patagonia, the Juan Fernandez Islands, Australia, and New Zealand.

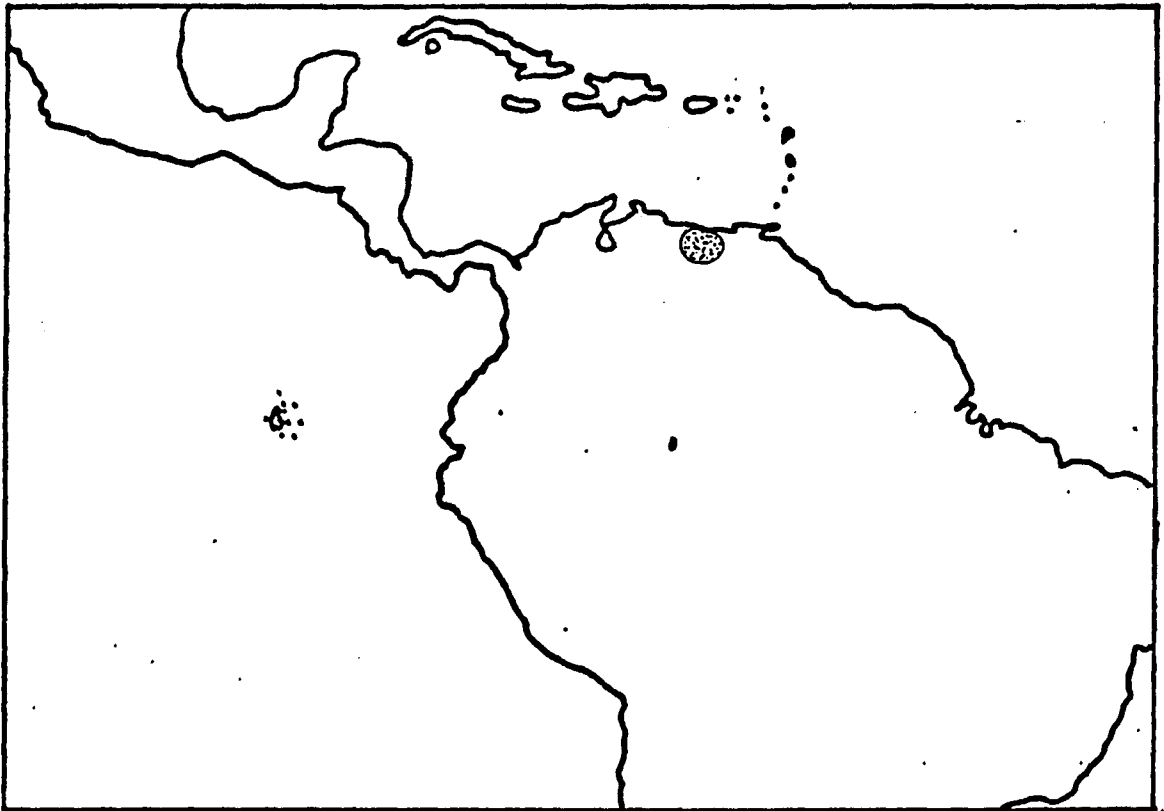


FIGURE 44 A.

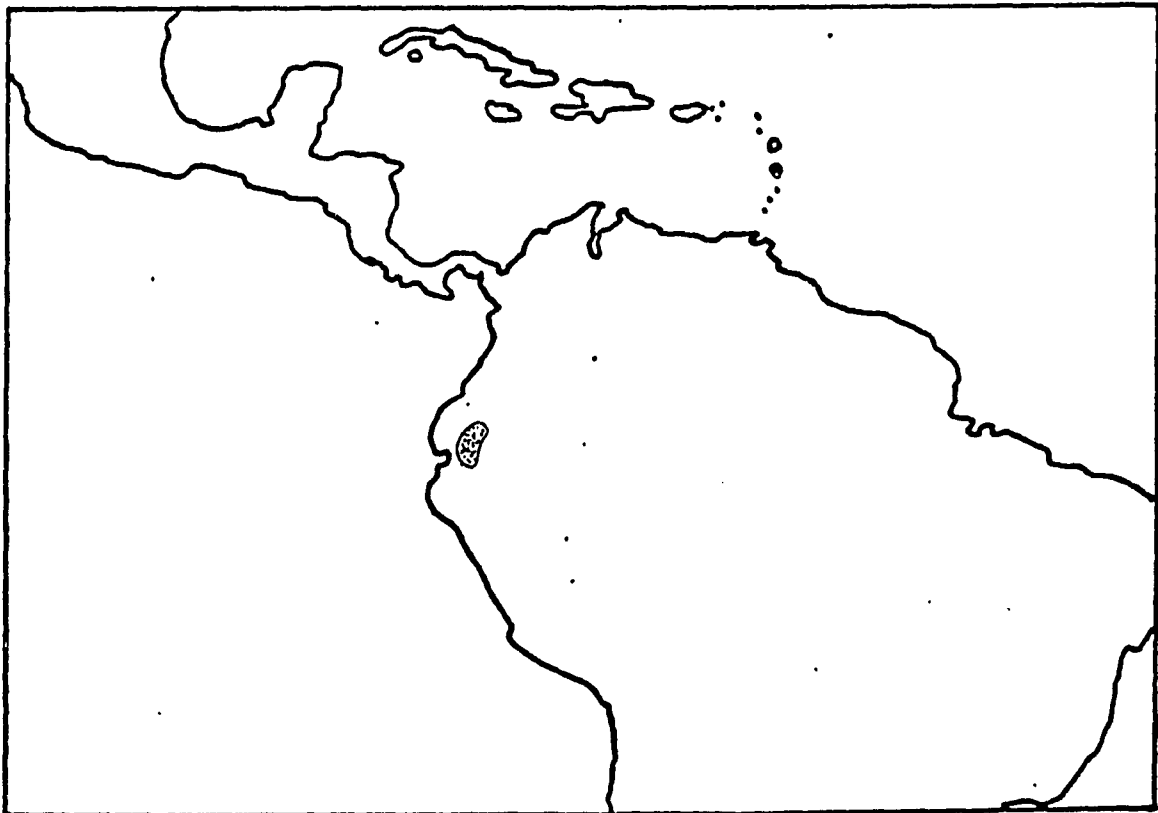


FIGURE 44 B.

but cited no specimens. According to Barros (1953, 1962) it is also found in the provinces of Catamarca, Tucumán and Río Negro in Argentina and in Santa Catarina in Brazil (under the synonym J. leersii), but this is based on misidentifications of J. effusus. It is here reported from one locality in Venezuela, to which it might easily have been introduced by man. Hultén (1958) shows a map of the total distribution.

VENEZUELA. Aragua, Colonia Tovar, 1900 m, 25 Dec 1921, Pittier 9961 (GH).

Juncus conglomeratus is closely related to J. effusus and has often been confused with that species. Linnaeus, who named both, mixed them in his own herbarium, and the nomenclature has only recently been straightened out. Linnaeus (1753) distinguished J. effusus by its lax inflorescence and J. conglomeratus by its condensed inflorescence. This character is not constant in either species. The best distinguishing character is the culm anatomy as pointed out by Snogerup (1970, 1971, 1980) and Hämet-Ahti (1980). Juncus effusus has many (40-60) fine, subepidermal sclerenchyma strands, which are not connected with any modifications of the overlaying epidermis. The culms therefore appear finely striate. Juncus conglomeratus has fewer (12-30) and larger subepidermal sclerenchyma strands, which are connected with enlarged epidermal cells that protrude as prominent, longitudinal ridges. This distinction was not clear to earlier workers. Meyer (1819) thus united them as one species, J. communis, with two varieties, α conglomeratus and β effusus. This confusion, and the fact that Linnaeus' her-

barium was mixed, led Buchenau (1890, 1906) to apply the later name Juncus leersii to avoid confusion. Dandy (1969) argued that J. conglomeratus should be considered a synonym of J. effusus, and that J. subuliflorus was an older name than J. leersii, and therefore the earliest name for what had been called J. conglomeratus. By selecting a type in the Van Royen herbarium at Leiden (L), which Linnaeus cited, Snogerup (1970) secured the name J. conglomeratus for what has been called so in most recent European floras. The synonyms mentioned above are only those which are relevant for this discussion of the nomenclatorial confusion. A full synonymy would include more names based on European types.

It should be mentioned that Krisa (1962), in a study of the Czechoslovakian populations of J. effusus L. s.s. and J. conglomeratus L. s.s., concluded that they are mere extremes of one 'conspecies' connected by a whole system of morphological and anatomical transition types. Agnew (1968) disagreed with that view and stated that the two species are clearly morphologically and phenologically separable in the British Isles, though they do form hybrids, especially at higher altitudes, where the phenological separation is less distinct.

13. *Juncus patens* E. Meyer, Synops. Luzularum 28. 1823. Type. USA.

California: Monterey, Haenke s.n., n.v.

Similar to *Juncus effusus* in general habit but 30-90 cm high, which is on the average shorter, with 6, not 3, stamens, the anthers as long as the filaments, and the capsule subglobose, shorter than the perianth segments and spreading them.

Distribution. Occurs along the west coast of North America from Oregon to Baja California in moist places from the shore to the montane coniferous forest. Collected at one locality within the neotropical region.

Specimens examined. MEXICO. Puebla: Santa Barbara, Jul 1909, Nicolas s.n. (P).

14. *Juncus procerus* E. Meyer, *Linnaea* 3: 367. 1828. Type. Chile.

Chamisso s.n. (n.v., not at B, possibly at LE). Figs. 42 B, 44 B.

Juncus valdiviae Steudel, *Syn. pl. glum.* 2: 296. 1855. Type.

Chile. Valdivia, Philippi 43 (holotype, P; isotypes, G, GOET, K, MO, P, S).

Juncus pallidus R. Brown var. *triandrus* Cheeseman, *Man. New*

Zealand fl. 2 ed. 293. 1925. Type. New Zealand. Auckland,

St. John's College, Dec 1883, T. F. Cheeseman AK 2995 (lectotype, AK, n.v., selected by Edgar, 1964; isolectotype, CANTY 1941, n.v.)

Perennial densely caespitose herb, 60-140 cm high. Rhizome creeping, 4-8 mm diam., with brown scales, internodes short and the culms arising in densely crowded rows. Culms erect, terete, 1-5 mm diam., striate by longitudinal, subepidermal sclerenchyma strands, pith aerenchymatous of asteriform cells, interrupted by empty parts of varying length. Cataphylls (2-)3(-4) to each culm, lower one to 4 cm long, upper one to 20 cm long, with rudimentary needle like blade to 3 mm long, unfolding and loosely sheathing or sometimes diverging from the culm, light reddish brown basally, light brown upwards. Blade bearing leaves absent. Inflorescence pseudolateral, many flowered, lax or densely capitate, compound cymose, consisting of several congested cymes, the ultimate ones being unilateral drepania. Lower inflorescence bract appearing as a continuation of the culm, 5-10 cm long, constituting less than 1/10 of the total plant height, usually with a conspicuous constriction where it joins the culm, upper bracts membranaceous pro-

gressively shorter, the ultimate ones to 5 mm long. Each flower clasped by two 1-1.5 mm long bracteoles. Tepals unequal, lanceolate, stramineous, sometimes reddish tinged, margin never membranaceous, outer ones 2.3-2.8 mm long, slightly concave, inner ones 2.1-2.5 mm long, flat. Stamens 3, 1.1-1.4 mm long; anthers oblong to linear, 0.5-0.7 mm long. Capsule ellipsoidal to suborbicular, 2-2.5 x ca. 1.5 mm, light brown, spontaneously dehiscent, 3-septate. Seeds asymmetrical, oblong, broadly apiculate, 0.4-0.5 x ca. 0.2 mm, finely reticulate, yellowish brown.

Distribution. In southern Chile from Concepción to Puerto Montt, in Neuquen and Chubut in Argentina, on the Juan Fernandez Islands and in southern Ecuador. Introduced to Australia (Beadle et al., 1972) and New Zealand (Edgar, 1964; Moore & Edgar, 1970). Engelmann's report of this species from San Francisco, California, USA (Engelmann, 1866) has never been confirmed. In southern Ecuador it occurs in pastures, meadows and at ponds and along roadsides at altitudes between 2600 m and 3200 m.

Specimens examined. ECUADOR. Azuay: Nr Cuenca, Rose 22935 (GH, NY, US); Río Tarqui, 4-18 km S of Cuenca, 2550-2750 m, Camp E-2051 (NY, S); 3 km N of Tarqui (S of Cuenca), 2700 m, Balslev 1218 (NY); Cuenca-Loja rd, km 37, 3200 m, Balslev 1221 (NY), km 82, 3000 m, Balslev 1237 (NY); Soldados-Hacienda San Vicente, W of Cuenca, 3200-3300 m, Balslev 1536 (NY); 2-4 km W of Sayausí (W of Cuenca), 2900 m, Balslev 1565 (NY). Cañar: Tipococha, 3200 m, Penland & Summers 1026 (F, GH); Nr Azoguez, Rose 22779 (GH, NY, US). Loja: Zamora-Huiaco E of Loja,

2600-2800 m, Acosta Solis 20530 (US); Panamerican Highway 10-15 km N of Saraguro, 2900-3100 m, Balslev 1404 (NY); Santiago W of Panamerican Highway ca. 40 km N of Loja, 2400 m, Balslev 1360 (NY); Yangana-Zumbard, km 15-20, on N slope of Cordillera de Sabanilla, 2550 m, Balslev 1273 (NY).

Common name. 'Totorilla' in Ecuador, 'Juncillo' in Chile.

The Ecuadorean material of J. procerus was misidentified as J. effusus until it was separated by Balslev (1979). The two species both belong to Buchenau's (1906) informal group 'Junci genuini valleculati', characterized by subepidermal sclerenchyma strands that show up externally as fine longitudinal striae. Juncus procerus is distinct through the loosely sheathing and lighter colored cataphylls, the interrupted pith, the smaller stramineous tepals, and the shorter lower inflorescence bract, which is less than 1/10 of the total plant height. The lower inflorescence bract of J. procerus usually has a constriction where it joins the culm. This is not the case in J. effusus. The nearest relative of J. procerus is J. pallidus R. Brown from Australia and New Zealand. That species has 6 stamens, a pith which is not interrupted, pale green tepals occasionally tinged with pink and later becoming light brown.

15. *Juncus arcticus* Willdenow in Linnaeus, Sp. Pl. 4 ed. 2: 206. 1799.

Type. Norway (holotype, B).

Perennial herb, 20-170 cm high. Rhizome creeping, 2.5-10 mm diam., branching but with long unbranched segments, internodes very short or more often up to 4 cm long, the insertion of the culms accordingly varying from crowded to spaced, sometimes with a creeping part with long internodes and side branches with short internodes. Culms erect, 1-7 mm diam., smooth or slightly wrinkled striate, but only very rarely with longitudinal ridges. Cataphylls 2-3 to each culm, lower one 1-8 cm long, upper one 3-25 cm long, usually mucronate by a up to 3 mm long needle-like rudimentary blade, yellow to light brown or stramineous. Blade bearing leaves absent or in var. mexicanus present and then 1-2 to each culm, the blade laterally compressed, varying in length from very short to equalling the culm. Inflorescence pseudolateral, few- to many flowered, usually lax and then up to 15 x 7 cm, sometimes congested and only 2.5 x 2 cm, compound cymose, consisting of several congested cymes, the ultimate ones being unilateral drepania. Lower inflorescence bract appearing as a continuation of the culm, (2-)5-15(-25) cm long, or usually constituting between 1/10 and 1/5 of the total plant height, sometimes less, upper bracts progressively shorter, membranaceous. Each flower clasped by two 1.5-2.5 mm long, acute, membranaceous bracteoles. Tepals equal or outer ones longer, lanceolate, stramineous to dark brown or reddish brown, sometimes lighter colored along the midrib and at least inner ones often with membranaceous margins, outer ones 3-5.5 mm long, concave, acuminate, inner ones 3-5 mm long, flat to concave, acute. Stamens 6, 1.5-3 mm

long; filaments flat, widened towards the base; anthers linear 0.7-2.5 mm long, 1-6 times as long as filaments. Style 0.5-1.5 mm. Stigmas 1.5-3 mm. Capsule ellipsoidal to ovoidal, apiculate, round to trigonous or slightly 3-lobed, 2.5-4.5 x 1.5-2 mm, light to dark brown, often light basally changing to dark apically, glossy, 3-septate. Seeds ellipsoidal, oblong, ovoidal or irregularly shaped, short apiculate, 0.6-0.8 x 0.2-0.5 mm, rugose, light brown to reddish brown below a hyaline outer seed coat.

Distribution. In a broad circumscription, as here applied, this species is almost circumboreal and extends to the south through the Rocky Mountains in western North America, the Méxican Sierra Madres, and the Andes from Colombia to Patagonia.

Buchenau (1906) separated Juncus arcticus sensu stricto, J. lesueurii Bolander (type from pacific North America) and J. andicola Hooker (type from Ecuador) of the 'Junci genuini laevis' as three geographically restricted species. In addition, populations representing a wide array of morphological variation, distributed over the entire area of this complex, were referred to 11 varieties of J. balticus Willdenow. The neotropical populations of the complex were thus classified as belonging to three species, J. lesueurii, J. andicola and J. balticus, the latter with four varieties: Juncus arcticus sensu stricto does not reach the neotropical region. In our current, much expanded, collections of neotropical Juncaceae I have not found a basis for dividing this complex into distinct species. There is a strong geographically dependent variation which, however, is

overlaid by ecological modifications in such a way that the taxa are difficult to circumscribe. I have therefore found it best to classify the neotropical populations of this complex as three varieties. I have no evidence that these three varieties are more closely related to J. balticus sensu strictu (type from the Baltic Sea, herb. Willd. B), then they are to J. arcticus sensu stricto (type from Norway), and they are therefore treated as varieties of the latter which bears the older name.

Key to the neotropical varieties of

Juncus arcticus

1. Each culm with one or two blade bearing leaves. Culms and blades laterally compressed, usually twining. Western United States to México and southern Peru to Patagonia.
 - 15a. J. arcticus var. mexicanus.
1. Blade bearing leaves absent, the culms bearing only cataphylls. Culms terete.
 2. Tepals stramineous, or at least with lighter colored midrib. Western North America to central México.
 - 15b. J. arcticus var. montanus.
 2. Tepals dark reddish brown. Southern Colombia to Patagonia, and one station in México.
 - 15c. J. arcticus var. andicola.

15a. *Juncus arcticus* Willdenow var. *mexicanus* (Willdenow) Balslev, comb. nov. Basionym. *Juncus mexicanus* Willdenow ex Roemer & Schultes, Syst. veg. 7: 178. 1829. Fig. 45 A.

Juncus compressus Humboldt, Bonpland & Kunth, Nov. gen. sp. 1: 235. 1816. Type. México. Chapoltepec, San Agustín de las Cuevas et Real del Monte, altit. 1200-1430 hex. 18 Feb, Humboldt & Bonpland s.n. (holotype, P; isotype, B).

Juncus mexicanus Willdenow ex Romer & Schultes, Syst. veg. 7: 178. 1829. Type. Same as for *J. compressus* H.B.K. The duplicate sent to Berlin for study by Willdenow (holotype, B; isotype, P).

Juncus complanatus Roemer & Schultes, *ibid*, 185.

Basionym. *Juncus compressus* H.B.K.

Juncus orizabae Liebmann, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 39. 1850. Type. México. Vulkanen Orizaba, 3650 m, Sep 1841, Liebmann s.n. (holotype, C; fragment of holotype, W).

Juncus pictus Philippi, Linnaea 33: 268. 1864, pro parte. Type. Chile. Thermas 'de Chillan' dictus prope Corral, ad locum Rancho in insula Chiloe (holotype, SGO, n.v.; photo of holotype, GH; isotype, K).

Juncus balticus Willdenow var. *mexicanus* (Willdenow) Kuntze, Revis. gen. pl. 3 (2): 320. 1898.

Juncus balticus Willdenow var. *columnaris* Buchenau in Engler, Pflanzenreich 36, IV (Heft 25): 145. 1906. Type. Chile. Atacama: San Andres, 2400 m, 19 Jan 1904, Reiche s.n. (holotype, W).

Juncus balticus Willdenow var. durangensis Buchenau, *ibid.* 146.

Type. México. Durango, Apr-Nov 1896, Palmer 188 (holotype, W; isotypes, GH, MO, NY, G, K).

Juncus balticus Willdenow forma mexicanus (Willdenow) Parish,

Muhlenbergia 6: 119. 1910.

Perennial herb (5-)15-30(-70) cm high. Rhizome creeping, 2-6 mm in diam., internodes very short or up to 2 cm long, the culms accordingly crowded or spaced, often with short sidebranches with short internodes giving rise to crowded culms. Culms 0.5-2 mm diam., laterally compressed, often twisted. Blade-bearing leaves 1-2 to each culm, blades similar to the culm but often shorter. Inflorescence small usually less than 20-flowered and less than 3 x 2 cm. Tepals 4-5.5 mm long, dark reddish brown with green or gray midrib, becoming slightly shorter and stramineous at fruiting. Stamens 2-3 mm long with 1.5-1.8 mm long linear anthers. Style 1-1.5 mm long. Stigmas 1.5-3 mm long. Capsule ellipsoidal, apiculate, 3.5-4.5 mm long, slightly shorter than or as long as the tepals.

Distribution. Western United States to southern México and again in the Andes from southern Peru to Patagonia. Grows at altitudes between 1800 m and 3200 m in México, between 3000 m and 4000 m in Peru and Bolivia, and descending to sea level in Patagonia.

Representative specimens. MEXICO. Distrito Federal: San Barja, Mixcoac, Arsene 10991 (NY). Hidalgo: Rancho Nuevo, 2700 m, West K-9 (WIS). México: México-Toluca rd, km 22, 2900 m, McPherson 1050 (NY). Oaxaca: Sierra, 2150 m, Galeotti 5845 p.p. (P). Puebla: Lago Salido 253 km E of México, 2450 m, Weaver 859 (US). San Luis Potosí: Nr San Luis Potosí, Schaffner 554 (K). Veracruz: Llano Grande above Acultzingo, 3150 m, Sharp 44113 (NY).

PERU. Cuzco: Calca, Hacienda Paucartiva, 2950 m, Keel K-434B (NY); Cuzco, Sagsaywan ruins, 3550 m, Keel K-437 (NY); Kaira, 3220 m, Vargas 676 (F); Cuzco, Rose 19076 (NY, US). Puno: Granja de Salcedo nr Puno, 3960 m, Keel K-458 (NY); Chuquibambilla, 3850-3900 m, Pennell 13379 (F, GH); Yucay, Soukup 725 p.p. (F).

BOLIVIA. 1.5 km N of Ancoraimas, 3950 m, Lara & Parker 39-C (MO, NY).

The presence of blade bearing leaves in this variety requires comment since it is peculiar in, and actually an exception to, one of the main diagnostic features of the subg. Genuini. The blades are oval in cross section, laterally compressed but without sharp edges. They are linear with an aerenchymatous pith and may become as long as and twining like the culms. Presence of blades is a primitive feature in subg. Genuini, linking it to Poiophylli which always has blade bearing leaves. Juncus arcticus var. mexicanus is in all other respects well contained within the J. arcticus complex, and we should not be disturbed by the presence of this Poiophylli feature within Genuini. It only shows that biological taxa are not categorically defined - primitive features may well be retained in otherwise derived taxa.

FIGURE 45

- 45 A. The distribution of Juncus arcticus var. mexicanus in the neotropical region. In addition it occurs northwards into the Rocky Mountains, and southwards into the southern Andes.
- 45 B. The distribution of Juncus arcticus var. montanus in the neotropical region. In addition it occurs northwards into the Rocky Mountains.

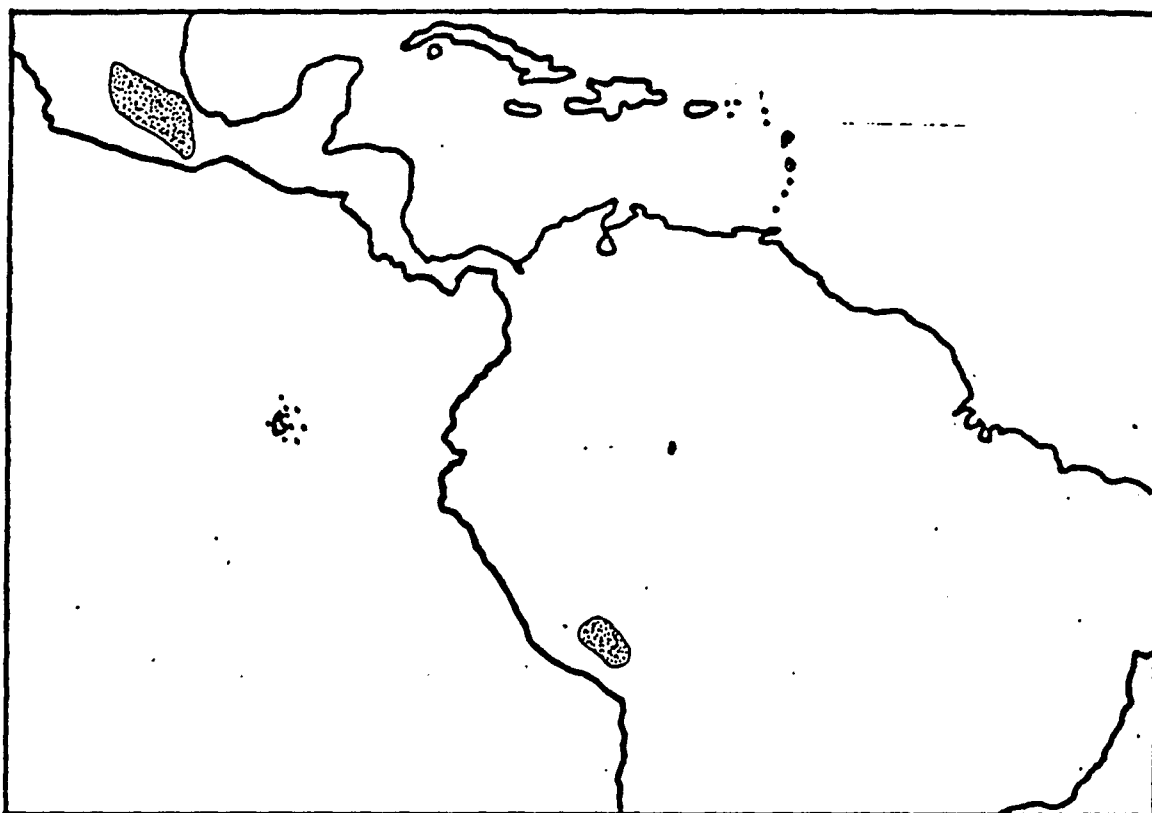


FIGURE 45 A.

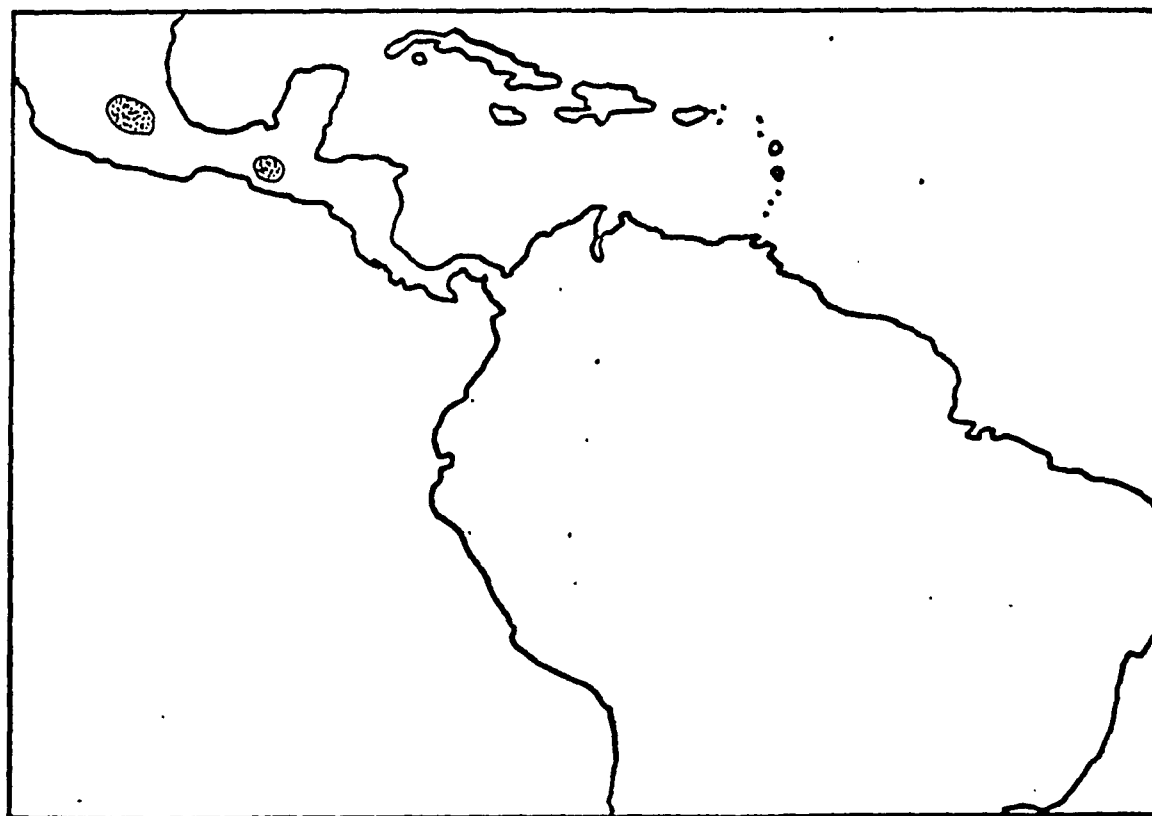


FIGURE 45 B.

15b. *Juncus arcticus* Willdenow var. *montanus* (Engelmann) Balslev, comb.

nov. Basionym. *Juncus balticus* var. *montanus* Engelmann.

Fig. 45 B.

Juncus balticus Willdenow var. *montanus* Engelmann, Trans. Acad.

Sci. St. Louis 2: 442. 1866. Type. No specimen cited.

Juncus balticus Willdenow var. *vallicola* Rydberg, Bull. Torrey

Bot. Club 31: 399. 1904. Type. USA. Wyoming: Point of Rocks, .

1901, Merrill & Wilcox 664 (holotype, NY).

Juncus ater Rydberg, Fl. Rocky mts. 1060. 1917 (1918). Basionym.

Juncus balticus Willdenow var. *montanus* Engelmann.

Juncus vallicola (Rydberg) Rydberg, *ibid.*

Juncus arcticus Willdenow subsp. *ater* (Rydberg) Hultén, Kongl.

Svenska Vetenskapsakad. Handl. IV, 8 (5): 24. 1962.

Juncus arcticus Willdenow subsp. *vallicola* (Rydberg) Lint. The

holotype of *J. balticus* var. *vallicola* Rydberg at NY is annota-

ted with this unpublished(?) name by Harold Lint in 1974.

Perennial herb, 40-120 cm high. Rhizome creeping, 3-7 mm diam.,
 plae brown with scattered thin membranaceous scales, internodes 1-3 cm
 long. Culms terete, 1.5-4 mm diam., not twisted. Blade-bearing
 absent. Inflorescence usually more than 20-flowered, 5-10 x 2-4 cm.
 Tepals 3.5-5 mm long, dark reddish brown with green or gray midrib,
 stramineous at fruit ripening. Stamens 1.5-2.5 mm long with 1.2-1.8
 mm long linear anthers. Style ca. 1 mm long. Stigmas ca. 2 mm long.
 Capsule ellipsoidal to ovoidal, apiculate, 3.5-4.5 mm long, shorter
 than or equalling the tepals.

Distribution. Western North America from Alaska to central México. From the Mexican collections of this variety no ecological information is available, but in the Intermountain region of western United States it grows in low, wet, often alkaline places, from the valleys and plains up to middle elevations in the mountains (Cronquist et al., 1977).

Specimens examined. MEXICO. México: Tlalnepantla, Rose et al. 8377 (NY); Valley of México, Schaffner 523 (MO). Puebla: Zacatepec, Fassett 22769 (MO, WIS), 29083 (WIS). Without locality: Wright 1720 (K).

GUATEMALA. Huehuetenango: Sierra de los Cuchumatanes, N of Tojiah, km 322 on Ruta Nacional 9N, 3200 m, Beaman 3924 (W).

This variety differs from var. mexicanus in usually being taller and more robust and in never having blade bearing leaves. Its flowers are similar to those of var. mexicanus, but the inflorescence is usually larger and with more flowers.

15c. *Juncus arcticus* Willdenow var. *andicola* (Hooker) Balslev, stat. nov.

Basionym. *Juncus andicola* W. J. Hooker.

Figs. 42 C, 46 A.

Juncus andicola W. J. Hooker, Icon. pl. Ser. 2.8, t. 714. 1848. Type.

Ecuador. Andes of Quito, Jameson 51 (holotype, K; isotypes, BM, G).

Juncus conceptionis Steudel, Syn. pl. glum. 2: 296. 1855. Type.

Chile. Concepción, Urville s.n., n.v.

Juncus Antonianus Steudel in Lechler, Berberid. Amer. austral. 56.

1857. Nom. nud. Original collection. Peru. San Antonio, Jun

1854, Lechler 1808 (G, GOET, K, MO, P).

Juncus deserticola Philippi, Florula Atacamensis 52. 1860. Syn-

types. Chile. Atacama desert, Cachinal de la Sierra 25° lat. m.,

7000 p.s.m., Philippi s.n., n.v.; Zorras 248' lat. m., 9600

p.s.m., Philippi s.n. (SGO, n.v.; photo at GH).

Juncus balticus Willdenow var. *crassiculmis* Buchenau in Grisebach,

Pl. lorentz. 219. 1874, also published in Abh. Königl. Ges. Wiss.

Göttingen 19: 267. 1874. Type. Argentina. Catamarca: in salsis

10000', Lorentz 448 (syntypes, GOET, W), remaining syntypes not

seen.

Juncus Antonianus Steudel ex Buchenau, Abh. Naturwiss. Vereine

Bremen 6: 383. 1879, nom. in syn. Original collection. Peru.

San Antonio, Jun 1854, Lechler 1808 (G, GOET, K, MO, P).

Juncus andicola W. J. Hooker var. *Schulz-Korthii* Macbride, Field

Mus. Nat. Hist., Bot. Ser. 11: 44. 1931. Type. Peru. Puno:

Pucará, 3600 m, Weberbauer 1367 (holotype destroyed at B; photo

at F).

Juncus crassiculmis (Buchenau) Herter, Rev. Sudamer. Bot. 6: 149.

1940.

Perennial herb, 20-170 cm high. Rhizome short- or long-creeping, 2.5-10 mm diam., pale yellow to brown, with thin membranaceous or thick somewhat hardened scales, internodes 1-4 mm long. Culms terete, 1-10 mm in diam., not twisted. Blade bearing leaves absent. Inflorescence with more than 20 and up to several hundred flowers, 2-15 x 2-10 cm. Tepals 3.5-5.5 mm long, dark reddish brown. Stamens 1.5-2.5 mm long with 0.7-2 mm long. linear anthers. Style 1-1.5 mm long. Stigmas 1-1.5 mm long. Capsule ellipsoidal to obovoidal, acute to truncate, apiculate, 2.5-5 mm long, equalling or shorter than the tepals.

Distribution. Along the Andes from Nariño in southern Colombia to Patagonia. A few collections from the state of México in México fit best here on morphological grounds, though the phytogeography of this mainly Andean variety becomes less distinct by accepting them here. This variety has been collected at altitudes between 2700 m and 4000 m. In Ecuador where I have seen it in the field, it is usually found in grazed páramos or in other places under human influence. A form in southern Peru and Bolivia usually grows at the margin of eutrophic ponds and little lakes.

Representative specimens. MEXICO. Mexico: Valle de Mexico, Lago Zempoala, Morelos, 3000 m, Matuda 25606 (NY). Puebla: Laguna Preciosa (=Laguna de las Minas), Dickerman 1045 (MIN).

COLOMBIA. Nariño: Mt Cumbal, Laguna Bolsa, 2740-2980 m, Ewan 16134 (NY, US).

ECUADOR. Carchi: Páramo El Angel, 28 km N of El Angel, 3400 m, Balslev & Quintana AAU-23904 (AAU, NY). Chimborazo: Panamerican Highway 20 km N of Riobamba, 3450 m, Balslev 1048 (NY). Cotopaxi: 8 km S of Cotopaxi railroad station on rd to Mt Cotopaxi, 3450 m, Balslev 1186 (NY). Pichincha: Quito-Papallacta rd, between Pifo and Páramo de Guamani, Balslev AAU-24182 (AAU, NY). Tungurahua: N slope of Mt Chimborazo at Ambato-Guaranda rd, 3900 m, Balslev 998 (NY). Zamora-Chinchipe: Loja-Zamora rd, km 15-16, 2700-2800 m, Balslev 1254 (NY).

PERU. Ancash: Recuay, Carpa-Pachacoto, 3450 m, López et al. 8330 (AAU, MO, NY). Arequipa: Nr Arequipa, Rose 18825 (NY, US). Cuzco: Calca, Hacienda Urco Calca, 2900 m, Vargas 2446 (BM, F, MO). Huanuco: Huanuco, summit of Mt Carpish, 2750 m, Luteyn & Lebrón-Luteyn 5484 (NY). Junín: Yauli, 4100 m, Asplund 11691 (B, S). La Libertad: Sánchez Carrión, Laguna Sausacocha, 3000 m, Sagástegui 9440 (MO, NY).

BOLIVIA. La Paz: Laguna Jacha Kkota ca. 8 km straight S of La Paz, 3750 m, Balslev 1141 (NY); Ingari, Huacullani, granja Cordepaz, 3840 m, Beck 2472 (LPB, NY); Murillo, Anchocalla nr La Paz, 3720 m, Beck 1883 (LPB, NY).

This variety exhibits much ecological variation. On the northern slopes of Mt. Cayambe in Ecuador I observed it growing in a gradient from loose humus rich soil towards the edge of a gravel road. Culms from the same clone correspondingly decreased in height from 170 cm to 30 cm, and in diameter from 5-6 mm to 1 mm. In southern Peru and Bolivia some very large specimens, from plants usually growing along the margins of ponds and little lakes with high nutrient content from cattle droppings,

seem to represent a genetically controlled variation. They have large flowers with ca. 5.5 mm long tepals and ca. 5 mm long capsules, but even if this is genetically controlled they are connected to the average form of this variety by all intermediates.

FIGURE 46

- 46 A. The distribution of Juncus arcticus var. andicola in the neotropical region. In addition it occurs southwards along the Andes until Patagonia.
- 46 B. The distribution of Juncus ramboi subsp. colombianus. The typical subsp. of J. ramboi occurs in southeastern Brasil.

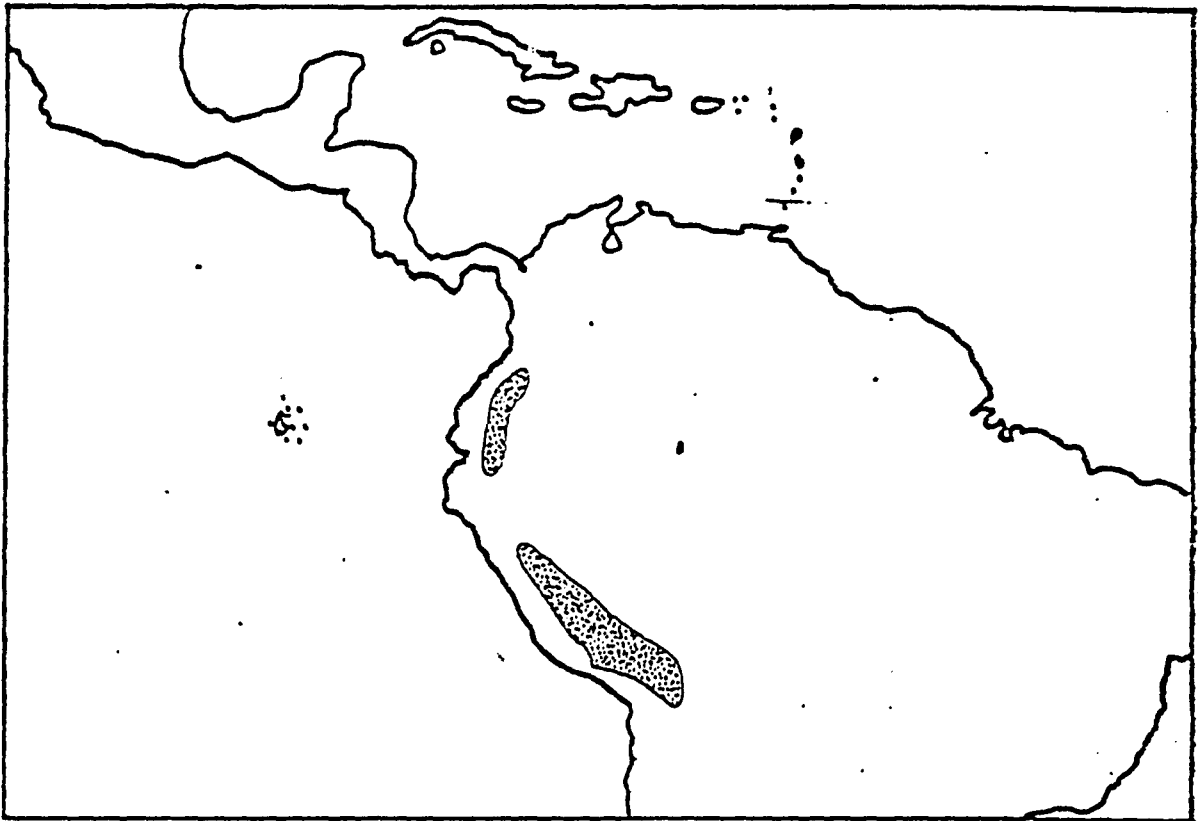


FIGURE 46 A.

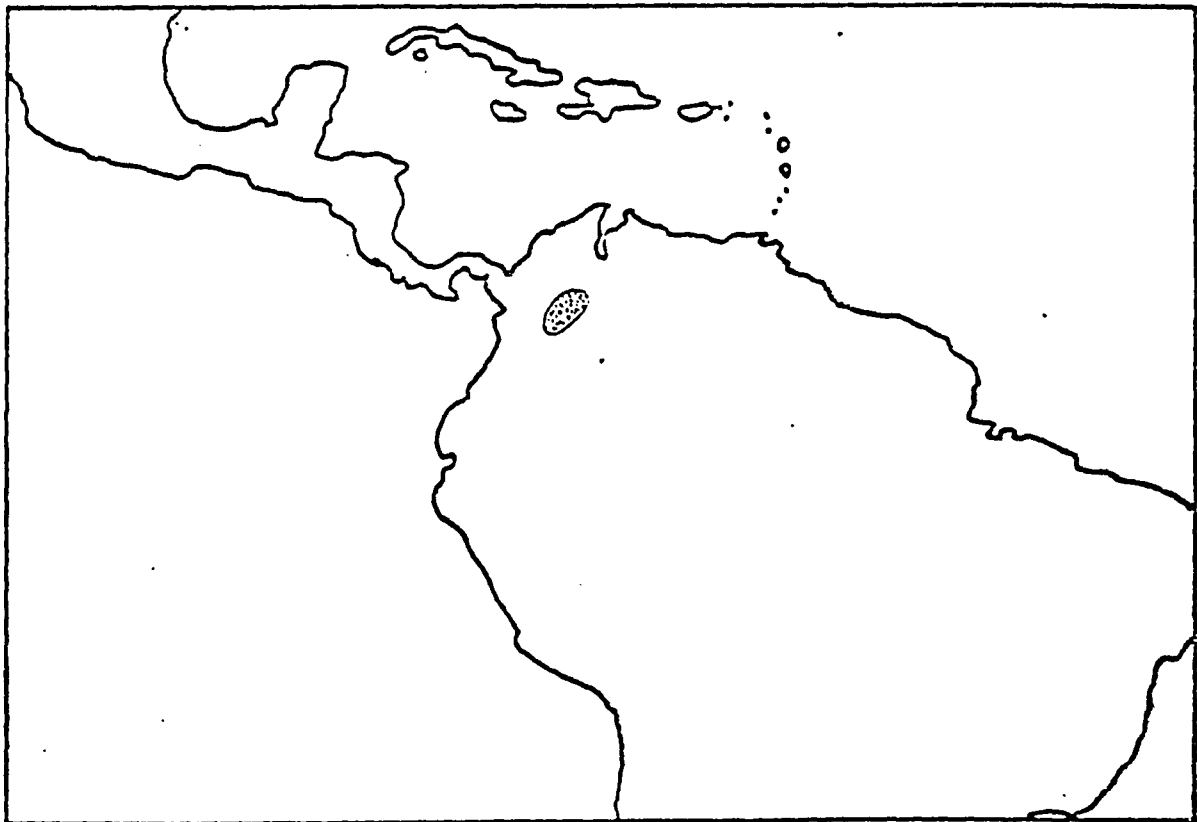


FIGURE 46 B.

16. *Juncus ramboi* Barros subsp. *colombianus* Balslev, subsp. nov. Type.

Colombia. Cundinamarca: Macizo de Bogotá, Quebrada de las Delicias, 2650-2770 m, 11 Jul 1939, Cuatrecasas 5437 (holotype, COL; isotypes, F, US). Figs. 46 B, 47.

Perennial densely caespitose herb, 20-30(-65) cm high. Rhizome creeping, ca. 2 mm in diam., densely branching, covered with stramineous or brown, to 5 mm long scales, internodes short and the culms arising densely crowded. Culms erect, 0.6-1.2 mm diam., equally thick from base to top, with 12-18 longitudinal ridges, pith continuous, parenchymatous. Blade bearing leaves absent. Cataphylls 3-4 to each culm, the uppermost and longest one to 4.5 cm long with an up to 4 mm long, needle like rudimentary blade, castaneous. Inflorescence pseudolateral, capitate, 10-20 flowered, composed of 2-4 densely crowded cymes. Lower inflorescence bract appearing as a continuation of the culm, 2-5 (-9) cm long, round in cross-section, upper bracts obtuse, membranaceous, ca. 1 mm long. Each flower clasped by two 1.5-2 mm long obtuse, castaneous or membranaceous bracteoles. Tepals subequal, lanceolate, acute, castaneous, often pale green along the midrib, turning stramineous, outer ones 3.5-4.5 mm long, concave, inner ones slightly smaller and flat or slightly concave. Stamens 6, 1.6-2 mm long; filaments flat, widened at the base; anthers linear, 0.5-0.8 mm long. Capsule ovoidal to obovoidal, round to trigonous in cross section, 2.5-3.5 x 1.5-2.2 mm, castaneous, sometimes pale brown basally, 3-septate. Seeds ellipsoidal or curved, apiculate, 0.5-0.6 x 0.2-0.3 mm, reticulate by longitudinal ridges and transverse lines, reddish brown below a hyaline outer seed coat.

Distribution. In the eastern cordillera of the northern Andes of Colombia in the departments of Boyacá and Cundinamarca. Grows in páramos at altitudes between 2650 m and 3200 m, on moss covered damp soil along quebrada (Langenheim 3644) or in 5 cm of water on open plateau (Galen Smith 1373).

Specimens examined. COLOMBIA. Without further locality: Mutis 6187 (US), 6190 (US). Boyacá: Páramo de Guantiva nr km marker 230 on rd between Belén and Susacón, 3200 m, Langenheim 3644 (US); Esparto, Pombo s.n. (COL). Cundinamarca: Alto de Páramo ca. 15 km NW of Zipaguira, 3200 m, Galen Smith 1373 (COL, F, GH, US).

Juncus ramboi is peculiar in having a parenchymatous, dense pith instead of aerenchymatous, loose pith of asteriform cells, which is usually found in subg. Genuini. It is also very distinct through the wiry, thin culms and the rigid castaneous flowers. The typical variety is known from only a handful of collections in Rio Grande do Sul and Santa Catarina in southeastern Brazil, where it grows in bogs, pastures, dry woods and brook banks at altitudes between 900 m and 1600 m. This new subsp. colombianus differs from the typical one in being smaller in all dimensions. The two taxa are both geographically restricted and quite far removed.

	subsp. <u>ramboi</u>	subsp. <u>colombianus</u>
Height	60-80 (-110) cm	20-30 (-65) cm
Culm diameter	0.9-1.2 mm	0.6-1.2 mm
Longest cataphyll	5.5-8.5 cm	4.5 cm
Flowers per inflorescence	20-40	10-20

FIGURE 47

Habit and detail of Juncus ramboi subsp. colombianus (Drawn from Cuatrecasas 5437, US).

- 47A. Habit showing the densely caespitose growth form.
- 47B. Single culm showing the basal sheathing cataphylls, the leafless culm, and the pseudolateral inflorescence.
- 47C. Inflorescence.
- 47D. Flower at fruiting stage.
- 47E. Capsule.
- 47F. Adaxial view of inner tepal and stamen.
- 47F. Adaxial view of outer tepal and stamen.

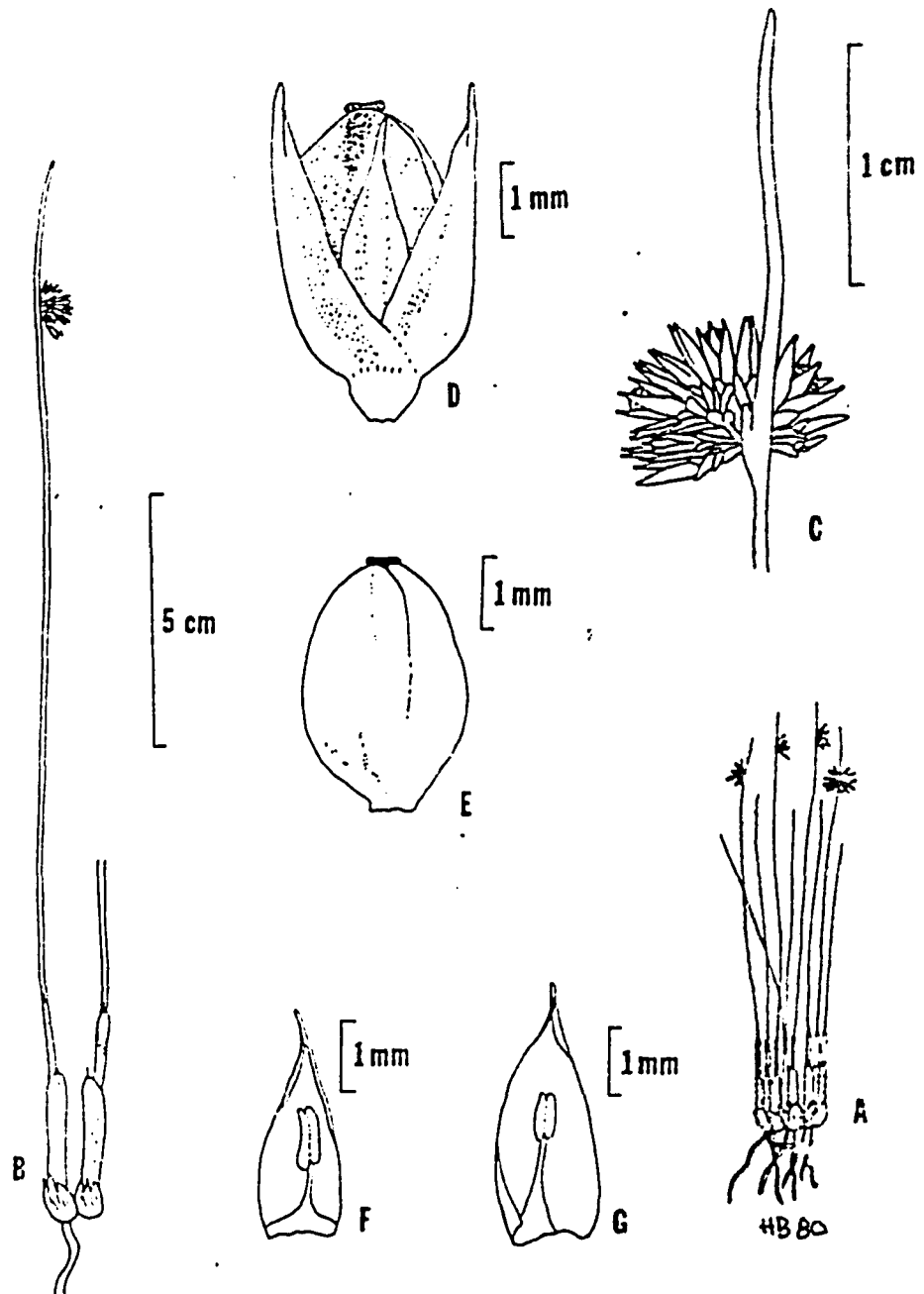


FIGURE 47.

Juncus subg. *Graminifolii* Buchenau, Abh. Naturwiss. Vereine Bremen

4: 407, 441. 1875. Type species. To be selected among the South African species treated by Buchenau (1875).

Cephaloxys Desvaux, J. Bot. (Desvaux) 1: 321. 1809. Type species. Cephaloxys flabellata Desvaux (= J. repens Michaux).

Perennial herbs to 100 cm high. Rhizome densely branching and the plants caespitose, or the rhizome loosely branching-ascending and the plants not caespitose, sometimes with long runners. Culms erect or ascending, terete or compressed, smooth. Leaves basal and cauline; sheaths auriculate and densely enveloping the culm or not auriculate and bending away from the culm; blade flat, not dorsiventrally differentiated. Inflorescence compound with the flowers congested into heads which are anthelately arranged, each flower originating in the axil of a floral bract, but without bracteoles on the pedicel.

Distribution. About 25 species. Most common in North America where nine species occur and in southern Africa where eight species occur. Australia and New Zealand have four species and the neotropical region has three species. Of the neotropical species one is strictly South American, J. cyperoides, and two are North American species extending into the tropical region, J. marginatus and J. repens. In temperate South America there is one species with Antarctic distribution, J. planifolius.

This subgenus is easily recognized by the flat (grass like !!) leaf blades, the cross section is equally thick throughout, and there is no obvious macroscopical dorsiventral differentiation. The inflorescence, in which the flower heads are anthelately arranged, and the lack of two bracteoles clasping each flower are furthermore characteristic features, but they are shared with the subgenera Septati and Ensifolii.

Key to the neotropical species of

Juncus subg. Graminifolii

1. Rhizome branching-ascending, gradually changing into the culm.
Leaves not in basal rosettes, all spaced along the length of the culm. 18. J. cyperoides.
1. Rhizome densely branching, culms arising in dense tufts. Leaves in dense basal rosettes, some also on the culms or in tufts along runners.
2. Small plants to 15 cm high, long runners with evenly spaced tufts of leaves often present. Capsule linear to lanceolate, trigonous. 19. J. repens.
2. Plants larger, 40-100 cm high, runners not present. Capsule broadly ellipsoidal, round in cross section. 17. J. marginatus.

17. Juncus marginatus Rostkovius, de lunc 38, t.2, f.3. 1801. Coville, Proc. Biol. Soc. Wash. 8: 121-128. 1893. Type. USA. Pennsylvania. Collector and specimen unknown, but the illustration of the protologue leaves no doubt about the identity of this name. Fig. 48 A.

Juncus triglumis Walter, Fl. Caroliniana 24: 1788, not Linnaeus (1753), not Weber (1780). Type. USA. Carolina: Collector unknown, n.v.

Juncus aristulatus Michaux, Fl. bor.-Am. 1: 192. 1803. Type. USA. in Georgia et Carolina (holotype, P). The holotype is marked 'Juncus aristatus' in Michaux's hand.

Juncus aristatus Persoon, Synops. pl. 1: 385. 1805. Orthographic error for J. aristulatus Michaux, but corresponding to Michaux's annotation of the holotype.

Luzula juncoides Poirer, Encycl. Suppl. 3: 535. 1813. Type. USA. croit a la Caroline, Bosc s.n. (holotype, P).

Juncus biflorus Elliot, Sketch bot. S. Carolina 1: 407. 1821. Type. USA. Georgia: ten miles from Savannah, on the road to Augusta, Elliot s.n. (holotype, n.v., the Juncaceae missing from Elliot's herbarium at CHARL and NY; isotype fragment, GH).

Juncus marginatus Rostkovius var. odoratus Torrey, Fl. N. & Middle U.S. 1: 362. 1824. Type. USA. New York: Bloomingdales woods, Torrey s.n. (a specimen at NY is probably the holotype).

Juncus triandrus Bosc ex Roemer & Schultes, Syst. veg. 7: 220. 1829. nom. in syn.

Juncus heteranthos Nuttall, Trans. Amer. Philos. Soc. (New Ser.)

5: 153. 1837. Type. USA. Arkansas: in the woods of Arkansas,
Nuttall s.n. (holotype lost, see Coville, 1893, p. 126).

Juncus cylindricus M. A. Curtis, Amer. J. Sci. Arts 44: 83.

1843. Type. USA. N. Carolina: Lincolnton, Curtis s.n.
(holotype, n.v.; isotype, NY).

Juncus canaliculatus Liebmann, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjøbenhavn 43. 1850. Type. México. Vera Cruz: S. Antonio Huatusco, Aug 1841, Liebmann 726 (holotype, C; isotypes, C, W fragment).

Juncus odoratus (Torrey) Steudel, Syn. pl. glum. 2: 304. 1855.

Juncus marginatus Rostkovius var. α vulgaris Engelmann, Trans.

Acad. Sci. St. Louis 2: 455. 1866. 'The common form', type
same as J. marginatus Rostkovius.

Juncus marginatus Rostkovius var. β biflorus (Elliot) Engelmann,
ibid.

Juncus marginatus Rostkovius var. γ paucicapitatus Engelmann,

ibid. Type. USA. New Jersey: Long Branch, C. W. Short s.n.,
(holotype, n.v., probably at MO; isotype, P).

Juncus marginatus Rostkovius var. setosus Coville, Proc. Biol.

Soc. Wash. 8: 124. 1893. Type. USA. Arizona: Santa Catalina
mountains, 4 Jun 1882, C. G. Pringle s.n. (holotype, US, n.v.;
isotypes, NY, P).

Juncus marginatus Rostkovius var. aristulatus (Michaux) Coville,

Proc. Biol. Soc. Wash. 8: 123. 1893.

Juncus Buchenavi Svedelius, Bih. Kongl. Svenska Vetensk.-Akad.

Handl. 23 (3): 6. 1897. Type. Brazil. Rio Grande do Sul:

Lindman 857 (holotype, S; isotypes, GH, W).

Juncus aristulatus Michaux var. pinetorum Coville in Small, Fl.

southeastern U.S. 259. 1903. Type. USA. in sandy pine woods from N. Carolina to Florida (no specimen cited in the protologue, several syntypes at K, NY, P).

Juncus setosus (Coville) Small, *ibid*, 248.

Juncus longii Fernald, *Rhodora* 39: 397. 1937. Type. USA.

Virginia: Sussex Co., Coddysore, 20 Jul 1936, Fernald & Long 6144 (holotype, GH; isotypes, NY, PH).

Perennial caespitose herb, 40-100 cm high. Rhizome short, densely branching, 2-4 mm diam. Culms sometimes basally bulbous, erect, slightly compressed, 0.5-3 mm diam., smooth. Cataphylls absent. Blade bearing leaves basal and cauline; basal ones 2-5 to each culm, sheaths to 9 cm long with the margins terminating in two 0.5-1(-3) mm long, rounded auricles, blade 10-30 x 0.1-0.5 cm, flat, usually with one abaxial and two adaxial nerves clearly visible, but otherwise without macroscopical bifacial differentiation; cauline leaves spaced along the culm, similar to basal leaves but progressively shorter upwards. Inflorescence compound, anthelate, 4-15 x 2-10 cm, principal branches to 10 cm long and 1 mm diam., upper ones shorter, the ultimate ones ca. 0.3 mm diam., flower heads (5-)10-40(-60), 5-7 mm diam., 3-5(-10) flowered, stramineous to dark brown. Lower inflorescence bract resembling cauline leaf, as long or shorter than the inflorescence, upper ones progressively

shorter, floral bracts lanceolate, acute, membranaceous, as long as or shorter than the flowers, bracteoles absent. Tepals unequal, outer ones 2-2.8(-3) mm long, shortest, lanceolate, apically obtuse to acute or sometimes shortly awned, concave, membranaceous towards the margin, inner ones 2.4-3 mm long, longest, lanceolate, apically obtuse to acute, with membranaceous margin inflexed to form a little cap when young, flat. Stamens 3, 1.2-2.2(-3) mm long; filaments linear, somewhat flattened; anthers oblong 0.4-1(-1.5) mm long, usually obviously shorter than the filaments but occasionally as long, dark reddish brown, robust in appearance, often protruding between the tepals after anthesis. Style ca. 0.1 mm long. Stigmas 0.5-1 mm long. Capsule about as long as the tepals, broadly ellipsoidal, round in cross section, 2-2.5 x 1.8-2 mm, dark brown with shiny surface, 3-septate, dehiscing apically, apiculate, the lobes becoming inflexed. Seeds narrowly and obliquely ellipsoidal, apiculate, 0.5-0.6 x 0.15-0.2 mm, with longitudinal ribs and transverse lines, yellowish brown.

Distribution. Widely distributed in eastern North America from Nova Scotia southwards to Florida and eastwards to Arizona. In Central America it occurs in the highlands of México and southwards to Honduras, and in the West Indies on Bermuda and western Cuba. In South America this species is represented by a single collection from the state of Sucre in Venezuela, and occurs in southeastern Brazil, in Uruguay, Argentina (Corrientes, Misiones) and Paraguay. It is found at low altitudes in temperate areas, but the Central American and Venezuelan collections were made between 1200 m and 2000 m altitude. It grows in wet places along ditches and streams.

Representative specimens. MEXICO. Chiapas: Tenejapa, Sibakte'el, 1800 m, Breedlove 14803 (NY); Teopisco, 1800 m, Breedlove 15069 (NY); 12 km N of Jitotol, 2000 m, Breedlove & Thorne 21445 (NY). Durango: Los Corralitos, 2100 m, Soule 2206 (MO). Jalisco: Río Blanco, Palmer 13 (NY). Oaxaca: Ayutla, Camp 2748 (NY). Vera Cruz: Swamps nr Jalapa, 1200 m, Pringle 8123 (MO, NY); Coatzacoalcos, Tehuantepec Isthmus, Smith 1121 (MO, NY).

GUATEMALA. Alta Verapaz: San Juan Chamelco, 1350 m, Standley 92445 (NY); Coban, 1350 m, Tuckerheim 3796 (ECON); nr Santa Cruz at San Cristobal rd, 1350 m, Standley 92844 (NY).

BELIZE. Cayo: San Luis-Cuevas rd at Macaw river, Dwyer 10754 (MO).

HONDURAS. Comayagua: Potrerillos S of Siguatepeque, Hazlett 1481 (MO). La Paz: Quebrada El Cerron 8 km from Marcala, 1500 m, Molina & Molina 24247 (MO, NY). Morazan: Zambrano-San Francisco de Soroguara rd, km 2.5, 1370 m, Davidse & Pohl 2241 (MO, NY).

CUBA. Las Villas: Vedado, Habana, Savanna of Manacas, León 5881 (GH, NY). Piñar de Río: Mateo Sancher, Ekman 17931 (NY, US); Herradura, Ekman 10782 (NY), 10833 (US). Santa Clara: Manacas, Ekman 17109 (NY, US).

VENEZUELA. Sucre: Mt Turumuquire between Ríos Manzanares and de Amana, 1900-2000 m, Steyermark 62700 (F, NY).

Engelmann (1866) divided Juncus marginatus into three varieties based on number of flower heads and the number of flowers in each head. Coville (1893) added characters of the seeds and also he divided this species into three varieties, though differently circumscribed than those of Engelmann. Small (1903) raised Coville's varieties to species rank,

but most recent North American floras have accepted two species, J. marginatus and J. biflorus, the former with two varieties, var. marginatus and var. setosus. Juncus biflorus is said to have many 2-3 flowered heads, and J. marginatus is said to have few 5-12 flowered heads; var. marginatus is said to have brown capsules and obtuse to acute tepals, var. setosus is said to have glossy capsules and aristate inner tepals. It has not been possible for me to arrange the neotropical and temperate South American material within that classification.

FIGURE 48

48 A. The distribution of Juncus marginatus in the neotropical region.

In addition it is widespread in temperate North America, and also occurs in temperate South America.

48 B. The distribution of Juncus repens in the neotropical region.

In addition it occurs along the North American east coast.

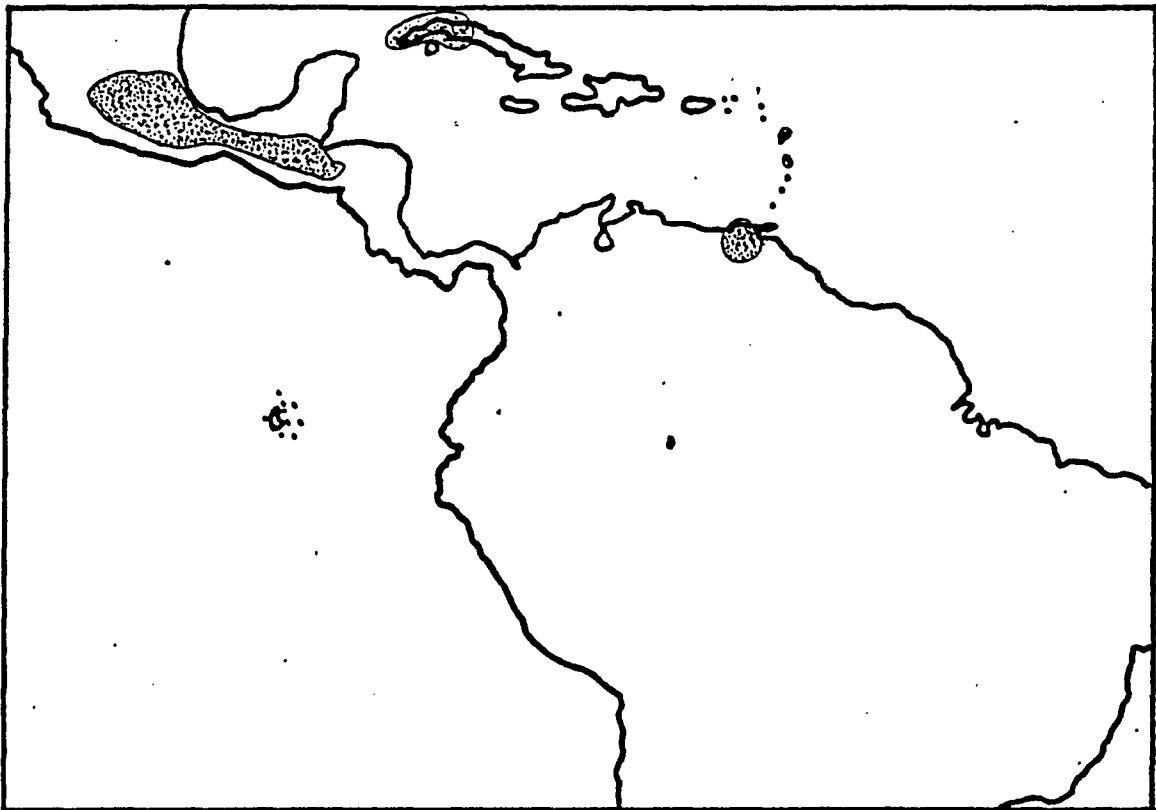


FIGURE 48 A.

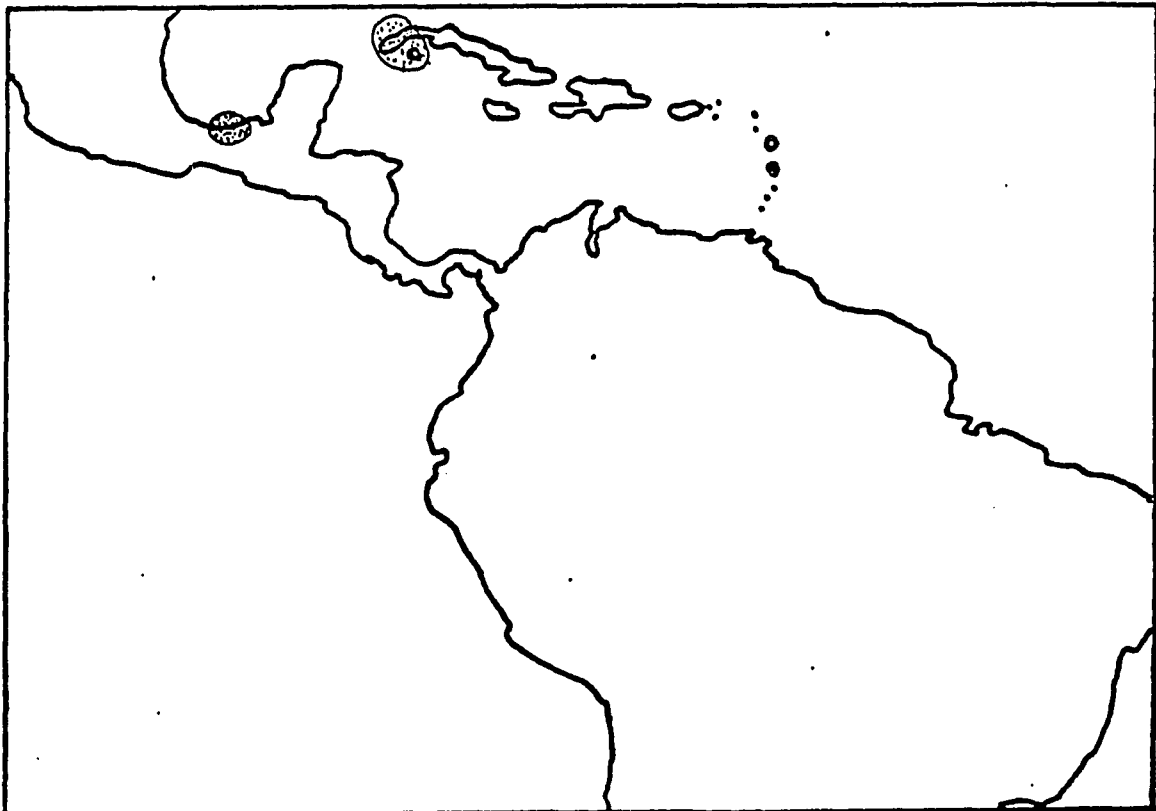


FIGURE 48 B.

18. *Juncus cyperoides* Laharpe, Essai monogr. jonc. 57. 1825, also published in Mem. Soc. Hist. Nat. Paris. 3: 145. 1827. Type. L'Amerique méridionale, Née s.n. (holotype, G). Figs. 49, 50 A.

Juncus graminifolius E. Meyer in Presl, Rel. Haenkeana 1: 144.

1827. Type. Peru. in montanis Peruviae Huanoccensis, Haenke s.n. (holotype among three sheets at W with Meyers handwriting).

Juncus rivularis Poeppig ex Kunth, Enum. pl. 3: 343. 1841, nom. in syn.

Cephaloxys graminifolia (E. Meyer) Nees & Meyen in Meyen, Reise um die Erde, Theil 4 (Beiträge zur Botanik): 128. 1843, also published as Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 16 Suppl. 2, which is at the same time vol. 19 Suppl. 1.

Perennial herb, 5-30 cm high. Rhizome creeping and branching ascending, gradually changing into the culm, 0.7-1.5 mm diam., internodes to 3 cm long, with up to 1.5 cm long membranaceous scales and protruding adventitious roots at the nodes. Cataphylls usually absent, or 1-3 to each culm, inconspicuous, membranaceous, 0.5-2 cm long, with rudimentary blade to 3 mm long. Blade bearing leaves 5-15 to each culm, separately and somewhat distantly inserted, sometimes somewhat clustered basally, linear, 3-12 x 0.1-0.7 cm, flat, without raised margins and therefore not bifacially differentiated; sheaths 0.5-3 cm long, not differing from the blade, upper parts with or without membranaceous margin, without auricles. Inflorescence anthelately compound of (1-)5-40 flower heads on delicate 0.2-0.3 mm thick branchlets; heads (3-)5-10 flowered, some-

FIGURE 49

Habit of Juncus cyperoides (Drawn from Holm-Nielsen et al. 4697,
AAU; from Balslev, 1979a).



Tind
FIGURE 49

5 cm.

times with viviparous shootlets. Lower inflorescence bracts resembling cauline leaves, to 9 cm long, upper ones progressively shorter, floral bracts membranaceous, to 5 mm long. Tepals linear to lanceolate, equal or subequal, 2.2-4(-5) mm long, green with narrow membranaceous margin, turning reddish brown and finally light brown, outer ones concave, inner ones flat. Stamens 6, 2-3 mm long; filaments filiform; anthers linear, 0.5-1 mm long, much shorter than the filaments. Style ca. 0.5 mm long. Stigmas 1.5-2 mm long. Capsule ellipsoidal, trigonous, 2-3.5 x 1-1.5 mm, with ca. 0.5 mm long beak, about as long as the tepals, thin walled, 3-septate. Seeds ellipsoidal, apiculate, 0.4 x 0.2 mm, reticulate, reddish brown, ca. 40 per capsule.

Distribution. Somewhat disjunctely distributed in the Andes. One area is in the northern Andes where it has been collected from Colombia to northern Peru at altitudes between 2000 m and 3700 m. According to A. Cleef (personal communication) it may be found up to + 4000 m in the eastern cordillera of Colombia, where 'it is present in all páramos...in bogs and in the bamboo páramo'. From southern Ecuador and northern Peru several collections were made in dry scrub or chaparral vegetation, though it was confined to occasional wet places. The other area is in the southern Andes where it is found in Chile and Argentina from Tucumán in the north to Aysen in the south. The ecology of the species in this southern area is similar to that in the northern Andes, but the altitudinal range is quite different. It may be found at sea level in southern Chile. The upper altitudinal limit depends

FIGURE 50

50 A. The distribution of Juncus cyperoides in the neotropical region.

In addition it occurs along the Andes southwards to Patagonia.

50 B. The distribution of Juncus microcephalus in the neotropical

region. In addition it occurs in temperate South America.

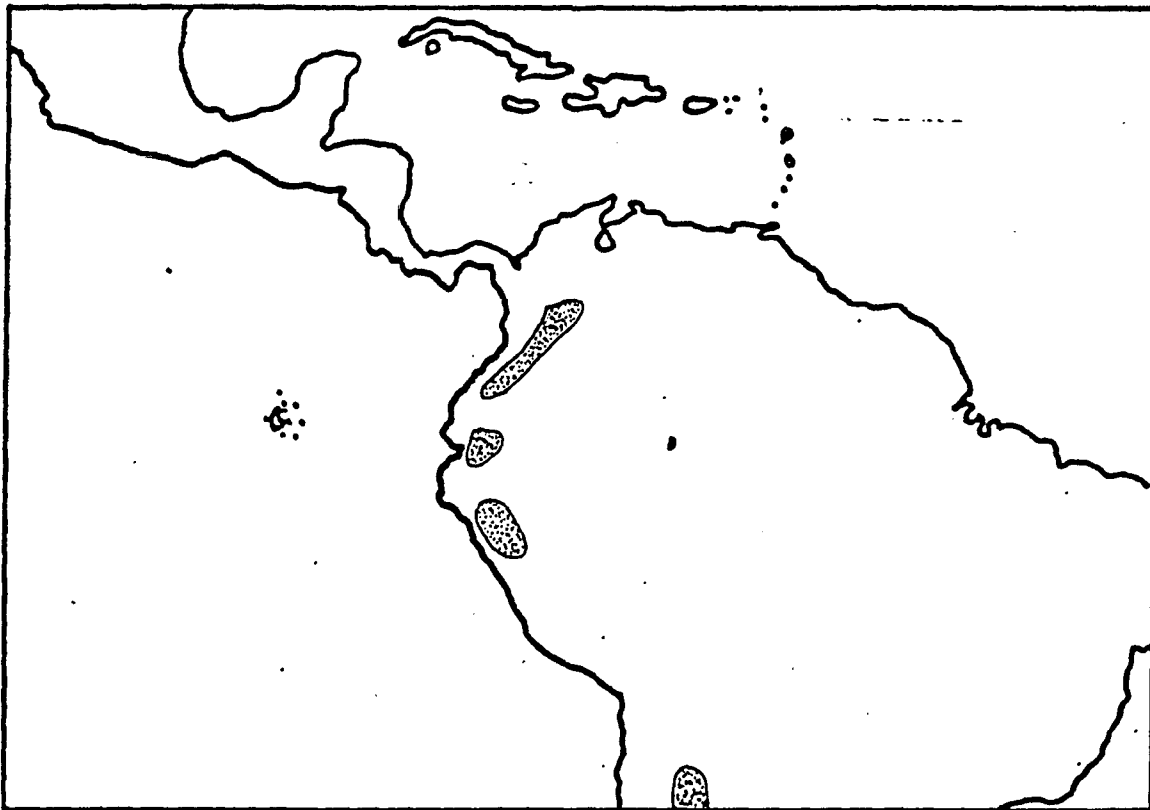


FIGURE 50 A.

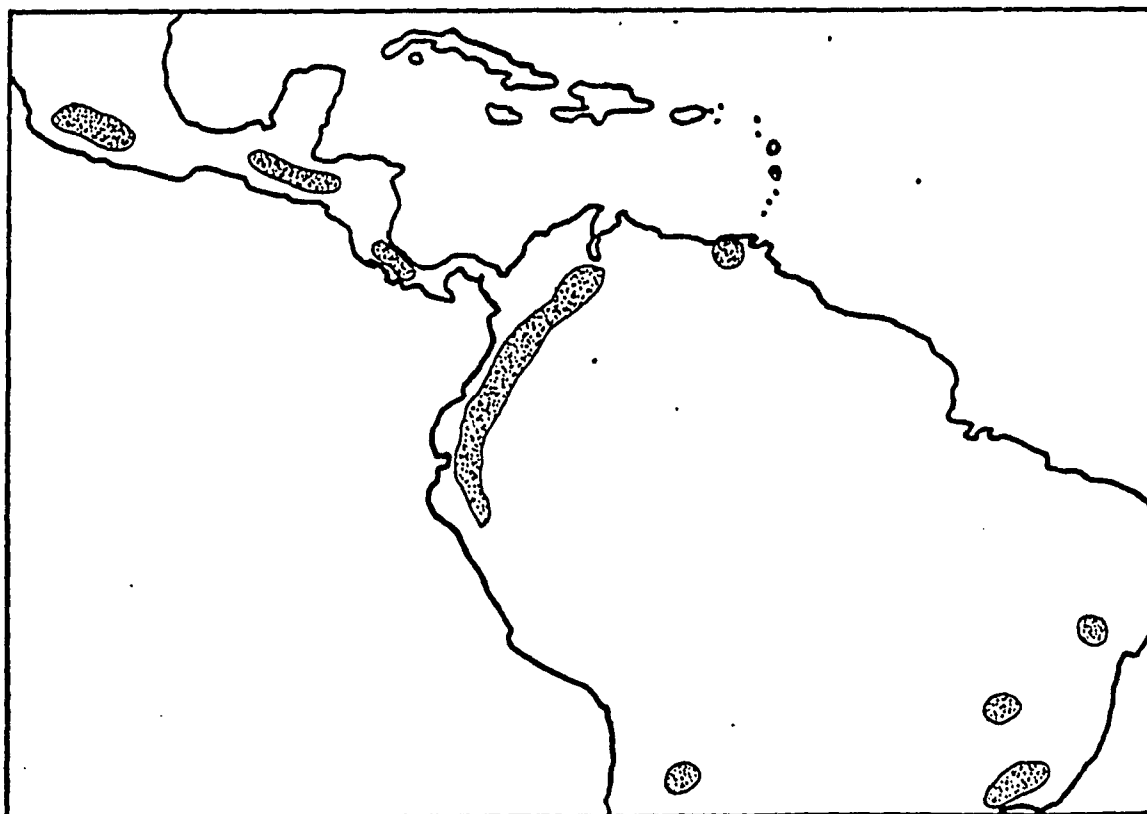


FIGURE 50 B.

on the latitude, reaching 3600 m in Tucumán. In this southern area it grows in bogs, meadows, swamps, ditches and other wet or humid places.

Specimens examined. COLOMBIA. Boyacá: Sierra Nevada del Cocuy, S of Laguna Cuadrada, 4060 m, Cleef 5578A (COL); Páramo de Pisva, Socha-La Punta rd, km 61.5, 3580 m, Cleef 4372A (COL), 4391A (COL), 4406A (COL), 4410A (COL), km 72, 3500 m, Cleef 4274 (U), 4278A (COL), 4285A (COL). Cauca: Silvia, Popayan, 2300-2600 m, Lehmann 8473 (GH, K); Mt Puracé, 3600-3700 m, Pennell & Killip 6547 (GH, NY, US); Coconuco, 2400 m, von Sneider 2080 (G, NY); Río Palo, La Tolda above Tacueyo, 2000 m, Cuatre-casas 19458 (GH, US). Cundinamarca: Páramo de Sumapaz, Alto Caicedo between Andabobos and Media Naranja, 3845 m, Cleef 4824B (COL); Chisaca, Río S. Rosa ca. 1 km S of Laguna Larga, 3660 m, Cleef 5187 (AAU, P); Quebrada Chuza between Páramos Palacio and Chingaza, 3640 m, Cleef & Florschütz 5476 (P, U). Meta: Páramo de Sumapaz, Laguna la Guitarra, 3450 m, Cleef 871A (COL).

ECUADOR. Azuay: Sevilla de Oro, 2500 m, Harling 1160 (S); Sayausí, 3100-3300 m, Harling et al. 8385 (GB); 10-15 km W of Sayausí, 3200-3400 m, Balslev 1567 (NY); Soldados-Hacienda San Vicente, 3200-3300 m, Balslev 1554 (NY); Laguna Zurrucuchu, 3650 m, Prescott 779 (NY); Nudo de Portete, 2750 m, Camp E-2113 (AAU, NY, S); Panamerican Highway 37 km S of Cuenca, 3200 m, Balslev 1233 (NY), 82 km S of Cuenca, 3000 m, Balslev 1239 (NY). Cañar: El Gun, 3000 m, Acosta Solis 21335 (US), 21353 (US); San Marcos 5-8 km NE of Azogues, Camp & Prieto E-2627 (AAU, NY, S); El Tambo, 3000 m, Camp E-3983 (AAU, NY, S); El Triunfo-Cañar rd, 5 km W of Suscal, 2700 m, Balslev 1197 (NY); Panamerican

Highway at highest point between Cañar and Biblian, 3500 m, Balslev 1202 (NY); ca. 10 km N of Biblián, 3000 m, Balslev 1212 (NY). Carchi: El Pun-Tulcán, 3000 m, Asplund 16894 (G, K, NY, S, US). Chimborazo: Chunchi-Sibambe, 2200 m, Fagerlind & Wibom 753 (S). Loja: Loma de Oro, 10 km S of Saraguro, 3000-3200 m, Balslev 1366 (NY), Barclay & Juajibioy 8535 (US); 10 km N of Loja, 2000 m, Balslev 1351 (NY); 51 km N of Loja, 2900 m, Holm-Nielsen et al. 4697 (AAU, NY, S); Loja-Malacatos rd, km 13-15, 2100-2200 m, Balslev 1318 (NY). Zamora-Chinchipe: Loja-Zamora rd, km 15-16, 2700-2800 m, Sparre 16511 (S), Balslev 1250 (NY).

PERU. Ancash: Monserrate, 3100 m, Ferreyra s.n. (USM). Cajamarca: Hualgayoc, Llapa, 2200 m, Muños 1016 (USM); Sunchubamba, 3680 m, Ellenberg 1856 (U). Huánuco, Carpish, 2800 m, Asplund 12751 (G), 12887 (US). Junín: Mito, 2750 m, MacBride 3319 (F). La Libertad: Huamachuco, Río Munmalka, Hacienda Cochabamba, 3200 m, Lopes Miranda 1483 (NY, US).

19. *Juncus repens* Michaux, Fl. bor.-Am. 1: 191. 1803. Type. USA.

Hab. in Carolina et Georgia (holotype, P; isotype, P). Fig. 48 B.

Cephaloxys flabellata Desvaux, J. Bot. (Desvaux) 1: 324. 1809.

Basionym. Juncus repens Michaux.

Juncus subincurvus Steudel, Syn. pl. glum. 2: 303. 1855. Type.

USA. Louisiana, Hartmann 86 (holotype, P; isotype, P).

Perennial heteromorphic herb. One form is caespitose, 5-15 cm high with one to several short erect culms bearing 1-4(-8) flower heads, another form is prostrate with the creeping stems rooting and producing leaf rosettes 5-10 cm apart, and a third form is floating with leaf rosettes evenly spaced along the stems. Rhizome absent in prostrate plants, weakly developed, densely branching and 0.5-1.5 mm diam. in caespitose plants. Culms flattened 0.8-2 mm diam., smooth shorter than the rosette leaves, creeping and floating stems 1.5-2.5 mm diam. to 50 cm long with 5-10 cm long internodes. Blade bearing leaves in tufted rosettes, 2-15 x 0.1-0.4 cm, flat; sheaths 0.5-1.5 cm long, not obviously different from the blade, margin membranaceous, terminating in two 0.5 mm long rounded auricles. Inflorescence consisting of one terminal flower head that does not reach above the leaves, or of up to eight flower heads in anthelate arrangement that do reach above the leaves, flower heads conical to hemispherical, 7-13(-20) mm diam., 2-20-flowered. Lower inflorescence bracts resembling basal leaves, upper ones progressively shorter, floral bracts broadly lanceolate, mucronate, 1-2 mm long, bracteoles absent. Tepals unequal, green, sometimes reddish apically or throughout, outer ones 2.8-4.2 mm long, concave, membranaceous

towards the margin, inner ones distinctly longer, (3.5-)4-5 mm, flat, subulate, with distinct narrow involute membranaceous margin. Stamens 3, 2-3 mm long, opposite outer tepals; filaments delicately filiform, hyaline; anthers 0.3-1 mm, first linear and as long as the filaments, after anthesis shrivelling to 1/7 of filament length. Style ca. 0.2 mm long. Stigmas ca. 0.4 mm long. Capsule linear to lanceolate, apically truncate or three-keeled and retuse, trigonous, 2.5-3.5 x 0.7-1.1 mm, as long as or longer than outer tepals but shorter than inner tepals, basally thin walled and hyaline, apically thicker and stramineous or golden brown, trilocular with central columellar placentation and ascending ovules. Seeds oblique, ovoidal, apiculate, ca. 0.3 x 0.15 mm, finely rugose, reddish brown or whitish, 100 or more per capsule.

Distribution. In eastern United States from Delaware to Florida, westwards to Texas and inland to Oklahoma, Tennessee and Arkansas. Disjunct in lower California according to Small (1903, p. 258), on Cuba in the western province of Piñar del Río and on Isla de Pinos, and in Tabasco in México. It grows in muddy or sandy loam soils at the margin of fresh water and Cypress gum ponds, lakes, in swamps and bogs, and often in pine woods or pine barrens. On Cuba it has been collected in dried out stream beds.

Specimens examined. MEXICO. Tabasco: 10-40 km W of Huimanguillo, Barlow 30/138 (BM, WIS).

CUBA. Isle of Pines: San Pedro and vicinity, Britton & Wilson 14719 (NY); Santa Ana, Laguna Blanca, Britton & Wilson 15686 (NY);

Nueva Gerona, Jan 1904, Curtiss s.n. (NY). Piñar del Río: Lagoon
Jovero, León 15385 (NY); Herradura, sandy pine barrens, Ekman 10733
(NY), 10808 (NY); Coloma, Britton & Cowell 9677 (NY).

The morphological variation and anatomy of Juncus repens were described in some detail by Holm (1899). The growth is correlated to the nature of the habitat. When submerged it produces long shoots with long internodes and leaf rosettes at the nodes. In shallow water the long shoots may root at the nodes. When growing above the waterline it attains a tufted habit. Intermediate forms are often found.

Juncus subg. *Septati* Buchenau, Abh. Naturwiss. Vereine Bremen 4: 406.

1875. Type species. To be selected among the South African species treated by Buchenau (1875).

Juncus sectio *Ozophyllum* Dumortier, Fl. belg. 142. 1827.

Juncus sectio *Steirochloa* Grisebach, Spic. fl. rumel. 2: 407.

1845. pro parte.

Juncus subg. *Ozophyllum* (Dumortier) Kuntze in Post & Kuntze,

Lex. gen. phan. 303. 1904.

Juncus sectio *Septati* (Buchenau) Vierhapper in Engler & Prantl,

Nat. Pflanzenfam. 2 ed. 15a: 217. 1930.

Perennial herbs to 150 cm high. Rhizome creeping and the culms arising in rows, densely branched and the culms arising in clusters, or loosely branching-ascending and gradually changing into the culms. Culms erect, terete or slightly compressed, smooth. Leaves basal and cauline, blades linear, round to elliptical in cross section, tubular with an empty pith interrupted by septate partitions. Inflorescence compound and decompound, the flowers in one to many heads which are anthelately arranged, heads 3-50 flowered, each flower originating in the axil of a floral bract, but without bracteoles on the pedicel.

Distribution. Subg. *Septati* is the largest in *Juncus* with well over 80 species. It is distributed in all continents except Antarctica. The neotropical species are derived from several North American and south temperate species groups.

Subg. Septati is easily recognized by the round, hollow, and septate leaf blades. In fresh material the septa are not always easily visible on the outside, but they are easily revealed if the blade is pulled between two fingers. In dry condition the blades usually appear nodulated because of the septa. In very small species, such as Juncus stipulatus, the septa may be difficult to detect. The inflorescence of subg. Septati is similar to that of the subgenera Graminifolii and Ensifolii. It is composed of flower heads which are arranged in an anthela, and the flowers are without bracteoles on the pedicels. This feature holds these three subgenera together, and they must be distinguished by the structure of their leaf blades.

Key to the neotropical species of

Juncus subg. Septati

1. Rhizome stoloniferous and/or ascending branching.
 2. Plants 1-10 cm high. Leaves 1-8 cm long. Inflorescence of one or rarely two 2-5 flowered heads. Rhizome with branching, ascending part (Andes). 28. J. stipulatus.
 2. Plants 10-30 cm high, rarely only 5 cm. Leaves 4-25 cm long. Inflorescence of 2-8 semiglobose to globose (5-)10-20(-30) flowered heads. Rhizome without branching, ascending part (North to Central America and central Andes).
 3. Rhizome with bulbous thickenings at base of culms. Tepals subulate, rigid, light green to stramineous. Capsule 3-4.7 mm long with 0.5 mm long beak. 32. J. nodosus.
 3. Rhizome without bulbous thickening at base of culms. Tepals acute, flexuose, usually castaneous to reddish brown. Capsule 3-4 mm long with 1-2 mm long beak. 30. J. ebracteatus.
1. Rhizome short creeping or densely branching.
 4. Rhizome short creeping, horizontal. Cataphylls present and usually conspicuous.
 5. Inflorescence of 1-2 compound racemes with the ultimate branchlets terminated by 2-3 flowered clusters. Tepals acute flexuose. 29. J. liebmannii.
 5. Inflorescence with the flowers congested into obvious heads, each with usually more than 10 flowers. Tepals subulate, rigid.

6. Rhizome with bulbous thickening at base of culms.

32. J. nodosus.

6. Rhizome without bulbous thickening at base of culms.

7. Flower heads dark reddish brown or castaneous.

8. Inflorescence 1-2 headed (northern Andes).

34. J. echinocephalus.

8. Inflorescence 5-50 headed (southeastern Brasil).

35. J. ustulatus.

7. Flower heads stramineous or rarely reddish brown.

9. Plants 65-135 cm high with the rhizome 3-8 mm diam.

and less than twice as thick as the culm. Outer
tepals usually longest and the capsule shorter than
these.

33. J. densiflorus.

9. Plants 50-85 cm high with the rhizome 4-9 mm diam.

and more than twice as thick as the culm. Inner
and outer tepals usually equally long and the cap-
sule longer than these.

31. J. micranthus.

4. Rhizome densely branching. Cataphylls absent or inconspicuous.

10. Capsule longer than the tepals (J. micranthus and J. nodosus
keyed out above also have capsules longer than tepals).

11. Capsule acute or acuminate.

12. Capsule 4-6 mm long. Plants to 150 cm high (Gua-
deloupe).

25. J. guadeloupensis.

12. Capsule ca. 3 mm long. Plants 15-50 cm high

(Mexico and North America).

27. J. debilis.

11. Capsule extended into a 1-2 mm long beak.

30. J. ebracteatus.

10. Capsule as long as or shorter than the tepals.

13. Plants less than 10 cm high.

14. Rhizome branching ascending. 28. J. stipulatus.

14. Rhizome densely branching.

15. Lower inflorescence bract much overtopping
the inflorescence. 24. J. breviculmis.

15. Lower inflorescence bract about as long as the
inflorescence. 26. J. achalensis.

13. Plants more than 10 cm high.

16. Inflorescence of 1-2 compound racemes with the
ultimate branchlets terminated by 2-3 flowered
clusters. 29. J. liebmanni.

16. Inflorescence with the flowers congested into globo-
se or semiglobose heads, each with usually more than
ten flowers.

17. Culm shorter than the blade bearing leaves.
Lower inflorescence bract much overtopping the
inflorescence. 24. J. breviculmis.

17. Culm longer than the blade bearing leaves.
Lower inflorescence bract shorter than the in-
florescence or rarely slightly overtopping it.

18. Plants less than 20 cm high. Inflorescence
of 1-2 flower heads. Lower inflorescence
bract scale-like, ca. 1 cm long.

26. J. achalensis

18. Plants more than 20 cm high. Inflorescence
of 3-100 flower heads, rarely only one.

Lower inflorescence bract resembling a small cauline leaf, 1-20 cm long.

19. Seeds 0.7-0.9 mm long. Capsule 2.9-4.4 mm long. 23. J. ecuadoriensis.

19. Seeds to 0.5 mm long. Capsule 2-3.5 mm long.

20. Ultimate head bearing branches more than 0.45 mm diam. Flower heads relatively few, usually less than seven. Tepals thick and rigid (Andes). 21. J. pallescens.

20. Ultimate head bearing branches less than 0.4 mm diam. Flower heads relatively numerous, usually more than ten. Tepals thin (North and South America).

21. Stamens 3, rarely 6 (North America southwards to Honduras).

22. J. acuminatus.

21. Stamens 6, rarely 3 (South America to central Mexico).

20. J. microcephalus.

20. *Juncus microcephalus* Humboldt, Bonpland & Kunth, Nov. gen. sp.

1: 237. 1816. Type. Colombia. Quindio, Humboldt & Bonpland s.n.

(holotype, P; isotypes, B, GH, MO fragment). Figs. 50 B, 51 C-D.

Juncus floribundus Humboldt, Bonpland & Kunth, *ibid.* Type.

Venezuela. sylvarum Orinocensium, juxta Esmeraldam, Humboldt & Bonpland s.n. (holotype, P; isotypes, B, MO fragment, P). Type-locality doubtful, the specimen probably originates in Colombia and is mislabelled.

Juncus dichotomus Willdenow ex E. Meyer, Synops. Luzularum 30.

1823. Pro syn. Willdenow's herbarium name on the isotype of *J. microcephalus* H.B.K. at B.

Juncus microcephalus Humboldt, Bonpland & Kunth var. major

Roemer & Schultes, Syst. veg. 7: 195. 1829. Type. Same as for *J. floribundus* H.B.K.

Juncus microcephalus Humboldt, Bonpland & Kunth var. intermedius

Meyer in Roemer & Schultes, *ibid.* Type. Not cited in protologue, but reference given to 'Mart. Fl. brasil. ined.', which, when published in 1847, cited a specimen from 'Villa Rica provincia Minarum', that I have not seen.

Juncus microcephalus Humboldt, Bonpland & Kunth var. floribundus

(Humboldt, Bonpland & Kunth) Kunth, Enum. pl. 3: 324. 1841.

Juncus rudis Kunth, *ibid.*, 333. Type. Brazil. São Paulo, Sellow

s.n. (holotype, destroyed at B; isotype fragment, MO).

Juncus sellowianus Kunth, *ibid.*, 336. Type. Brazil. Brasilia

meridionalis, Sellow s.n. (holotype, destroyed at B; isotype fragment, MO).

Juncus luzuloxiphium Grisebach, Pl. lorentz. 220. 1874, also published in Abh. Königl. Ges. Wiss. Göttingen 19: 268. 1874.

Type. Argentina. Cienaga, 31 Mar 1872, Lorentz 96 (holotype, GOET).

Juncus microcephalus Humboldt, Bonpland & Kunth var. typicus

Buchenau, Abh. Naturwiss. Vereine Bremen 6: 408. 1879. Basionym. Juncus microcephalus Humboldt, Bonpland & Kunth.

Juncus microcephalus Humboldt, Bonpland & Kunth var. virens

Grisebach, Symb. fl. argent. 317. 1879, also published in Abh. Königl. Ges. Wiss. Göttingen 24 (1): 317. 1879. Type. Argentina. Quebrada de Tala, Nov 1872, Lorentz & Hieronymus 444 (holotype, GOET).

Perennial caespitose herb, 20-100 cm high. Rhizome densely branching, 1-4 mm diam., with few thin membranaceous scales. Culms erect, 0.5-4 mm diam., terete, smooth or striate. Cataphylls 0-2 to each culm, to 15 cm long, green or reddish tinged, with distinct membranaceous margin. Blade bearing leaves 1-3 basal and 1-2 cauline to each culm, (5-)10-50 cm long; sheaths (1.5-)5-15 cm long, with membranaceous margins terminating in two 0.5-5 mm long rounded auricles; blades 0.7-4 mm diam., round to elliptical in cross-section, conspicuously septate, sometimes with obvious adaxial groove basally. Inflorescence decompound, anthelate, (3-)5-20(-30) x (1.5-)3-10(-15) cm, flower heads (3-)7-50(-100), conical to globose, 5-10 mm diam., (3-)10-35 flowered, stramineous or brown, ultimate head bearing branches less than 0.4 mm diam. Lower inflorescence bract to 5(-9) cm long, much shorter than the inflorescence, scale like with reduced blade but occasionally resembling a small basal leaf with a well developed blade, upper bracts progressively shorter, floral bracts acuminate, ca. 3 mm long, membranaceous, usually not contrasting tepal color. Tepals

subequal, 1-3.5(-5) mm long, lanceolate, acute, outer ones concave and membranaceous towards the margin, inner ones flat with distinct membranaceous margin. Stamens 6 or 3, 1-2 mm long; filaments flat, linear; anthers oblong to linear, 0.3-0.7 mm long, or about half as long as the filaments. Capsule ellipsoidal to obovoidal, obtuse to bluntly acute and shortly mucronate, 3-lobed to trigonous, 2-3.5 x 1-1.5 mm, stramineous to brown or almost black, unilocular. Seeds ellipsoidal, apiculate, 0.4-0.5 x ca. 0.2 mm, reticulate, yellowish brown with a hyaline outer seed coat.

Distribution. Throughout the highlands of the neotropical region, from central México in the north to Bolivia and southeastern Brazil in the south. In the Andes it is apparently somewhat displaced by Juncus palleescens from central Peru and southwards.

Representative specimens. MEXICO. Chiapas: Pueblo Nuevo Solistahuacán, 1700 m, Breedlove & Thorne 21530 (MO). Jalisco: Río Grande de Santiago nr Atequiza, Pringle 3131 (MO, NY). México: San Felipe, Cunatitlan, Mitastein 108 (WIS). Morelos: Cuernavaca, 2000 m, Pringle 6509 (MO, NY).

HONDURAS. Comayagua: 12 km E of Siguatepeque, 1350 m, Davidse 2232 (MO, NY). Morazan: Mt Uyuca, 1500 m, Molina 12797 (NY). Ocotopeque: El Moral on Cordillera Merendón, 1600 m, Molina 22255 (NY).

COSTA RICA. Hereida: 12.5 km NE of Varxa Blanca, 2200 m, Davidse & Pohl 893 (MO).

PANAMA. Chiriquí: Dos Lagunas rd, 2 km W of El Hato del Volcán, 1300 m, Mori & Bolten 7389 (MO).

COLOMBIA. Antioquia: Monte del Diablo (La Ceja), Daniel 3306 (US). Boyacá: Paipa, 2550 m, Fassett 25900 (US). Cundinamarca: SW of Las Cuces, Bogotá, 2600-2700 m, Pennell 2134 (GH, NY). Norte de Santander: Río Chitaga, Vega Colombia, 2880-3000 m, Cuetre Casas et al. 10067 (F). Putumayo: Valle de Sibundoy, 2-5 km N of San Pedro, 2250-2700 m, Chindoy 172 (GH). Santander: Mesa de los Santos, 1500 m, Killip & Smith 15173 (GH, NY).

VENEZUELA. Sucre: Valley between Mt Diablo and Mt Neverí, 2000 m, Steyermark 62722 (F). Táchira: SW side of Páramo de Tamá to La Linea, 3100-3200 m, Luteyn et al. 5878 (NY). Trujillo: Below Páramo de Guaramacal between Boconó and Guaramacal, 2800 m, Steyermark 104792 (U). ECUADOR. Azuay: 10-15 km W of Sayausí (W of Cuenca), 3200-3400 m, Balslev 1569 (NY). Cañar: El Tirufo-Cañar rd nr Rodeo, 1800 m, Balslev 1191 (NY). Carchi: Playón de San Francisco-J. Andrade rd, km 2, 3050-3150 m, Løjtnant et al. 12450 (AAU). Loja: Loja-Malacatos rd, km 13-15, 2100-2200 m, Balslev 1312 (NY). Napo: Cordillera de Huancamayos on Tena-Baeza rd, 2000 m, Balslev 1603 (NY). Pichincha: Old rd Quito-Sto. Domingo 23-27 km W of Chillogallo, 2800-3100 m, Balslev 1657 (NY). Zamora-Chinchipe: Zamora-Loja rd, km 1, 1200 m, Balslev 1269 (NY).

PERU. Amazonas: Murica, Cevasco s.n. (USM). Chachapoyas: Mt Calla Calla 18 km above Leimebamba on rd to Balsas, 3100 m, Hutchinson & Wright 5697 (F, G, K, M, MO, NY, P, US, USM). Without department: Sunchubamba, 3680 m, Ellenberg 1855 (U).

BRAZIL. Bahia: Serra de Agua de Rega, Seabre-Agua de Rega rd, km 27, 1000 m, Irwin et al. 31012 (F, NY). Distr. Federal: Nr Sobre-dinho, Prance et al. 59078 (F, NY, S). Goias: Serra dos Cristais, 6 km S of Cristalina, 1175 m, Irwin et al. 9749 (NY). Minas Gerais: Serra do Espinhaco, Pico de Itacolom, ca. 3 km S of Ouro Preto, 1650 m, Irwin et al. 29620 (F, NY). Rio de Janeiro: Mt Itatiaia, Monte Serrat-Ponte Maromba rd, Estacao Biologica, 800-1200 m, Smith 1613 (F, NY). São Paulo: Reserva Carlos Botelho, between São Miguel Arcanje and Sete Barras, 800 m, Prance et al. 6911 (NY).

BOLIVIA. Tarija, Fries 1259a (S, US). Calderillo, Fiebrig 2884 (F).

PARAGUAY. San Pedro: Alto Paraguay, Primavera, Woolston 602 (NY).

FIGURE 51

Habit and details of Juncus pallescens and J. microcephalus (From Balslev, 1979a).

51A. Habit of J. pallescens (Drawn from Sparre 15080, S).

51B. Detail of same.

51C. Habit of J. microcephalus (Drawn from Harling et al. 10408, GB).

51D. Detail of same.

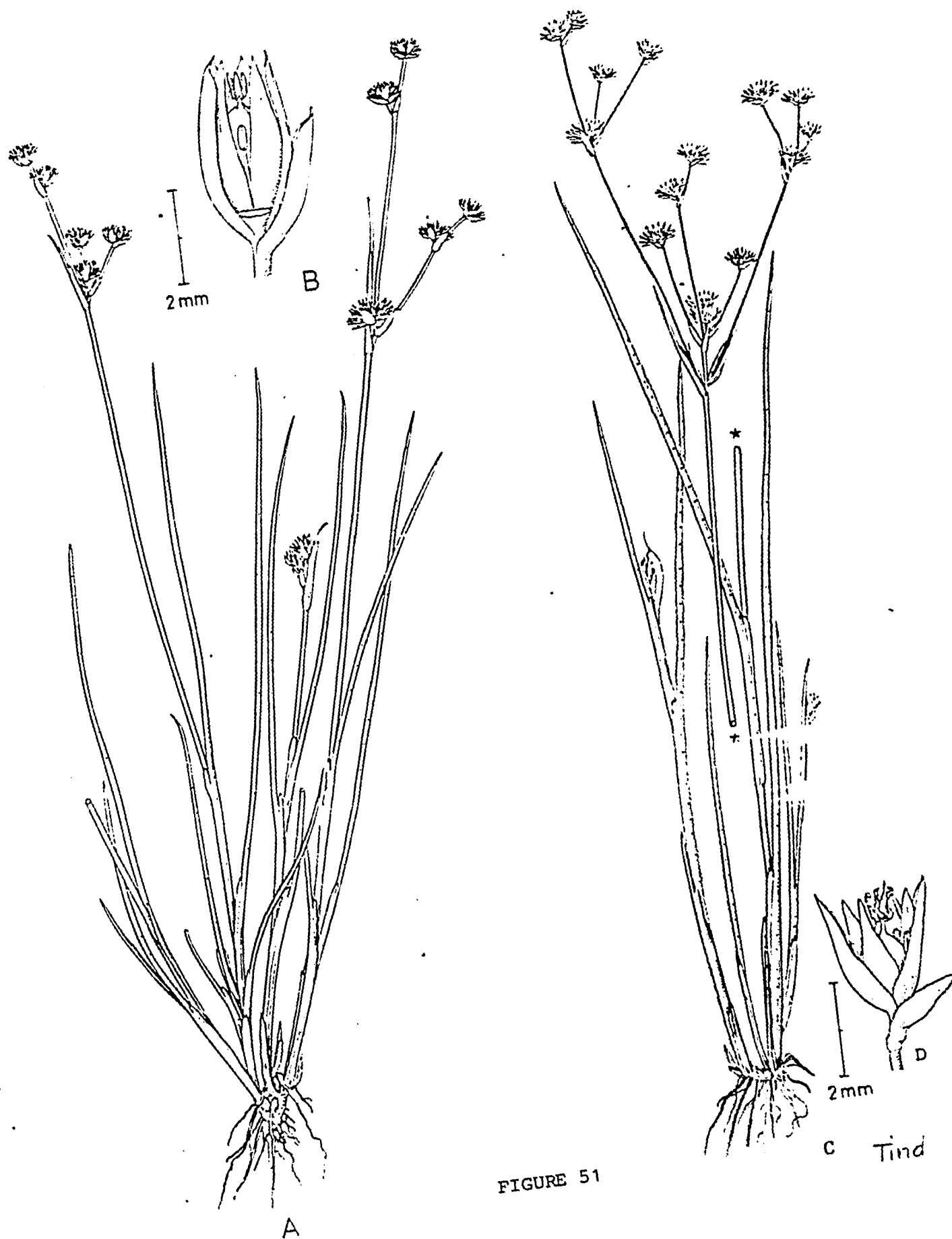


FIGURE 51

21. *Juncus pallescens* Lamarck, Encycl. 3: 268. 1789. Type. Argentina.

Buenos Ayres, 1767, Commerson s.n. (holotype, P; isotype, P).

Figs. 51 A-B, 52 A.

Juncus dombeyanus J. Gay ex Laharpe, Essai monogr. jonc. 44.

1825, also published in Mem. Soc. Hist. Nat. Paris 3: 132.

1827. Type. Perou, Dombey s.n. (holotype, P; isotypes, MO, P).

Juncus commixtus Steudel, Syn. pl. glum. 2: 300. 1855. Type.

Chile. Quillota, Feb 1829, Bertero 1059 ex parte (holotype, P; isotype, MO).

Juncus proximus Steudel, ibid. Type. Chile. Valdivia, Lechler 292 (holotype, P; isotype, MO).

Juncus fernandezianus Steudel, ibid, 302. Type. Chile. Juan

Fernandez Islands, Bertero 1468 (holotype, P; isotype, K).

Juncus dombeyanus Gay ex Laharpe var. typicus Buchenau, Abh.

Naturwiss. Vereine Bremen 6: 408. 1879. Basionym. *Juncus dombeyanus* Gay ex Laharpe.

Perennial caespitose herb, 20-45 cm high. Rhizome densely branching or short-creeping, 1.5-2.5 mm diam., with few small membranaceous scales. Culms erect 0.8-2 mm diam., terete, smooth. Cataphylls 0-2 to each culm, to 5 cm long, thin. Blade-bearing leaves 2-3 basal and 0-1 cauline to each culm, 10-25 cm long; sheaths 2-7 cm long with membranaceous margins terminating in two 1.5-3.5 mm long, rounded auricles; blades 1.5-2 mm diam., round to elliptic in cross section, septate but sometimes inconspicuously so. Inflorescence decomposed, antherlate, 1.5-10 x 1.5-4 cm, flower heads (1-)3-10(-20), globose at maturity,

0.5-1 cm diam., (4-)8-20-flowered, usually strongly reddish brown, ultimate head-bearing branches more than 0.45 mm diam. Lower inflorescence bract 1-5 cm long, shorter than the inflorescence, resembling blade-bearing leaves or scale-like, upper bracts progressively shorter, floral bracts acuminate ca. 3 mm long, membranaceous, whitish, usually contrasting the tepal color. Tepals subequal, 3-4.5 mm long, lanceolate, acuminate, robust rigid, outer ones concave and membranaceous towards the margin, inner ones flat with distinct membranaceous margin. Stamens usually 6 or rarely 3, 1-2 mm long; anthers 0.5-0.9 mm long, usually about half as long as the filament. Capsule ellipsoidal to obovoidal, truncate to bluntly acute, 3-lobed to trigonous, (2.2-)2.5-3 x 1.2-1.3(-1.6) mm, green basally, brown apically, glossy, unilocular. Seeds broadly ellipsoidal, conspicuously apiculate, 0.3-0.4 x ca. 0.2 mm, reticulate, yellowish brown with a hyaline outer seed coat.

Distribution. Juncus pallescens occurs in the Andes from central Ecuador to southern Chile and also in eastern South America from Rio Grande do Sul in Brazil to Buenos Aires in Argentina. In Ecuador, Peru and Bolivia it has been collected at altitudes between 2000 m and 3600 m. It is most common in seepage areas along roads and in pastures. Just south of Cuenca in Ecuador, for instance, I found it growing in a thin mudlayer which had accumulated in a pool on top of the paved Panamerican Highway. It also grows in more natural habitats such as Sphagnum bogs and edges of páramo lakes.

Specimens examined. ECUADOR. Azuay: Cuenca, 2500 m, Harling 653 (S); Panamerican Highway immediately S of Cuenca, 2600 m, Balslev 1213 (NY); Narancajo ca. 10 km S of Cuenca, 2650 m, Balslev 1217 (NY); Panamerican Highway 37 km S of Cuenca, 3200 m, Balslev 1236 (NY); Laguna Zurrucuchu, 3650 m, Prescott 781 (NY). Cañar: El Triunfu-Cañar rd, km 5 W of Suscal, 2700 m, Balslev 1198 (NY). Imbabura: S of Gonzales, 2700-3000 m, Fagerlind & Wibom 1299 (S). Loja: Cajanuma 18 km S of Loja, 2000 m, Espinosa 1633 (GH); Catacocha between El Almendral and La Hamaca, 1800-2200 m, Acosta Solis 7906 (F, US); Panamerican Highway ca. 30 km N of Loja, 2100 m, Balslev 1359 (NY). Pichincha: Alóag-Sto. Domingo rd, km 7, 2800 m, Sparre 15080 (S); old rd, Quito-Sto. Domingo, 23-27 km W of Chillogallo, 2800-3100 m, Balslev 1658 (NY); between Pifo and Los Coralles, 2800 m, Asplund 6998 (G, K, NY, S, US).

PERU. Ancash: Bolognesi, Chiquiau (Umpay), 3350 m, Cerrate 3211 (US). Cajamarca: Hualgayoc, San Miguel, 2750 m, Diaz s.n. (US); Cajamarca nr airport, 2670 m, Sagástegui 8021 (F, MO, NY); Contumaza, San Benito, Jeton-Guzmango, 2000 m, Sagástegui et al. 6361 (NY); Cruz Grande-Contumaza, 2700 m, Sagástegui et al. 6479 (NY). Huánuco: Huánuco, 2750 m, Asplund 13101 (G, K, NY, S). Junín: Jauja-La Oroya rd, 19 km NW of Parco, 3500 m, Balslev 1083 (NY). La Libertad: Otuzco, Motil-Chota, 2850 m, Lopez & Sagástegui 8036 (AAU, MO, NY); Huamachuco, Munmalca, Hacienda Cochabamba, 3200 m, Lopez 1469 (NY, US); Stgo. Chuco, La Yeguada (Mollebamba), 3100 m, Lopez 1104 (US); slopes above Yamobamba, 3000-3100 m, Conrad 2731 (MO). Without department: Tarma, 2150 m, Macbride & Featherstone 1030 (F, S, US); Mito, 2750 m, Macbride & Featherstone 1450 (F, G, GH, NY, US).

BOLIVIA. La Paz: Sud Yungas 69 km E of La Paz, Calacoto, Ikiko station nr Mt Illimani, 3100 m, Beck 3897 (LPB, NY); Inquisivi-Circuata rd, km 3, 2600 m, Beck 4442 (LPB, NY).

Uncertainty surrounding the name Juncus pallescens Lamarck led subsequent monographers to discard it. The species to which it belongs has been known under the later name Juncus dombeyanus Gay ex Laharpe.

In the protologue of J. pallescens, Lamarck (1789) states that it grows in both North and South America. The North American occurrence is documented only by the two literature references: 'Pluk. Alm. t. 92, f. 9' and 'Moris. Hist. 3, p. 228. Sec. 8, t. 9, f. 15'. The South American occurrence on the other hand, is documented by reference to a specimen collected by Commerson at 'Buenos-Ayres'. This collection is preserved with two sheets (one in the Lamarck herbarium at P, and one in the general herbarium at P), both annotated as 'Juncus pallescens' in Lamarck's hand. Since this is the only collection of J. pallescens seen by Lamarck it is obviously the type. The holotype in the Lamarck herbarium is juvenile and difficult to identify. The isotype in the general herbarium is mature and belongs to what has been called Juncus dombeyanus Gay ex Laharpe. The exact locality of this collection is doubtful since the isotype, in addition to 'Buenos-Ayres', also bears the locality annotation 'promotorium Montevideo' (=Cerro de Montevideo). This uncertainty, however, does not affect the correct application of the name.

Confusion around J. pallescens arose when Meyer (1822, p. 31) placed the North American Juncus acuminatus Michaux in synonymy of J. pallescens Lamarck. Laharpe (1825, p. 48; 1827, p. 136) argued that the

specimen of J. pallescens in Lamarck's herbarium was too young and undeveloped to serve as the basis of a name. He thus put J. pallescens in synonymy with J. acuminatus even though he realized that the South American specimens in the Lamarck herbarium belonged to what he called J. dombeyanus. By emphasizing Lamarck's references to literature dealing with North American plants and by paying less attention to the specimens actually available to Lamarck, the name J. pallescens therefore became attached to the North American species J. acuminatus, but as a synonym because of its vague definition. Later North American workers, starting with Engelmann (1866, p. 464), discarded the name because it was based only on South American specimens. Buchenau (1879) realized that the name J. pallescens Lamarck belonged to a South American taxon. As he knew only the undeveloped specimen in the Lamarck herbarium he could not decide its taxonomic affinities. Instead he assigned it as 'Sammel-Typus' for J. microcephalus H.B.K. and J. dombeyanus Gay ex Laharpe, which meant that he was not sure to which of those two taxa it belonged. In later writings Buchenau (1890, 1906) simply cited J. pallescens as a synonym of both J. microcephalus and J. dombeyanus.

Now that we have the well-developed isotype with Lamarck's annotation at our disposal, it is obvious that Juncus pallescens Lamarck (1789) is an older name and has to replace Juncus dombeyanus Gay ex Laharpe.

Juncus punctorius Lamarck (1789) has been cited as a synonym of J. dombeyanus (Laharpe, 1825, 1827; Buchenau, 1890, 1906). This name was, however, not published by Lamarck but by Linnaeus filius (1781), and it belongs to a South African species. Lamarck (1789) cited a collection of Dombey from Lima, Peru, under J. punctorius. This specimen is the type of J. dombeyanus Gay ex Laharpe, and this coincidence

led to the misleading citations.

The specimens of Juncus dombeyanus Gay ex Laharpe cited in the protologue are from 'Monte-Video' (Dombey s.n.) and 'Buenos-Ayres' (Commerson s.n.). One specimen at P with the annotation 'Juncus Dombeyanus N.' in J. Gay's hand is the holotype since Laharpe assigns this name to J. Gay. The specimen, however, has the locality 'Perou' rather than 'Monte-Video' as cited in the protologue. Since Dombey never was in Montevideo, the citation in the protologue must be wrong. The other specimen (Buenos-Ayres, Commerson s.n.) is a 'cotype' and happens to be an isotype of Juncus pallescens Lamarck at the same time.

Juncus pallescens is closely related to J. microcephalus and mature specimens are necessary to distinguish the two species with certainty. Juncus pallescens is most easily recognized by its inflorescence, the branches of which are more robust than those of J. microcephalus. The ultimate branches are more than 0.45 mm diam. below the flower heads. In addition, the flower heads have a strong reddish brown color from the tepals, and the floral bracts usually contrast this by being whitish. The tepals of J. pallescens are more robust and rigid than those of J. microcephalus and the flowers have a cup-like circumference and are thicker. The seeds are broadly ellipsoidal, 0.3-0.4 mm long instead of narrowly ellipsoidal, 0.4-0.5 mm long as in J. microcephalus. In its northern Andean range J. pallescens has fewer flower heads (e.g., usually fewer than seven in Ecuador), but southwards and in eastern South America this does not hold true.

FIGURE 52

52 A. The distribution of Juncus pallescens in the neotropical region.

In addition it occurs in temperate South America.

52 B. The distribution of Juncus acuminatus in the neotropical region.

In addition it occurs in temperate North America.

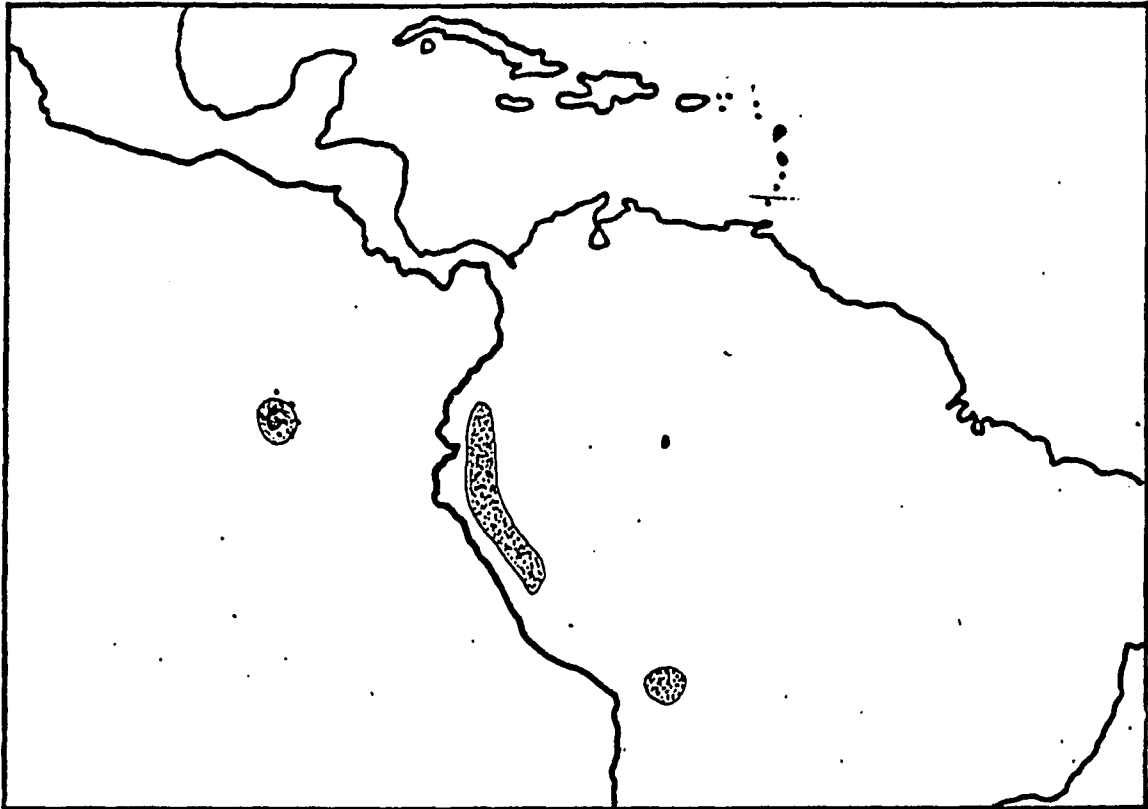


FIGURE 52 A.

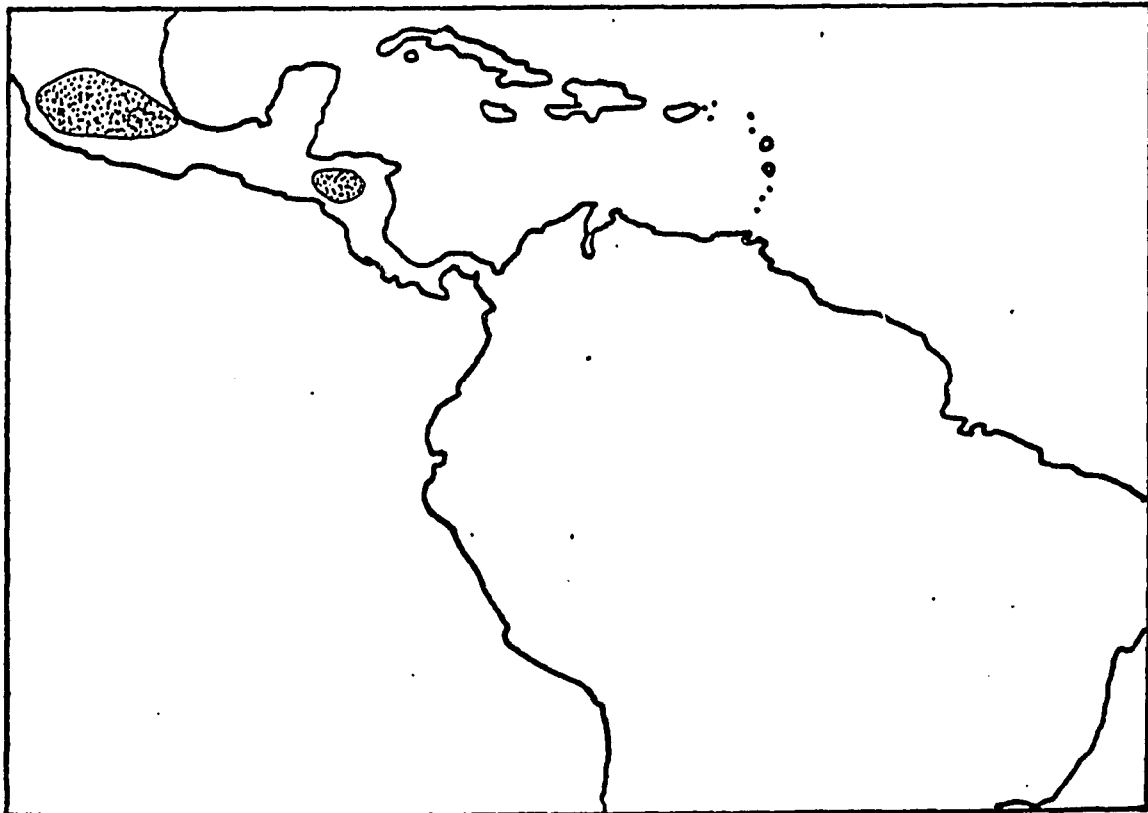


FIGURE 52 B.

22. *Juncus acuminatus* Michaux, Fl. bor.-Am. 1: 192. 1803. Type. USA.

Carolina (holotype, P).

Fig. 52 B.

Juncus acuminatus Michaux var. *legitimus* Engelmann, Trans. Acad.

Sci. St. Louis 2: 463. 1868. Basionym. *J. acuminatus* Michaux.

Perennial caespitose herb, 30-100 cm high. Rhizome densely branching, 2-4 mm diam., with thin inconspicuous scales. Culms clustered, erect, 1-3 mm diam., terete, smooth. Cataphylls 1-3 to each culm, to 10 cm long, green or reddish tinged, with distinct membranaceous margin. Blade bearing leaves 1-3 to each culm, to 30 cm long; sheath to 10 cm long, with membranaceous margin terminating in two rounded, 1.5-5 mm long auricles; blade 1-2 mm diam., terete, conspicuously septate. Inflorescence decompound, anthelate, (3-)5-15(-20) x 3-8 cm, flower heads 3-35, conical to globose, 5-10 mm diam., 10-40 flowered, stramineous, ultimate head bearing branches less than 0.4 mm diam. Lower inflorescence bract 1-5 cm long, much shorter than the inflorescence, with a reduced, terete blade, upper bracts progressively shorter, floral bracts acuminate, to 3 mm long, membranaceous. Tepals 2.5-3.5 mm long, linear-lanceolate, acute to acuminate, outer ones concave or V-shaped in cross section, inner ones flat. Stamens 3 or occasionally 6, 1.5-2 mm long; filaments filiform; anthers oblong to linear, 0.5-0.7 mm long, shorter than the filaments. Capsule about equalling the tepals, ovoidal, trigonous, 3-3.5 x 0.9-1.3 mm, with ca. 0.3 mm long beak, light brown to stramineous, unilocular, the carpel margin involuting at dehiscence. Seeds oblong-ellipsoidal, apiculate, 0.3-0.5 x 0.2-0.25 mm, reticulate, yellowish brown with hyaline outer seed coat.

Distribution. Throughout most of temperate North America from Maine to British Columbia, southwards to Georgia and California, and in the Méxican and Central American highlands. It grows in swamps and at river banks at altitudes between 1200 m and 2200 m.

Specimens examined. MEXICO. Guanajuato: Irapuato, Kenoyer 1864 p.p. (GH). Hidalgo: Barranca below Trinidad Iron works, 1650 m, Pringle 13226 (MO); Lake Atexca below Molango, 1400 m, Moore 3474 (GH); Tepeoco-Tianguistengo, 2200 m, Moore 2351 (GH); Tulacingo-Pachuca rd, 2200 m, Moore 2059 (GH). México: Valley of México nr San Augustin, Schaffner 525 (MO); Temascaltepec, Las Mesas, 2000 m, Hinton 3726 (GH); Peñon, 1700 m, Hinton 5601 (MO, NY); Ypericones, 1500 m, Hinton 3905 (GH). Michoacan: Zamora Valley, 1500 m, Pringle 9464 (GH, MO, NY). Nayarit: Santiago Ixc. Mezcaltitán, Ortega 5542 (GH). San Luis Potosí: Nr the town, Schaffner 217 (GOET, NY, P); 22°N lat., Parry & Palmer 893, 895 (GH, MO, NY). Veracruz: Nr Jalapa, Rose & Hough 4309 (GH).

HONDURAS. Intibuca: Quebrada El Huise 9 km E of La Esperanza, 1800 m, Molina 13994, 14025 (NY); Mt Opalaca 8 km from La Esperanza, 2000 m, Molina 7882 (GH); La Esperanza airfield, 2000 m, Molina 6260 (GH). La Paz: La Correa 3 km from Marcala, 1200 m, Molina 24412 (NY). Morazán: Las Tablas-Lepaterique, 1600 m, Molina 7847 (GH).

23. *Juncus ecuadoriensis* Balslev, Fl. Ecuador 11: 36. 1979. Type.

Ecuador. Azuay: Cerro Soldados W of Sayausí, 3400 m, 25 Apr

1968, Harling, Storm & Ström 8753 (holotype, GB; isotype, AAU).

Figs. 53, 54 A.

Perennial loosely caespitose herb, (20-)35-80 cm high. Rhizome densely and irregularly branching, 2.5-3.5 mm diam., rarely collected and apparently soon decaying. Culms erect, 1-4 mm diam, terete, smooth or basally with small elongate transverse nodules. Cataphylls usually absent, sometimes present as a membranaceous sheathing, but never conspicuously different from the leaf sheaths. Blade-bearing leaves 1-3 basal and 1-2 cauline to each culm, 20-70 cm long; sheaths 5-15 cm long, sometimes nodulated like the culm, margin membranaceous and terminating in two 1-3.5 mm long, scarious, rounded auricles; blades 2-5 mm diam., round to elliptic in cross section, nodulated by conspicuous septa 1-4 cm apart. Inflorescence varying from one terminal flower head to a 20-headed one to three times branched anthela, up to 7 x 15 cm, heads first conical, becoming semiglobose to almost globose towards fruit ripening, 1-1.5 cm diam., many flowered, ultimate head bearing branches relatively robust and more than 0.4 mm diam. Lower inflorescence bract 3-13 cm long, resembling basal and cauline leaves but much shorter, upper bracts progressively shorter, the ultimate ones scale like and about 1 cm long, floral bracts to 3.5 mm long, reddish brown to stramineous with membranaceous margins. Tepals equal, 3.8-4.6 mm long, lanceolate, acute, green with membranaceous margins, turning stramineous or more often castaneous, outer ones concave, inner ones a little narrower than outer ones, flat. Stamens 3, 1.4-1.8 mm long; anthers oblong to linear 0.5-0.8(-1) mm long or usually shorter than the

FIGURE 53

Habit and detail of Juncus ecuaçoriensis (From Balslev, 1979a).

53A. Habit (Drawn from Harling et al. 8753, GB).

53B. Twice divided inflorescence of the northern form (Drawn from
Asplund 16884, S).

53C. Flower (Drawn from Harling et al. 8753, GB).

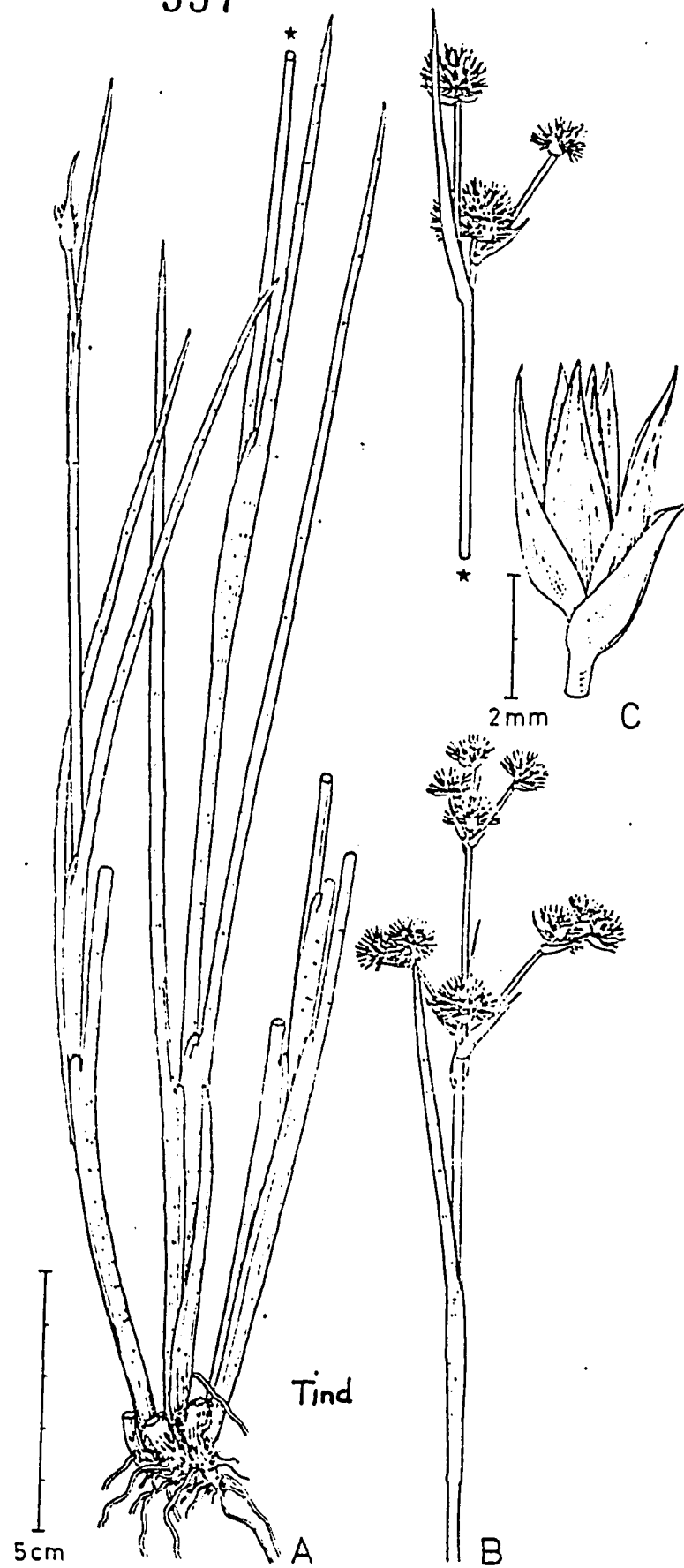


FIGURE 53

filament. Capsule narrowly ellipsoidal, acute and apiculate, trigonous, 2.9-4.4 x 1-1.3 mm, light brown basally, dark brown to almost black on the apical sometimes protruding part, unilocular. Seeds narrowly ellipsoidal, apiculate, 0.7-0.9 x ca. 0.3 mm, reticulate, yellowish brown.

Distribution. Juncus ecuadoriensis occurs interruptedly in the Andes from Venezuela to southern Ecuador. It grows in wet places at altitudes between 2400 m and 3500 m. In Ecuador I have collected it in seepage areas along roads and in Sphagnum bogs.

COLOMBIA. Boyacá: Río Cusiana 1 km E of Vado Hondo, 2880 m, Cleef 9225B (COL); Páramo de la Sarna between Sogamoso and Vado Hondo valley, 3405 m, Cleef 9406A (COL); Páramo de la Rusia between La Osera and Quebrada de la Esperanza on Duitania-Charala rd, 3624 m, Langenheim 3503 (US). Cauca: Páramo de las Barbillas nr Guachicón, 3100 m, Core 985 (US); Las Papas valley nr Valencia, 2700 m, Core 1004 (US); Paletara, 2950-3100 m, Pennell 6909 (GH, NY, US). Cundinamarca: Páramo de Sumapaz, Lagunitas 4.5 km S of San Juan, 3455 m, Cleef 8447 (COL); Páramo de Guasca, 3200-3400 m, Barclay & Juajibioy 6522 (US), Cuatrecasas 9488 (GH, US), Fosberg & Valencia 21464 (F, US), Black 46-673 (US); Páramo de Palacio, 3375 m, Cleef 4000 (P, U); Páramo de Cruz Verde, 3300-3500 m, Pennell 2049 (GH, NY); S of Usme between La Regadera and El Hato, 3000-3100 m, Idrobo 431 (GH, MO, US); 15 km NW of Zipaguira, 3200 m, Galen Smith 1370 (GH, MO, US); Villavicencio rd above Chipaque, 3000 m, Fosberg 20243 (US). Nariño: Laguna Cocha, André 3093 (GH, NY). Norte de Santander: Alto de Almorgadero N of Cerrito, 3800 m, Fassett 25995 (US).

Santander: Páramo del Almorzadero, Peralonso, 3200 m, Cuatrecasas

9876 (US); Páramo N of Carrito, 3050 m, Fassett 25927 (US).

VENEZUELA. Mérida: Páramo de los Conejos, Sergeant 21 (US); Sierra Nevada, Páramo de Mucubaji, Finca la Corcovada, Río Sto. Domingo, 3200 m, Shulz 740 (U). Táchira: NNE slopes of Pata de Judío, 3100-3500 m, Luteyn et al. 5954 (NY).

ECUADOR. Azuay: Panamerican Highway 91 km N of Loja, 2900 m, Holm-Nielsen et al. 5082 (AAU, F, NY, S), km 85, 2850-2950 m, Holm-Nielsen et al. 4792 (AAU, NY, S); Sígüig-Gualquiza rd, Campamento Molón, 2900-3000 m, Harling et al. 8215 (AAU, GB); Mt Soldados W of Sayausí, 3400 m, Harling et al. 8753 (AAU, GB); 10-15 km W of Sayausí, 3200-3400 m, Balslev 1587 (NY). Cañar: 5-8 km NE of Azogues nr San Marcos, Camp & Prieto E-2618 (AAU, NY, S). Carchi: E slopes of Mt Chiles, 3400 m, Drew E475a (GH, US); Páramo El Angel, Prescott 628 (NY); Tulcán-El Carmelo rd, km 18, 3300 m, Balslev & Quintana AAU-23847 (AAU, NY). Loja: Nr Tablon de Oña, Rose et al. 23125 (GH, NY, US); Loma de Oro pass 10 km S of Saraguro, 3200 m, Balslev 1364 (NY); Panamerican Highway 10-15 km N of Saraguro, 2900-3100 m, Balslev 1406 (NY). Zamora-Chinchiipe: Loja-Zamora rd, km 17, 2400 m, Holm-Nielsen et al 3540 (AAU, NY, S), km 15-16, 2700-2800 m, Balslev 1258 (NY).

This species has commonly been misidentified as J. brunneus in the herbaria. That name is a synonym of J. ebracteatus, with which J. ecuadoriensis has very little in common. For instance, J. ebracteatus has stoloniferous rhizome and long protruding styles, none of which are found in J. ecuadoriensis.

The morphological variation of the inflorescence of this species is geographically correlated. Populations from Venezuela, Colombia and the Carchi province in northern Ecuador usually have the inflorescence twice or three times branched and with up to 20 flower heads in the anthela, but sometimes only once branched. The populations from southern Ecuador, in contrast, usually has only one terminal flower head, or at most the inflorescence only once branched and with no more than 3-4 flower heads.

24. *Juncus breviculmis* Balslev, sp. nov. Type. Venezuela. Mérida:

Páramo at Laguna de Mucubaji, near Apartaderos and San Rafael,
35 km NE of Mérida, 3800 m, 18 Oct 1953, Maguire 39428 (holotype,
NY). Fig. 54 B.

Perennial soft caespitose herb, 10-40 cm high. Rhizome densely and irregularly branching, ca. 2 mm diam. Culms erect, 1-20 cm long and always shorter than the leaves, 1-2.5 mm diam., terete, smooth or with small transverse nodules, sometimes branching in the axils of cauline leaves. Cataphylls absent or inconspicuous. Blade bearing leaves 1-2 basal and 0-2 cauline to each culm, 6-40 cm long; sheaths 1-6 cm long, membranaceous towards the margin and terminating in two rounded, 1-2.5 mm long auricles; blades 1.5-2.5 mm diam., round in cross section but usually flat in pressed specimens, conspicuously transverse septate. Inflorescence a terminal flower head or a once to twice branched and up to 7-headed anthela to 10 x 7 cm, flower heads globose, 10 mm diam. and up to 40-flowered when single, or conical, 5 mm diam and only 6-7 flowered in many headed inflorescences. Lower inflorescence bract 4-20 cm long, resembling a cauline leaf, always conspicuously overtopping the inflorescence, sometimes straight, longer than the culm and appearing as a continuation of it except for being cross-septate, sheaths 1-5 cm long, blades 1-2.5 mm diam., floral bracts lanceolate, acuminate, 2-3 mm long, membranaceous. Tepals equal, 3-4 mm long, lanceolate, acute, brown to reddish with well marked white membranaceous margin. Stamens 6, ca. 1.5 mm long; filaments filiform, whitish; anthers oblong ca. 0.5 mm long, yellow. Capsule oblong to obovoidal, slightly apiculate and trigonous, 2.3-3 x 1.3-1.6 mm, thin

walled, golden to dark brown. Seeds ellipsoidal, apiculate, ca.

0.4 x 0.2 mm, reticulate, brown.

Distribution. In the northern Andes from the province of Mérida in Venezuela to Boyacá in Colombia. Grows, sometimes submerged, in ponds, lakes and streams in the páramos at altitudes from 3500 m to 4100 m.

Specimens examined. COLOMBIA. Santander: Páramo de Almorzadero, 3600-3800 m, Cuatrecasas 13509 (COL, US), Fassett 25999 (NY, US); Páramo de Santurban, 3600 m, Araque & Barkley 185722 (US). Boyacá: NW of Belen, Quebrada Minas NE of Laguna El Alcohol, 2850 m, Cleef 2061 (U); Sierra Nevada del Cocuy, Alto Valle Lagunillas, 3915 m, Cleef & Florschütz 5926 (U); Planos del Toldadero, 3950 m, Cuatrecasas 1557 (COL, US), Páramo de la Rusia, NW-N of Duitama, 3570 m, Cleef 7136 (COL), 6740 (P, U).

VENEZUELA. Mérida: Páramo de Mucuchies, 3600-4150 m, Humbert 26315 (P); Sierra de Sto. Domingo, Laguna de Mucubaji, 3500-3800 m, Gines 1674 (US), Barclay & Juajibioy 9600 (US).

This new species of septate-leaved Juncus is recognized most easily by its short culm, which never lifts the inflorescence up and above the tips of the blade-bearing leaves. The length of the culm and the degree of congestion of the inflorescence both vary considerably, but in a correlated manner, probably reflecting ecological modifications. Thus, small plants with 1-3 cm long culms usually have the inflorescence

FIGURE 54

54 A. The distribution of Juncus ecuadoriensis.

54 B. The distribution of Juncus breviculmis.

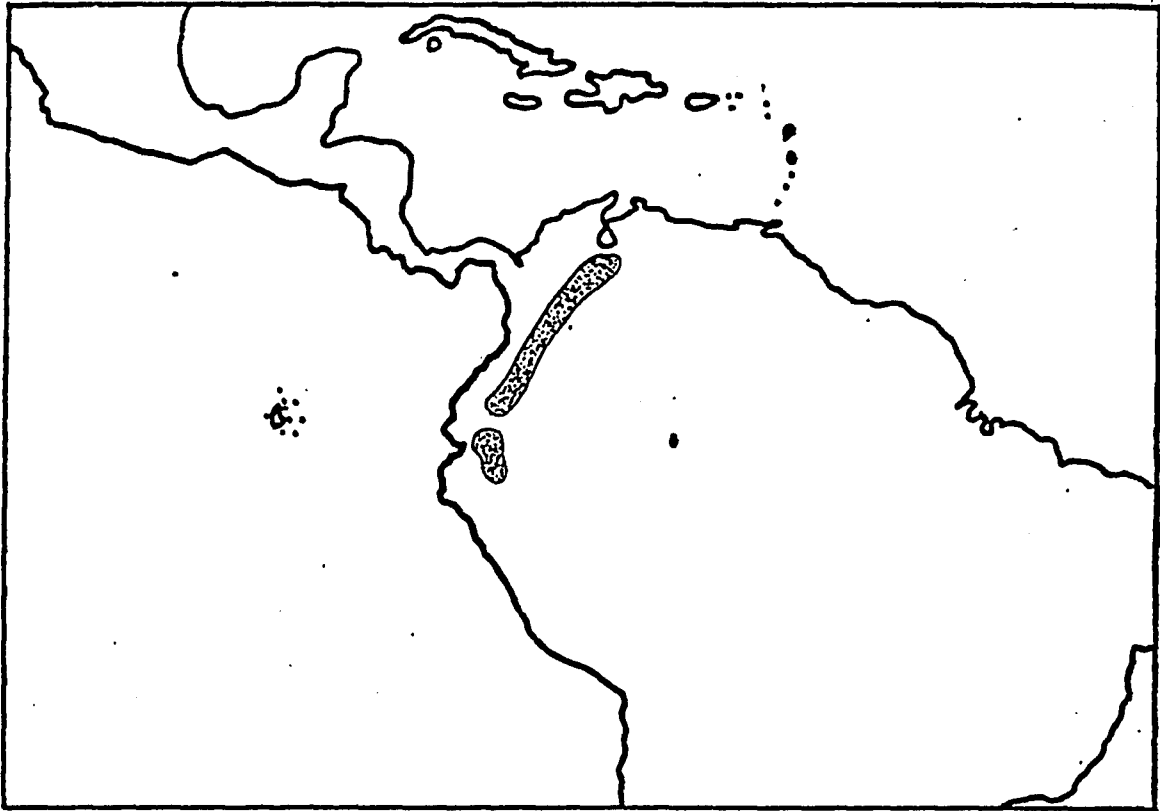


FIGURE 54 A.

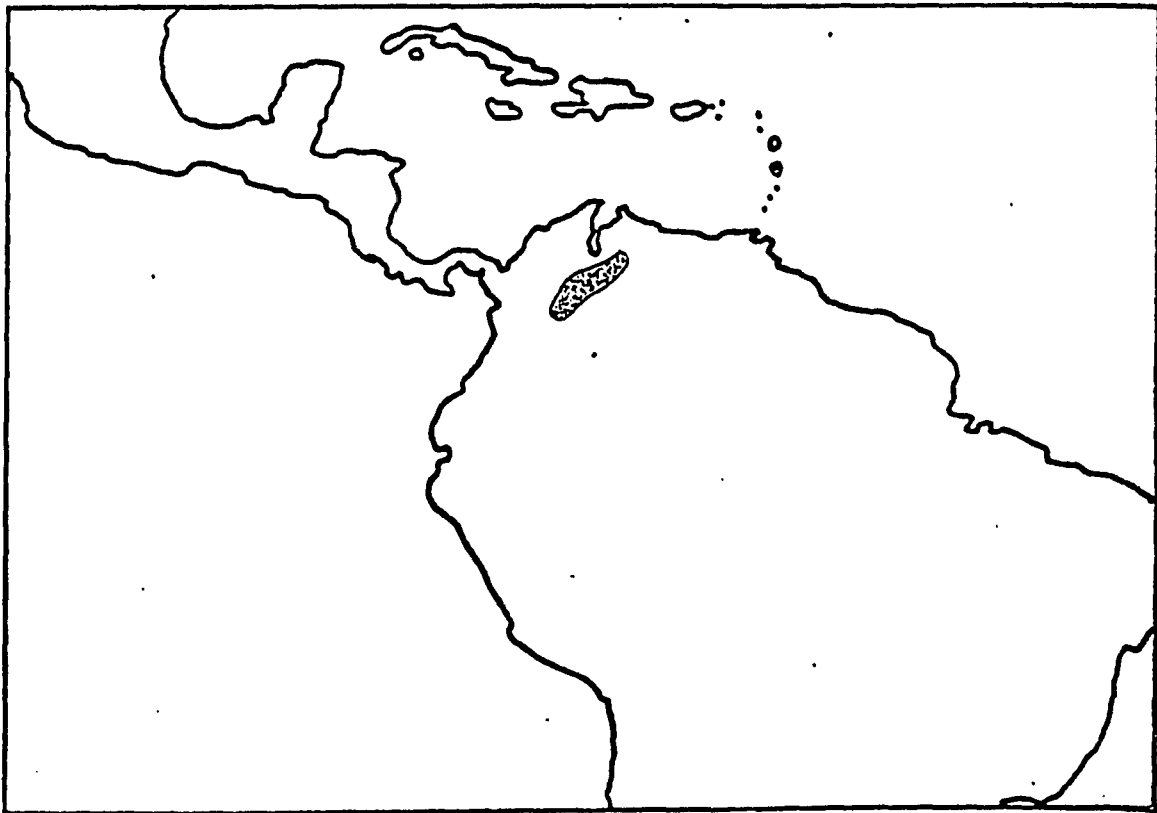


FIGURE 54 B.

quite congested, often consisting of a single flower head, 1 x 1 cm, terminating the culm, whereas taller plants with 15-20 cm long culms have more open inflorescences with several flower heads, each bearing 6-7 flowers, and the entire inflorescence being up to 10 x 7 cm.

All intermediates occur. Cuatrecasas 1557 was growing submerged according to the label information. The variation described above probably reflects differences in water depth, or, alternatively, in not submerged plants, the degree of humidity of the soil and lushness of the surrounding herb layer.

25. *Juncus guadeloupensis* Buchenau in Urban, Symb. antill. 1: 496. 1900.

Type. Guadeloupe. resources de la riviere Glass, 995-1200 m,
19 May 1899, Duss 3996 (lectotype, NY; isoelectotypes, C, F, MO,
here selected, but see below). Husnot 46 (syntype, BM, K, P).

Fig. 55 A.

Perennial herb to 150 cm high. Rhizome not seen. Culms erect, terete, smooth. to 6 mm diam. Cataphylls 0-3 to each culm, inserted somewhat separated, to 10 cm long, margin membranaceous, apex rounded with rudimentary needle like blade to 4 mm long. Blade bearing leaves 3-7 evenly distributed along the culm, to 40 cm long; sheaths to 10 cm long with membranaceous margin terminating in two 4 mm long rounded auricles; blades 2-3(-4) mm diam., round in cross-section, hollow with septa 1-3 cm apart. Inflorescence decompound, repeatedly anthelate, up to 25 x 15 cm when fully developed, flower heads 15-35, globose at maturity, to 15 mm in diam, 10-30 flowered, principal branches 2-10 cm long and 0.5-1.5 mm diam. Lower inflorescence bract 2-6 cm long, much shorter than the inflorescence, resembling cauline leaves, upper bracts progressively shorter, floral bracts about half as long as the flowers, membranaceous. Tepals equal, 3-4.5 mm long, linear-lanceolate, acuminate, pale green with varying amounts of red pigmentation, margins narrowly but distinctly membranaceous, outer ones concave, at least basally, inner ones flat. Stamens 3, ca. 2.5 mm long or about 2/3 as long as the tepals, anthers oblong 0.9-1 mm long, shorter than the filiform filaments. Capsule obclavate, acute, basally trigonous, apically pyramidate, 4-6 x 1-1.5 mm, clearly exceeding the tepals, golden yellowish brown, unilocular. Seeds obliquely ellipsoidal, short tailed, 1-1.1 x 0.3 mm, reticulate, yellowish brown below a hyaline outer

seed coat.

Distribution. Endemic to Guadeloupe and possibly Martinique (Lesser Antilles) at altitudes between 1000 m and 1200 m. Howard (1979) states that recent collections from the upper slopes of the Soufriere volcano on Guadeloupe dispels fears that this endemic species may be endangered by recent eruptions.

Specimens examined. GUADELOUPE. Mateliane, 1200 m, Stehlé 682 (GH); Lac Flammarion, Citerne, Stehlé 1132 (NY); Basse-Terre, Massif de la Soufriere, La Citerne, Sastre et al. 2830 (A); Basse-Terre, Soufriere, Sastre 6087 (P); Soufriere, Funck & Schlim 52 (G); Soufriere, Piton Tarade, 1200 m, Sastre 6948 (P). Without locality: Bena s.n. (P).

MARTINIQUE. Lac de Palmistas, La Croix at Mt Pelée, 1000 m, Duss 4622 (NY) sterile.

Duss 4622 from Martinique cited above is a sterile septate leaved Juncus, but a definite identification is not possible. In 1902 the Lac des Palmistas and the plant life around it was destroyed by a volcanic eruption, so the Martinique occurrence of Juncus guadeloupensis can presumably not be verified.

Howard (1979) found several populations in 1978 on the Soufriere flowering prolifically and plantlets had established themselves epiphytically on adjacent shrubs. This is the only report of epiphytic Juncaceae. Sastre (personal communication, 1981) says that Juncus guadeloupensis is now spreading along trails and on compacted soil at

altitudes between 1000 m and 1300 m on Guadeloupe.

Howard (1979) designated Duss 3996 as lectotype, but as a lectotype must be a specimen, not a collection, I have selected Duss 3996 (NY) as the lectotype. Buchenau (in Urban, 1900) Buchenau (1906) and Fournet (1978) cite 'Juncus acuminatus Husnot & Coutance' as a synonym of J. guadeloupensis, but that name was never published by Husnot & Coutance, who merely misidentified a syntype (Husnot 46) as Juncus acuminatus Michaux (Husnot & Coutance, 1871).

FIGURE 55

55 A. The distribution of Juncus guadeloupensis.

55 B. The distribution of Juncus achalensis in the neotropical region.

In addition it occurs in Sierra de Cordoba in Argentina.

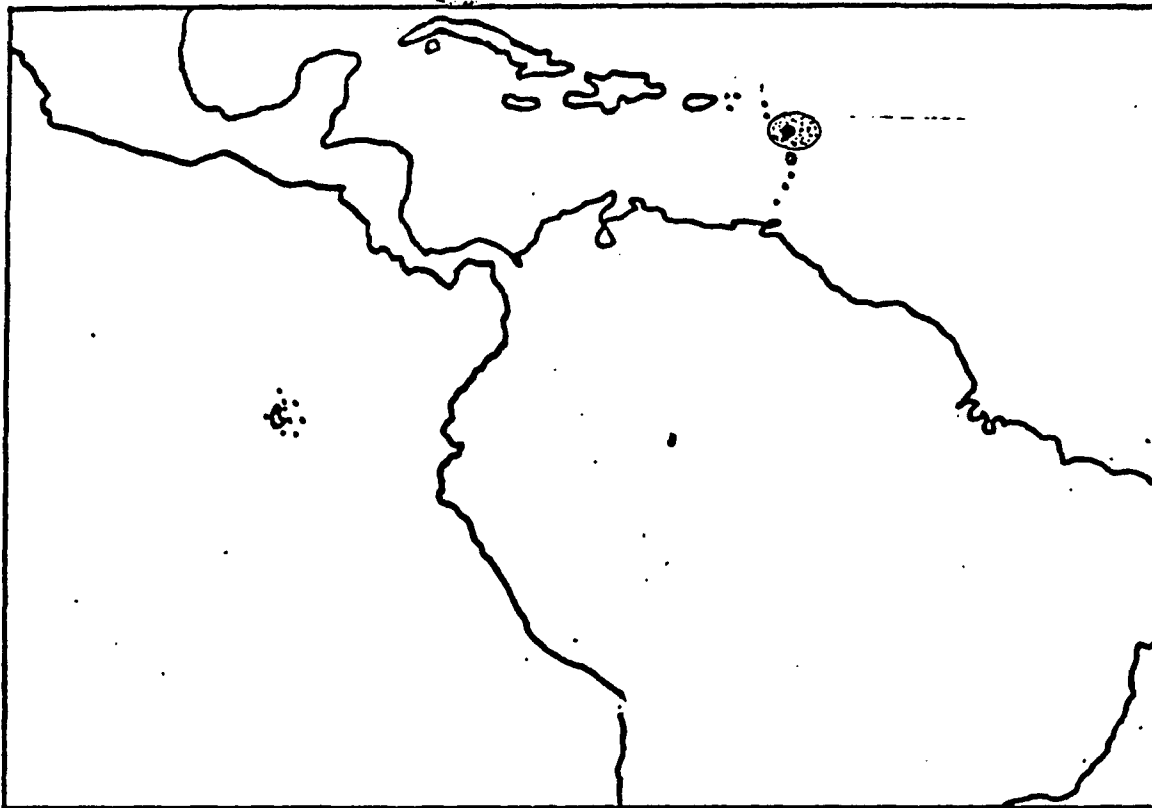


FIGURE 55 A.

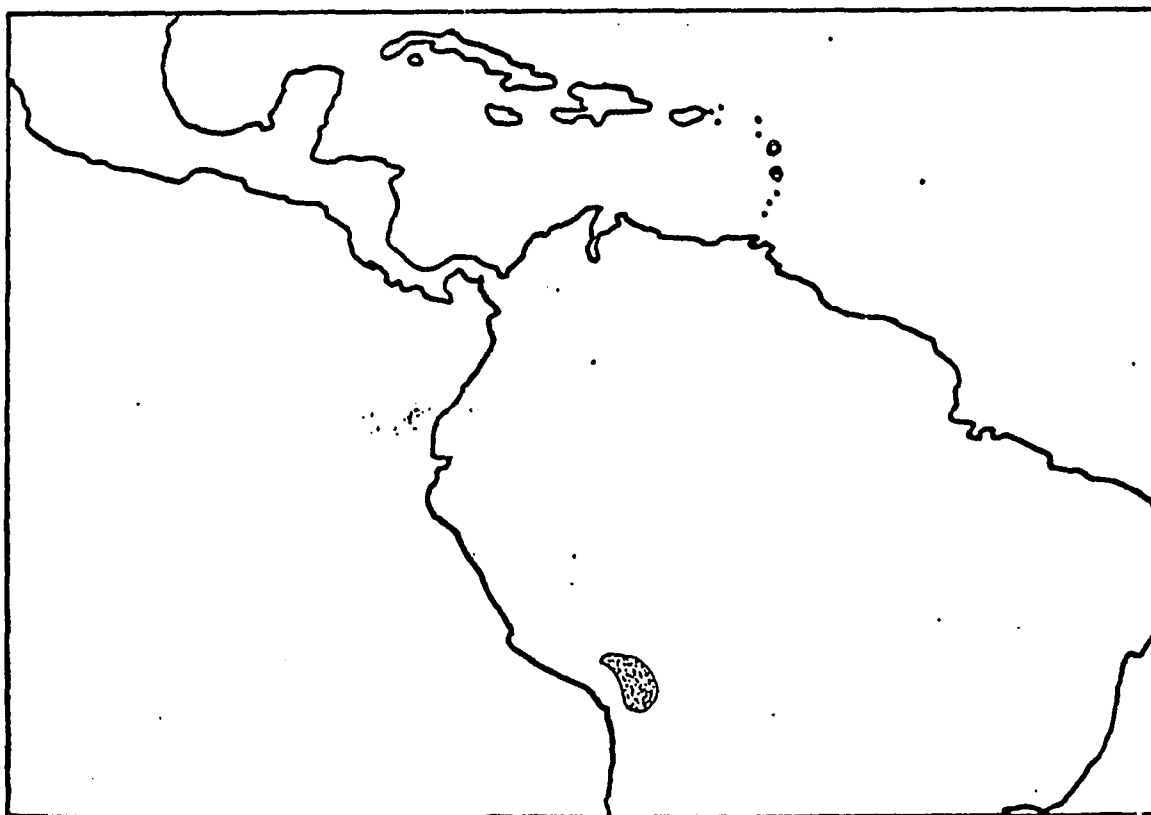


FIGURE 55 B.

26. *Juncus achalensis* Barros, Darwiniana 10: 449. 1953. Type. Argentina. Cordoba: Pampa de Achala, 5 Feb 1932, Castellanos BA-10347 (holotype, BA, n.v.). Fig. 55 B.

Perennial caespitose herb, 5-10(-20) cm high. Rhizome densely branching, clustered, ca. 1 mm diam. Culms erect, slightly curved, 0.6-1(-1.8) mm diam., terete or laterally compressed. Cataphylls absent or inconspicuous. Blade bearing leaves 1-3 basal and 0-1 cauline to each culm, 2-5(-9) cm long or shorter than the culms; sheaths 1-2 cm long, with membranaceous margins terminating in two 1 mm long auricles; blades round in cross-section, sometimes laterally compressed, transversally septate. Inflorescence a terminal semiglobose head about 1 cm in diam., sometimes two headed. Lower inflorescence bract ca. 1 cm long, scale like, lanceolate, acute, castaneous, with membranaceous margins, not differentiated into sheath and blade, floral bracts shorter than the flowers, acuminate, membranaceous, with castaneous midnerve. Tepals equal, ca. 4 mm long, lanceolate, acuminate, dark reddish brown or almost black with distinct white membranaceous margins giving the flower head a dark appearance with scattered white stripes. Stamens 3 (or 6), ca. 1.5 mm long; filaments filiform; anthers oblong, ca. 0.5 mm long, yellow. Capsule oblong, shortly or not apiculate, trigonous to 3-lobed, ca. 4 x 1 mm or as long as the tepals, brown, darker to almost black apically, unilocular. Seeds oblong, shortly apiculate, ca. 0.5 x 0.3 mm, reticulate, dark brown.

Distribution. Described from Sierra de Cordoba and collected at four localities in that isolated mountain range of central Argentina according to Barros (1953). It is here reported from Bolivia and southern Peru. The only indication of the ecology of this species is 'semiruderal' by Ellenberg.

Specimens examined. PERU. Puno: Huerta N of Puno, 4000 m, 22 Mar 1957, Ellenberg 2982 (U).

BOLIVIA. La Paz: Sorata, 3950 m, Feb 1886, Rusby 180 (NY).

I have neither seen the type nor any other collections referred to Juncus achalensis in the protologue, but from Barros' description and figure I believe the above cited specimens belong here. These two specimens are somewhat smaller than those mentioned by Barros (1953) and, in my description above, measurements mentioned in parenthesis refer to Barros' description. The Rusby collection cited above was identified as J. brevifolius var. quitensis (= J. liebmannii var. quitensis) by Buchenau in 1888, and as J. brunneus (= J. ebracteatus) by Rusby, but it has no affinities to either of those species. The two specimens are distinguished from other septate leaved Juncus species by their small size, one-headed inflorescence, the scale like lower inflorescence bract and almost blackish color of the flower head, sprinkled with fine white stripes from the membranaceous margins of the tepals.

27. *Juncus debilis* A. Gray, Manual 1 Ed. 506. 1848, 2 Ed. 481. 1856.

Basionym. *Juncus polycephalus* Michaux var. ? 3. *depauperatus*
Torrey. Fig. 56 A.

Juncus polycephalus Michaux var. ? 3. *depauperatus* Torrey, Fl.

State New York 2: 327. 1843. Type. USA. New York: Buffalo
Creek, Kinnicut & Gray s.n., n.v.

Juncus radicans Schlechtendal, Linnaea 18: 442. 1844. Type.

México. Vera Cruz: In aquis lente fluentibus, ad rivulos
Jalapae, Majo et Aug. nec non ad Jalcingo Nov. m., Schiede
s.n., n.v. Two collections destroyed at B during second
World War. ('Diese Pflanze erhielt ich in Schlechtendalschen
Original-Exemplaren von Jalapa in Mexico durch die grosse Gute
des Herrn O. Boeckler in Varel', Buchenau, 1873, p. 343).

Juncus acuminatus Michaux var. *debilis* (A. Gray) Engelmann,
Trans. Acad. Sci. St. Louis 2: 463, 1868.

Perennial loosely caespitose weak herb, 15-50 cm high. Rhizome
densely branching, clustered, ca. 1 mm diam. Culms erect or ascending,
0.5-1 mm diam., terete, smooth. Cataphylls absent or inconspicuous.
Blade bearing leaves 1-2 basal and 1-2 cauline to each culm, 5-20 cm
long; sheaths 1-5 cm long, with membranaceous margins terminating in
two 1 mm long, rounded auricles; blades ca. 1 mm diam., straight or
sometimes ascending, round to elliptical in cross-section, basally
slightly compressed, transversally septate. Inflorescence an up to
four times branched anthela to 15 x 10 cm, flower heads up to 50,
2-10 flowered, ultimate head bearing branches delicate ca. 0.3 mm diam.

Lower inflorescence bract usually $1/3$ or less as long as the inflorescence, resembling a small cauline leaf, upper bracts scale like, membranaceous, floral bracts membranaceous ca. 1.5 mm long. Tepals subequal, lanceolate, acute but not acuminate, green to stramineous, outer ones 2.2-2.8 mm, concave, inner ones 2.3-2.5 mm, flat. Stamens 3, ca. 1.5 mm long; anthers oblong ca. 0.5 mm long. Capsule narrowly ovoidal, acute and shortly apiculate, trigonous, ca. 3×1 mm and $1/4$ longer than the tepals, light brown, unilocular. Seeds ellipsoidal, apiculate, ca. 0.4×0.2 mm, reticulate, yellowish brown.

Distribution. Eastern North America from Connecticut to Florida, westwards to Texas and inland to Tennessee and Missouri. Also collected twice in southern México in the state of Veracruz (type of J. radicans) and once in the state of Chiapas.

Specimens examined. MEXICO. Chiapas: E side of Pueblo Nuevo Solistahuacan, 1700 m, 26 Oct 1971, Breedlove 21530 (NY).

This North American septate-leaved Juncus is recognized by its slender habit combined with the acute, 3 mm long trigonous capsules that protrude about $1/4$ from the perianth. Juncus diffusissimus Buckley, also from eastern North America, is similar, but has longer capsules that are even more protruding (4-5 mm long and 1.5-2 times as long as the tepals) and more profusely branched inflorescence.

FIGURE 56

56 A. The distribution of Juncus debilis in the neotropical region.

In addition it occurs in eastern North America.

56 B. The distribution of Juncus stipulatus in the neotropical region.

In addition it occurs southwards along the Andes until the
Magellan Strait.

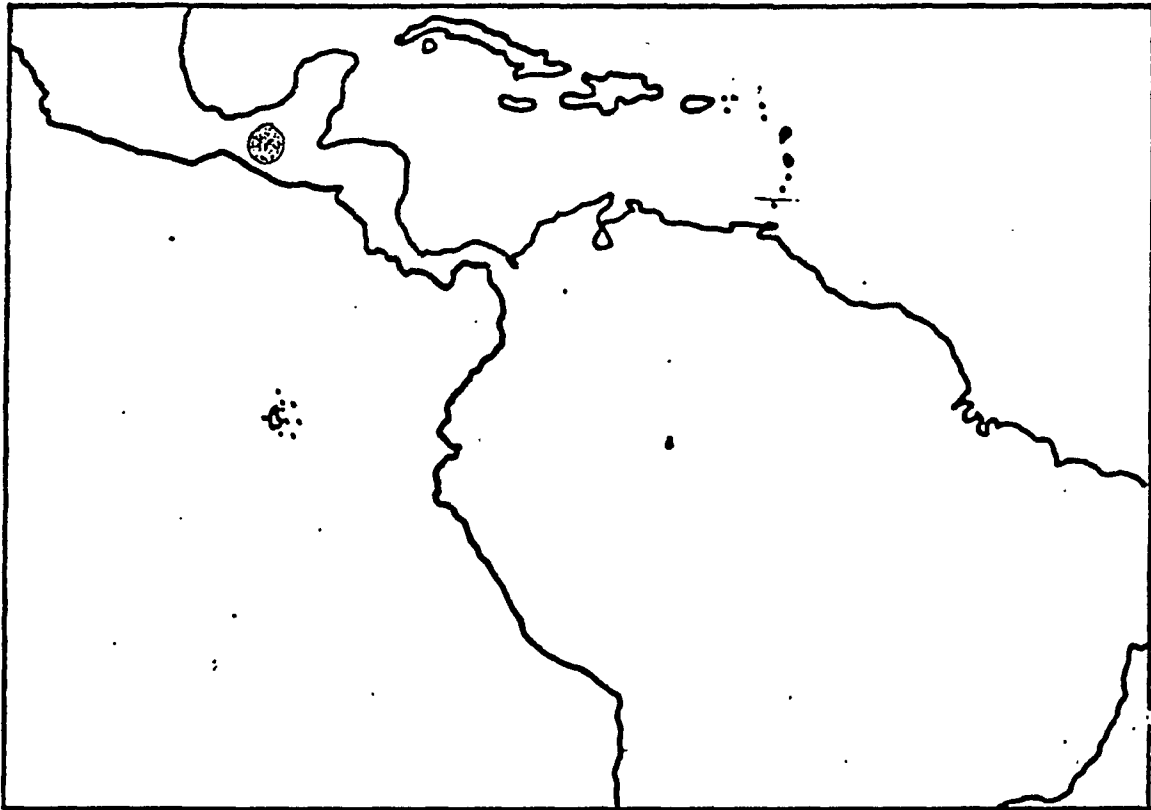


FIGURE 56 A.

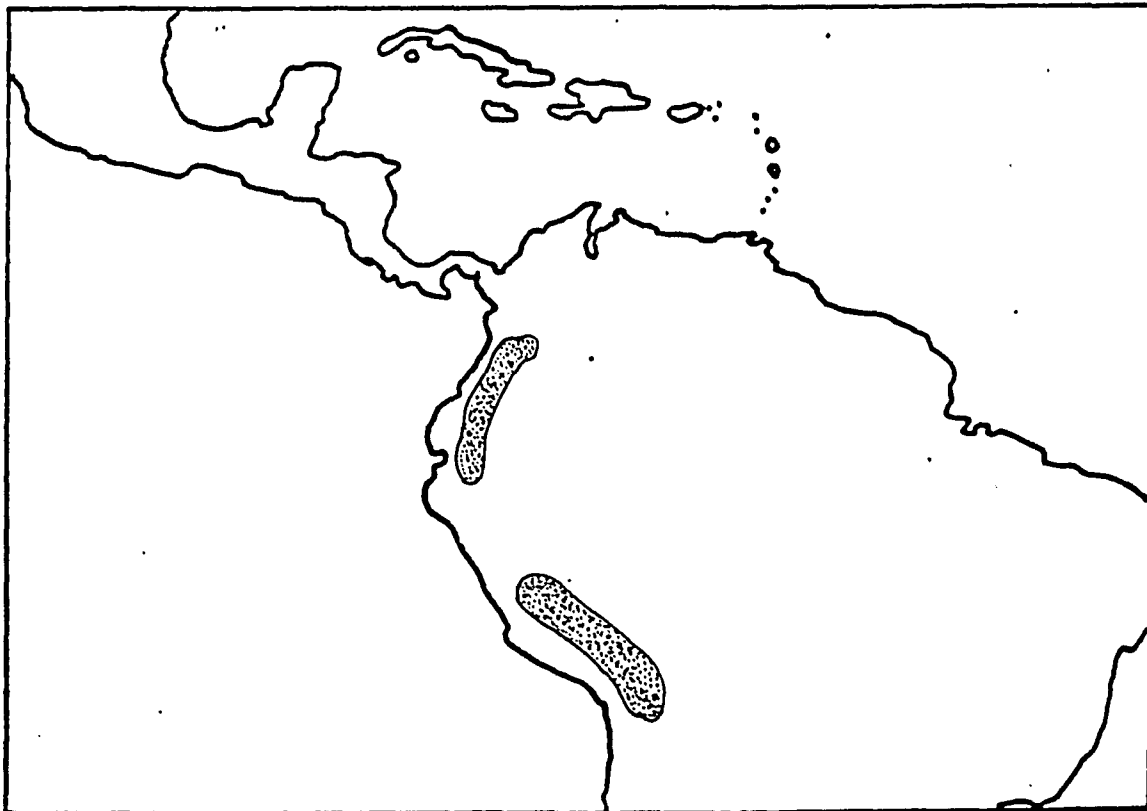


FIGURE 56 B.

28. *Juncus stipulatus* Nees & Meyen in Meyen, Reise um die Erde, Theil 4 (Beiträge zur Botanik): 126-127. 1843, also published as Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 16 Suppl. 2, which is at the same time Vol. 19 Suppl. 1; Lourteig, Comité National Français de Recherches Antarctique (CNFRA) 23 (Biologie): 33-49. 1968. Type. Chile. Valparaiso, Feb 1831, Meyen s.n. (holotype, PR, n.v., see Lourteig, 1968; 'in herb Lucaeana' according to Kunth, 1841, p. 324). Figs. 56 B, 57.

Juncus microcephalus Humboldt, Bonpland & Kunth β *pusillus*

E. Meyer, Rel. Haenkeana 1(2): 142. 1827; Kunth, Enum. pl.

3: 324. 1841 (as ♂ *pusillus*). Type. Peru. in montanis Peruviae, Haenke s.n. (holotype, probably at PR, n.v.).

Juncus chilensis Gay, Fl. chil. 6: 146. 1853. Type. Chile.

Colchagua: Cordillera de Talcaregüe, S. Fernando, 1833, Gay s.n. (holotype, P; isotypes, BREM, P).

Juncus gayanus Steudel, Syn. pl. glum. 2: 300. 1855. Type.

Chile. Colchagua: Cordillera de Talcaregüe, 1833, Gay s.n. (holotype, P).

Juncus oliganthus Philippi, Linnaea 29: 75. 1857. Type. Chile.

Valdivia: Corral, Philippi s.n. (holotype, SGO, n.v.; photo of holotype, GH; isotypes, BREM, G, K, P).

Juncus depauperatus Philippi, Florula Atacamensis 53. 1860. Type.

Chile. Antofagasta: Atacama Desert, Cachinal de la Sierra 25° lat. m., 7000 p.s.m., Philippi s.n. (syntype, n.v.); Valle Sardon 25°4' lat. m., c. 9000 p.s.m., Philippi s.n. (syntype, n. v.).

One specimen labelled 'des. Atac.' (Philippi s.n., K), was cited as isotype by Lourteig (1968).

Juncus corralensis Philippi, Linnaea 33: 269. 1864. Type. Chile. Valdivia: Corral, 1859, Krause s.n. (holotype, SGO, n.v.; photo of holotype, GH; isotype, P).

Juncus mandoni Buchenau, Abh. Naturwiss. Vereine Bremen 4: 121-123, pl.3, f.1-8. 1874. Type. Bolivia. La Paz: Larecaja, Viciniis Sorata; Gualata, Espadas etc. in paludosis, Regione temperata et alpina in paludosis, 2600-4100 m, Aug 1858-Feb 1859, Mandon 1440 (BM, G, GH, GOET, K, MO, NY, P). Lourteig (1968) cites the P-specimen as 'Type' (=holotype in her terminology), but Buchenau (1874) states that his description was based on a specimen at GOET or LUB.

Juncus stipulatus Nees & Meyen β corralensis (Philippi) Buchenau, Abh. Naturwiss. Vereine Bremen 6: 394. 1879.

Juncus biflorus Philippi ex Buchenau, ibid. nom. in syn.

Juncus melanocarpus Philippi ex Buchenau, ibid. nom. in syn.

Perennial herb, 1-10 cm high. Rhizome partly a long creeping, horizontal, occasionally branching stoloniferous part (rarely collected), at intervals producing erect or ascending, branching-ascending parts which gradually change into the culm, scales 5-10 mm long, membranaceous, light brown to stramineous, inserted 1-2 cm apart, enveloping the rhizome. Cataphylls absent, but basal leaves sometimes slightly reduced. Blade bearing leaves 10-15 to each culm, clustered or moderately spaced

FIGURE 57

Habit and detail of Juncus stipulatus (From Balslev, 1979a).

57A. Habit of depauperate specimen (Drawn from Øllgaard & Balslev
8206, AAU).

57B. Habit of normal specimen (Drawn from Øllgaard & Balslev 8536A,
AAU).

57C. Two flowered inflorescence of same.

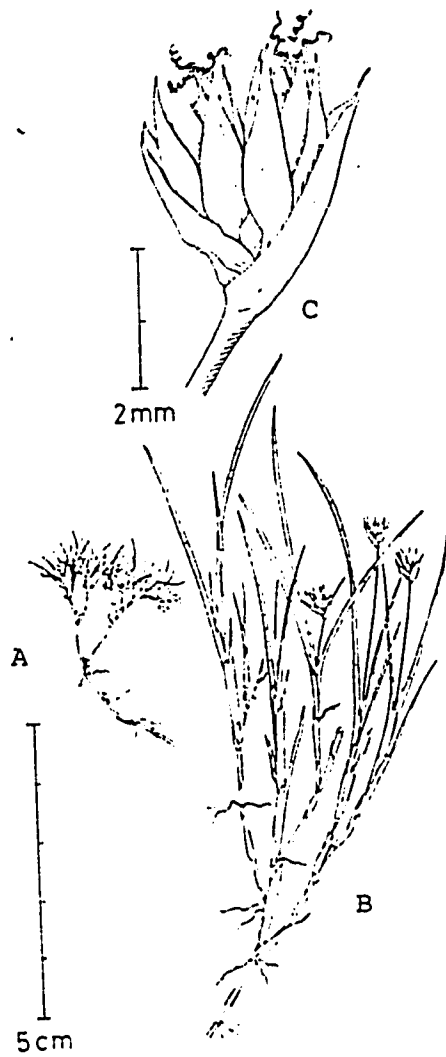


FIGURE 57

at the transition zone from rhizome to culm, 1-8 cm long; sheaths 2-15 mm long, margin membranaceous terminating in two 0.2-0.8 mm long rounded auricles; blade 0.2-0.3 mm diam., round to elliptical in cross-section, sometimes with adaxial groove basally, septa 1-3 mm apart, usually externally visible, sometimes absent or invisible in small leaves. Inflorescence one or rarely two 2-5 flowered heads terminal on and up to 7 cm long culm, sometimes reduced to a single flower on a pedicel equalling or slightly longer than the flower. Lower inflorescence bract resembling blade bearing leaves, to 2 cm long, sheath slightly shorter than the flower head, blade needle-like, floral bracts membranaceous, about as long as the flowers. Tepals equal or subequal, 2-3.5 mm long, lanceolate, acute, outer ones slightly wider than inner ones, midrib green turning reddish brown, margin reddish brown turning membranaceous. Stamens 6, 2.2-3.1 mm long, anthers linear, 0.8-1.3 mm long. Capsule ellipsoidal to suborbicular, apiculate, 2.5-3.5 x 1.5-2 mm, light brown to almost black, unilocular. Seeds broadly ellipsoidal, apiculate, 0.3-0.6 x 0.2-0.3 mm, usually reticulate, brown to reddish brown.

Distribution. In the Andes from Colombia to the Magellan Strait. In the northern Andes it is found above 3000 m altitude. It grows in a variety of situations from being a road side plant, a pioneer plant on landslides to being part of soft vegetation cover in suspended bogs. Correlated to these differences in growth conditions is a variation in habit from small, 1 cm high gnarled plants to up to 10 cm, more loosely branched and soft plants. Near stream sides or on lake shores this species may function as sand binder, forming mats on loose sediments

and being able to rapidly penetrate a new deposit of sediments to form a new mat.

Specimens examined. COLOMBIA. Caldas: Páramo del Quindio, 3700-4200 m, Pennell & Hazen 9963 (GH, K, NY, US). Cauca: Mt Puracé, 3450 m, von Sneider 2081 (F, G, NY, S), 3600-3700 m, Pennell & Killip 6543 (GH, NY). Cundinamarca: Páramo de Palacio, Laguna de Buitrago, 3620 m, Cleef 2351 (P); Páramo de Sumapaz, Chisaca, 3660 m, Cleef 3639 (AAU, P). Putumayo: Nr lake Cocha, 2700 m, Alston 8311 (US).

ECUADOR. Azuay: 10-15 km W of Sayausí (W of Cuenca), 3200-3400 m, Balslev 1574 (NY); Soldados-Angas rd, ca. km 8 (W of Cuenca), 3850 m, Balslev 1520 (NY); Páramo El Cajas W of Sayausí & Cuenca, 4100 m, Balslev 1452 (NY); Panamerican Highway 37 km S of Cuenca, 3200 m, Balslev 1235 (NY). Carchi: Páramo El Angel, 3500 m, Asplund 7102 (S, US); 7 km N of El Angel, 3700 m, Balslev & Quintana AAU-23905 (AAU, NY); 28 km N of El Angel, 3400 m, Balslev & Quintana AAU-23898 (AAU, NY), AAU-23899 (AAU, NY); Tulcán-Maldonado rd, km 53, 3150-3250 m, Holm-Nielsen et al. 5812 (AAU, F, MO, NY, S). Cotopaxi: Latacunga-Quevedo rd, km 18 W of Pujilí, 3700 m, Balslev 1053 (NY); 8 km S of Cotopaxi railroad station on rd to Mt Cotopaxi, 3450 m, Balslev 1185 (NY). Imbabura: Laguna Mojanda, 3600-3700 m, Øllgaard & Balslev 8778 (AAU), Balslev & Quintana AAU-24122 (AAU, NY). Loja: Panamerican Highway 19 km S of Oña, 3000 m, Balslev 1412 (NY). Napo: Quito-Baeza rd, 3-4 km W of Laguna Papallacta, 3550 m, Øllgaard & Balslev 8206 (AAU); Valle de Vicioso on E slope of Mt Cotopaxi, 3600 m, Holm-Nielsen & Balslev 23778 (AAU, NY). Pichincha: Mt Pichincha, Benoist 4380 (P); Lago San Marcos, NE slope of Mt Cayambe,

3400-3700 m, Holm-Nielsen & Balslev 23708 (AAU, NY), Cazalet & Pennington 5427 (K, NY); Mt Cayambe NE slope, 4000 m, Holm-Nielsen & Balslev 23682 (AAU, NY). Tungurahua: N slope Mt Chimborazo at Ambato-Guaranda rd, 3700-3900 m, Balslev 980, 989A (Ni).

PERU. Cuzco: La Convención, 3200-3900 m, White 123 (WIS). Puno: San Antonio de Esquilache, 4500 m, Stafford 1310 (F). Junín: Yauli, Pachachaca, 4000 m, Asplund 11629 (G, S).

BOLIVIA. La Paz: Murillo, La Paz, 3700-3800 m, Asplund 4347 (NY, S), 6374 (US), Buchtien 4353 (US); Palca valley, Huancapampa, 3700 m, Asplund 913 (NY, S), 1039 (NY, S); Pacajes, Ulloma, 3800 m, Asplund 2558 (NY, S); Pacajes, Calacota, 3800 m, Asplund 2808 (NY, S); Pacajes, Jeneral Campero, 3900 m, Asplund 2768 (S); Camancho, Ambana, 19 km towards Achacachi, 4300 m, Beck 4243 (NY); Larecaja, Sorata, 2600-4100 m, Mandon 1437 (G, GOET), 1440 (G); La Paz-Mina Kaluyo rd, 4100 m, Balslev & Beck 1152 (LPB, NY); 2 km N of Laguna Tuni, ca. 30 km due N of La Paz, 4500 m, Balslev & Beck 1151 (LPB, NY); Achacachi-Sorata rd, km 2.5, 3800 m, Balslev 1119 (LPB, NY); 3.5 km W of Comanche village, 4000 m, Balslev & Beck 1086 (LPB, NY); La Paz Airport-Achacachi rd, km 25, 3850 m, Balslev 1122 (LPB, NY); La Paz-Coroico rd, km 30, 3800 m, Balslev 1135 (LPB, NY); La Paz Airport-Achacachi rd, km 47 nr Chirapaca, 3850 m, Balslev 1120 (LPB, NY).

Juncus stipulatus belongs in the §29 of Buchenau (1906). He included 7 species in that group, 5 of which were South American. Barros (1953, 1969) accepted 6 South American species of this group. Louteig (1968) in a critical revision of the §29 included 5 species, one of which was described as new. Buchenau's 5 and Barros' 6 South

American species were reduced to 3 species: Juncus stipulatus, J. chilensis and J. scheuchzerioides. Of these J. scheuchzerioides supposedly does not reach north of the tropic of Capricorn, which leaves J. stipulatus and J. chilensis for consideration in this treatment of the neotropical Juncaceae. I have in vain tried to separate these two species, which, accordingly, have been lumped in my systematic treatment. To pay credit to Lourteig's detailed work, to avoid imposing my ignorance on my readers, and to encourage others to investigate the problem I present the differences that Lourteig (1968) based her taxonomy on in Table IV.

TABLE IV. The characters and features used by Lourteig (1968) to distinguish Juncus stipulatus, J. chilensis and J. scheuchzerioides.

	J. stipulatus	J. chilensis	J. scheuchzerioides
Phyllodes (=leaves)	Rigid, septa protruding adaxial furrow reaching from the stipules to the first few nodes, rarely longer	Less consistent, septa not visible. Blade + laterally compressed, longitudinal striae conspicuous	Adaxial furrow longer than in <u>J. stipulatus</u> , often reaching to the tip of the phyllode.
Stipules	Acute	Rounded	
Tepals		Light green, narrow, rather flat.	Reddish purple, closed, very acute, lanceolate, concave.
Capsule	Copper colored, + dark, oblong, apically rounded and mucronate, slightly longer than perianth.	Castaneous to light green, about as long as the perianth.	Castaneous to reddish, sometimes very dark, ovoidal to trigonous, mucronate, longer than the perianth.
Seeds	0.31-0.57 x 0.20-0.34 mm reticulation well marked but not as regular as in <u>J. chilensis</u> . Longitudinal ridges strong, more red than the rest of the surface. Ridge margin regularly dentate.	0.37-0.50 x 0.18-0.30 mm translucent. Polygons orderly arranged, slightly concave. Longitudinal margins with minute rounded teeth. Entire surface overrun by lines of fine tubercles. External envelope very fine and transparent.	(0.50-)0.66-0.70 x 0.33-0.40 mm dark. Reticulation fine, low regular. Polygon masks have rounded angles, and are less serrate in the equatorial region than at the poles.

29. *Juncus liebmannii* Macbride, Field Mus. Nat. Hist., Bot. Ser. 11,

1: 9. 1931 (as *J. liebmanni*). Basionym. *Juncus brevifolius*

Liebmann not. Rostkovius, 1801.

Figs. 58, 59.

Perennial herb, (15-)20-50(-65) cm high. Rhizome creeping, 1.5-3 mm diam., scales absent or few, membranaceous, internodes 0.5-1 cm long. Culms erect, often slightly curved, 1-2.5 mm diam. Cataphylls 0-3 to each culm, 1.5-7 cm long, reddish tinged when young, later light brown with distinct membranaceous margin, rudimentary blade to 2 mm long. Blade bearing leaves 1-4 basal and 1-2 cauline to each culm, 10-30 cm long; sheaths 3-12 cm long, with membranaceous margins terminating in two 0.3-1.3 mm long, involute auricles; blades 1-2.5 mm diam., elliptical to round in cross-section, laterally compressed, hollow, nodulated but sometimes inconspicuously so by septa 5-15 mm apart. Inflorescence terminal, compound racemose, usually divided into two subequal parts, one terminal on the culm and one laterally inserted, the lateral one usually overtopping the terminal one, ultimate branchlets with three to several flowers clustered together, but no distinct flower heads. Lower inflorescence bract to 12 cm long, resembling cauline leaves, sometimes membranaceous and shorter, to 2 cm long, upper bracts progressively shorter, the ultimate ones membranaceous to 4 mm long, floral bracts to 3 mm long. Tepals subequal, lanceolate, dark brown, sometimes with green midrib and reddish brown margin basally, outer ones 2.3-3 mm long, keeled to V-shaped in cross section, at least when young, inner ones 2-2.5 mm long, flat. Stamens 6, 1.1-1.8 mm long, inner whorl sometimes slightly shorter; filaments 0.8-1 mm long, flat

or filiform, slightly widened towards the base; anthers oblong, 0.4-0.8 mm long, shorter than the filament. Capsule ellipsoidal, apiculate, trigonous becoming 3-keeled before dehiscing, 2-3 x (0.9-)1.2-1.6 mm, sometimes longer than the tepals when mature, dark brown, unilocular. Seeds ellipsoidal, apiculate, ca. 0.5 x 0.2 mm, with conspicuous reticulate pattern, yellowish brown.

Distribution. Disjunct between México and northern Andes. The typical variety occurs from the Federal District of México to Guatemala, and var. quitensis occurs from the department of Nariño in southern Colombia to the province of Tungurahua in central Ecuador.

Key to the varieties of Juncus liebmannii

1. Culms to 1.2 mm in diam., usually 15-30 cm high, sometimes higher but the capsule then twice or more as long as wide. México and Guatemala. 29a. J. liebmannii var. liebmannii.
1. Culms to 2.5 mm diam., 20-50 cm high, capsules less than twice as long as wide. Colombia to Ecuador. 29b. J. liebmannii var. quitensis.

Juncus brevifolius Liebmann, Vidensk. Meddel. Dansk Naturhist.

Foren. Kjøbenhavn 40. 1850, not Rostkovius, 1801. Type.

México. Puebla: Chinautla, 2150 m, May 1841, Liebmann s.n.

(holotype, C; isotypes, C, G, GH, K, MO, P).

Juncus brevifolius Liebmann var. *mexicanus* Buchenau, Bot. Jahrb.

Syst. 12: 355. 1890. Basionym. *Juncus brevifolius* Liebmann.

Distinguished as indicated in the key.

Distribution. From the state of Chihuahua in México to Huehuetenango in Guatemala. Found in swamps and marshes and along creeks at altitudes between 2100 m and 2900 m.

Specimens examined. MEXICO. Chiapas: Tenejapa, Ach'lum, 2775 m, Breedlove 15252 (MO); NE side of Matsab hill, 2570-2800 m, Breedlove 15276 (MO), Ton 974 (NY). Hidalgo: Canales Station, 1850 m, Pringle 10011 (WIS). México. Valle de México, Deserta Negra, Bourgeau 1148 (P); Valle de México, 2450 m, Schaffner 532 (MO); Nevada de Toluca, Rose & Painter 7930 (NY); Temascaltepec, 2460 m, Hinton 1564 (NY). Vera Cruz: Cruz Blanca, Perote, 2300 m, Balls et al. B5501 (K); Actopan, Cofre de Perote, Balls et al. B5451 (K).

GUATEMALA. Huehuetenango: Nucá-Queztal, 2100-2500 m, Steyermark 49770 (NY). Totonicapan: Tecum Uman Ridge 20 km E of Totonicapan, 3340 m, Beaman 4186 (W). Without department: San Marcos, M. Gamain (?). 2000 m, Lehmann 157b (G).

This typical variety is morphologically less well circumscribed than var. quitensis, which may be caused by its geographically disrupted distribution. The northern populations are smaller and more delicate plants than those from the state of Chiapas in México and Guatemala. These southern populations of var. liebmannii may be up to 75 cm high which is more than the average plant of var. quitensis. The culms are, however, always slender, i.e. to 1.2 mm diam., so the appearance of the entire plant is less robust than that of var. quitensis, where the culms are up to 2.5 mm diam. These tall specimens of var. liebmannii also have more slender capsules, that are more than twice as long as wide, whereas var. quitensis always has capsules less than twice as long as wide. Maintaining the Mexican and Guatemalan populations as a variety of its own is therefore based as much on the geographical separation from var. quitensis as it is based on morphological evidence, where one has to depend on average values and combinations of features.

FIGURE 58

58 A. The distribution of Juncus liebmannii var. liebmannii.

58 B. The distribution of Juncus liebmannii var. quitensis.

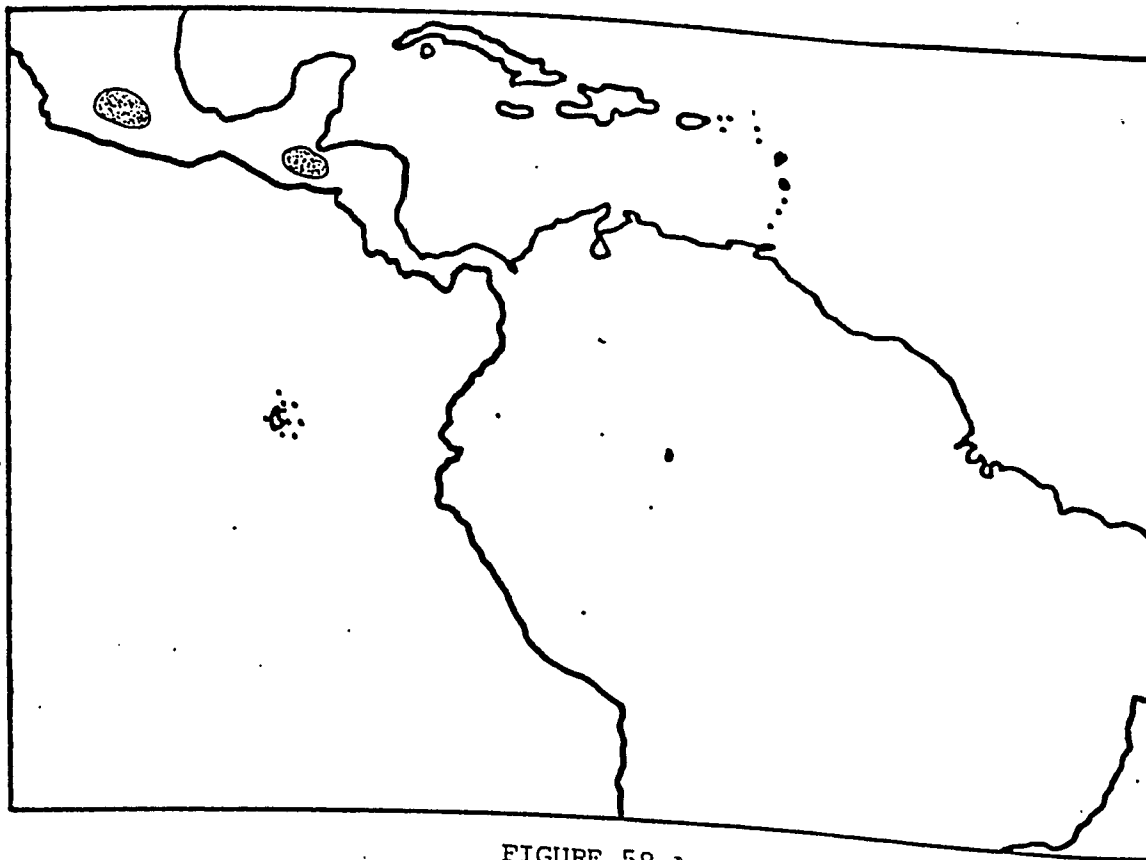


FIGURE 58 A.

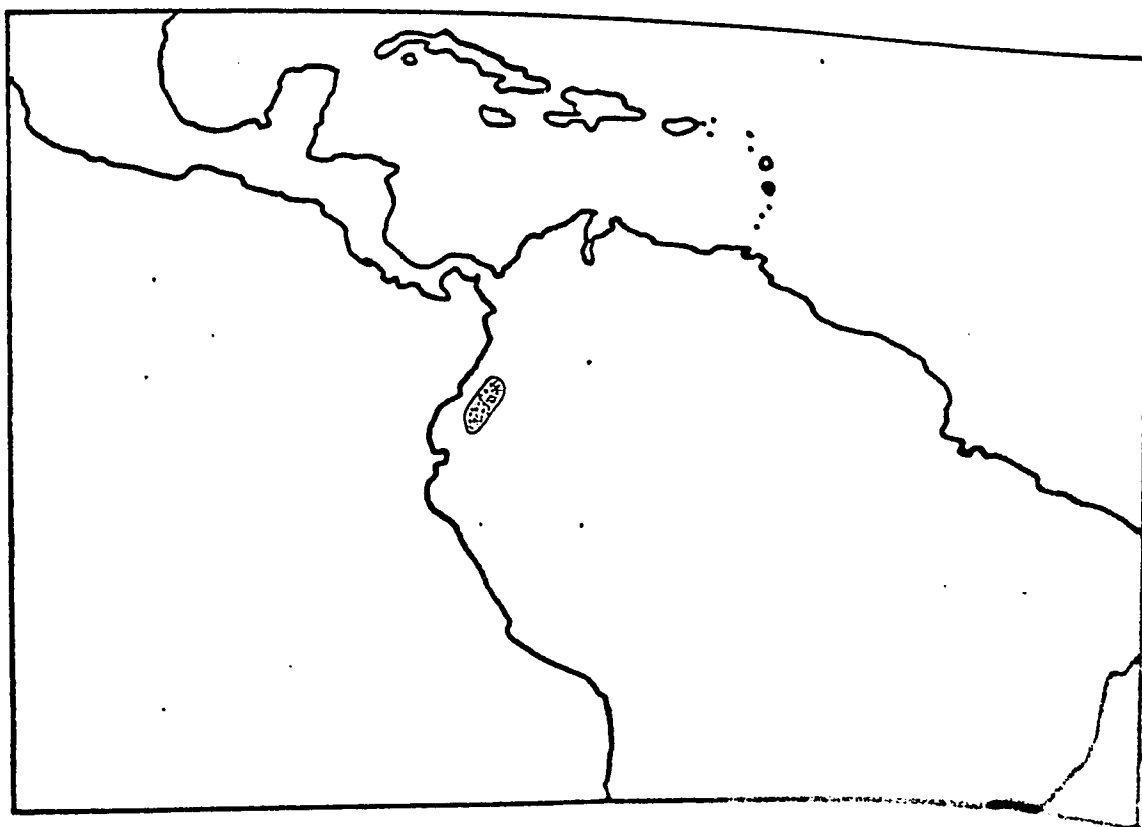


FIGURE 58 B.

29b. *Juncus liebmannii* Macbride var. *quitensis* (Buchenau) Balslev,

Fl. Ecuador 11: 40. 1979. Basionym. *Juncus brevifolius*

Liebmann var. *quitensis* Buchenau.

Figs. 58 B, 59.

Juncus brevifolius Liebmann var. *quitensis* Buchenau, Bot. Jahrb.

Syst. 12: 356. 1890. Type. Ecuador. Pichincha: Surubamba near

Quito, 1859, Jameson 880 (lectotype, K; isoelectotypes, BM, C,

G, GH, GOET, K, NY, P). Tungurahua: Baños, Feb 1859, Spruce

5942 (syntypes, BM, K).

Distinguished as indicated in the key.

Distribution. In both the eastern and the western cordilleras of the Andes from the department of Nariño in southern Colombia to the provinces of Chimborazo and Tungurahua in central Ecuador. It grows in pastures, meadows, along rivulets and in raised bogs at altitudes between 2800 m and 3500 m, as well in the páramos as in the cultivated land.

Specimens examined. COLOMBIA. Nariño: Upper Río Tescual above Córdoba, 2840-2890 m, Ewan 16298 (GH, US). Without locality: "New Granada", Triana 478 (K).

ECUADOR. Carchi: Tulcán-El Carmelo rd, km 18, 3300 m, Balslev & Quintana AAU-23846 (AAU, NY); E slopes of Mt Chiles nr Tufiño, 3500 m, Drew E-471 (COL, NY, US); Páramo El Angel, 3400-3500 m, Holm-Nielsen et al. 5317 (AAU, COL, F, NY, S), 5257 (AAU, F, NY, S), Sparre 14231 (S), Benoist 3655 (AAU); Tulcán-El Angel rd, 34 km S of Las Juntas, 3550 m, Balslev & Quintana 895 (NY). Chimborazo: Riobamba, Mille 358

FIGURE 59

Habit of Juncus liebmannii var. guitensis (Drawn from Sparre 14231, S (A), and Asplund 16241, S (B); from Balslev 1979a).



FIGURE 59

(US). Imbabura: Piñau, Mt Cotacachi, 3170 m, Drew E-106 (US); Laguna
Cunro, Prescott 280 (NY). Pichincha: Plains of Quito, Jameson 263 (K);
Quito, Benoist 2049 (P); San Juan-Quito, 3450 m, Asplund 16241 (S);
Lloa valley, 2600 m, Benoist 2720 (P), Holm-Nielsen & Balslev 23585
(AAU, NY); 8 km N of Cayambe village, 2850 m, Prescott 116 (NY);
Alóag 30 km S of Quito, 2890 m, Fosberg 22444 (US); Machachi, 2900 m,
Asplund 16029, 6227 (S); Mt Atacazo, Sodiro 186/2 (S); San Golqui,
2800 m, Asplund 6948 (S).

Common name. Hierba de Cienaga (Drew E-106).

30. *Juncus ebracteatus* E. Meyer, Synops. Junc. 28. 1822. Type.

México. Guerrero (?): Acapulco, 1791, Haenke s.n. (holotype, probably at PR, n.v.) Figs. 60, 61 A.

Juncus trinervis Liebmann & elatus Liebmann, Vidensk. Meddel.

Dansk. Naturhist. Foren. Kjøbenhavn 41. 1850. Type. México.

Puebla: Cerro Leon, 2135 m, Jul 1841, Liebmann 855 (holotype, c; isotype, C).

Juncus trinervis Liebmann β minor Liebmann, ibid. Type.

México. Oaxaca: Hacienda de Castresana in eastern Oaxaca, 2285 m, Jun 1842, Liebmann s.n. (holotype, C; isotypes, C, K, P).

Juncus brunneus Buchenau, Abh. Naturwiss. Vereine Bremen 6: 403.

1879. Type. Bolivia. La Paz: Larecaja, Viciniis Sorata prope capellam in glareosis et prope Locatia in paludosis, 2700-3800 m, Jan-Mar 1857, Mandon 1436 (syntypes, BM, G, MO, K, NY, P).

Peru. Azangaro, Jun 1854, Lechler 1749 (syntypes, G, K, P, S).

Perennial herb, (5-)15-30(-65) cm high. Rhizome stoloniferous, 1-2.5 mm diam., naked or with few membranaceous light brown to 5 mm long scales. Culms usually arising at nodes 1-5 cm apart or sometimes a few clustered together, erect or slightly curved, 0.7-2 mm diam., smooth or longitudinally wrinkled, not ridged, the basal internode sometimes elongated, separating the leaf rosette from the rhizome. Cataphylls 0-2 to each culm, up to 6.5 cm long, membranaceous or herbaceous, obtuse, mucronate or with rudimentary blade to 1.5 mm long. Blade bearing leaves 2-4(-7) to each culm, inserted below the middle of the culm, sometimes all basal, 4-20 cm long; sheaths 1.5-9 cm long,

with membranaceous margin terminating in two 0.5-1.5 mm long rounded auricles; blades linear, 0.5-3 mm diam., terete, hollow, nodulated by septa 1-15 mm apart. Inflorescence terminal, compound, anthelate, flower heads (1-)2-8(-11), semiglobose to globose at maturity, 7-12 (-14) mm diam.; (5-)10-20(-30) flowered, conspicuous by the protruding styles and beaks. Lower inflorescence bract to 5 cm long, resembling basal leaves with a sheath and a cross-septate blade or reduced to a sheath with a needle-like blade, upper bracts progressively shorter, floral bracts lanceolate, to 3.5 mm long, brown to castaneous. Pedicels sometimes up to 2 mm long and visible in the flower heads. Tepals subequal, 2.5-5 mm long, lanceolate, acute, castaneous to reddish brown, paler towards the base, sometimes pale or blackish brown throughout, outer ones concave or usually V-shaped in cross section, inner ones sometimes slightly shorter, flat, often with three clearly visible nerves. Stamens 6, 1.5-2.3 mm long; filaments flat, widened towards the base; anthers linear 1-1.8 mm long, much longer than the filaments, very light yellow to almost whitish at anthesis. Style 1-3 mm and stigmas 1-3 mm long, conspicuous. Capsule obovoidal to obclavate, basally 3-lobed, trigonous, 3-4 x 1-1.3 mm, tapering towards the 1-2 mm long protruding beak, light to dark brown, unilocular. Seeds ovoidal, apiculate, 0.4-0.5 x 0.2-0.3 mm, rugose, brown.

Distribution. Along the Méxican highlands and into Guatemala at altitudes between 1800 m and 3000 m, and again along the Andes from Ancash in northern Peru to the southern border of Bolivia, most commonly between 3000 m and 4000 m, but occasionally as low as 1800 m or 2000 m.

FIGURE 60

Habit and detail of Juncus ebracteatus.

60A. Habit (Drawn from Metcalf 30415, GH).

60B. Flower of same.

60C. Habit (Drawn from Buchtien 508, NY).

60D. Flower of same.

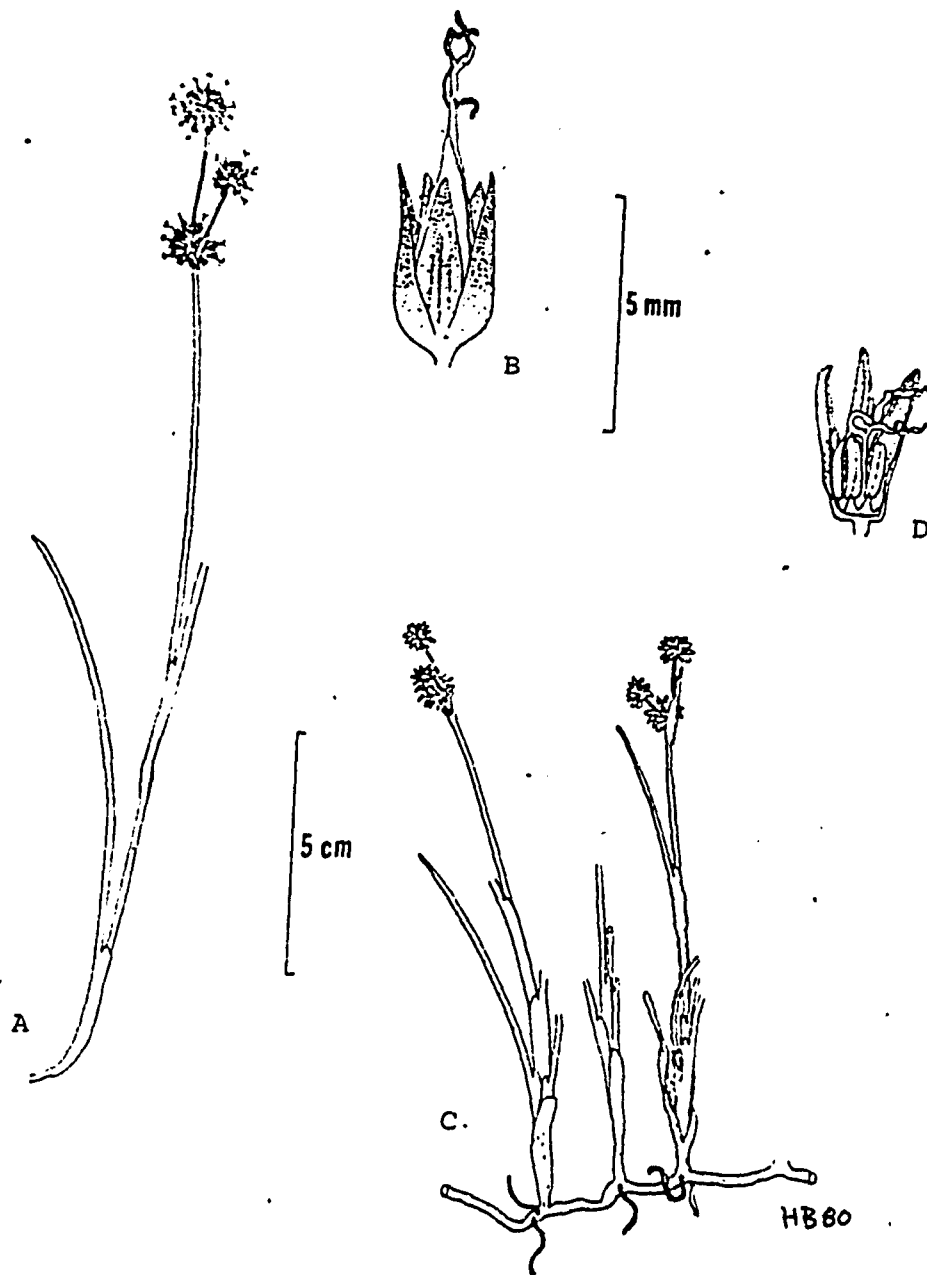


FIGURE 60

It grows in grassy swales, meadows, riverbeds and along creeks, always in places with waterlogged soil, sometimes even in flooded places.

Representative specimens. MEXICO. Chiapas: 25 miles NE of San Cristóbal Las Casas along highway 199, 2100 m, Croat 40469 (MO). Distrito Federal: Valle de México, Pringle 6652 (G, GOET, K, MO, NY, P, WU). Hidalgo: Rancho Nuevo 16 km ENE of Apam, 2700 m, West K-3 (WIS). Jalisco: Guadalajara, Palmer 241 (NY, P, WU). México: Tequexquipan, Temascaltepec, 2480 m, Hinton 1332 (MO, NY). Michoacán: Morelia, Loma Sta. Maria, Arséne 6687 (P). Oaxaca: 6 km S of Mt Pelon, 2743 m, Hill 1738 (NY). Puebla: Acatzingo, Cepeaca, 1900 m, Arséne 1918 (NY). San Luis Potosí: Sierra de San Miguelito S of San Luis Potosí, 1900-2000 m, Pennell 17713 (NY). Veracruz: Orizaba, Mueller 1954 (NY), 1955 (P), 7955 (P).

GUATEMALA. Huehuetenango: Sierra de los Cuchumatanes 2.5 miles E of San Mateo Ixtatan, 2500 m, Steyermark 49880 (NY). Sololá: Sierra Madre Mts, 10-12 km NW of Los Encuentros nr Maria Tecum, 3000 m, Williams et al. 27332 (NY). Totonicapán: 5 miles E of Totonicapán, 2950 m, Webster et al. (MO). Quezaltenango: Sierra Madre Mts ca. 4 km N of Olientepeque, 2600 m, Williams et al. 22864 (NY).

PERU. Ancash: Carhuas, Cordillera Blanca, Río Marcará valley, Vicos, 2960 m, Hutchinson & Wright 4294 (F, NY, US, USM). Arequipa: Nr Arequipa, Harrison s.n. (GH). Ayacucho: La Quinua-Tambo rd, km 1, 15 km E of Ayacucho, 3290 m, Keel K-411 (NY). Cuzco: Cusco, Sajsaihuaman, 2600 m, Vargaz 252 (F, MO). Huancavelica: Tayacaja, N of Pampas, 3250 m, Stork & Horton 10233 (F). Junín: Huancayo, Soukup 3973

(COL, F, GH). Puno: Huancané-Conima, 3900 m, Aguilar 335 (USM).

Tacna: Tarata-Juro Nanny trail, km 7, 2600 m, Metcalf 30415 (G, GH, MO).

BOLIVIA. Cochabamba: Cochabamba, Bang 1076 (G, GH, K, MO, NY, US, WIS). La Paz: Achacachi-Sorata rd, km 2.5, 3800 m, Balslev 1118 (LPB, NY). Potosí: Linares, Tambillos, Hammarlund 420 (S). Tarija: Tucumilla, 3000 m, Fiebrig 2640 (G, GH).

Juncus ebracteatus is most easily recognized by its long creeping stoloniferous rhizome and the long protruding styles which remain through fruit maturation as long beaks on the capsules. The very light yellow or white anthers which are several times longer than the filaments are also characteristic. The Peruvian and Bolivian populations have hitherto been known as J. brunneus, and the Central American and Mexican populations as J. trinervis, but there is no basis for maintaining two separate taxa. Buchenau (1890, 1906) was well aware of Meyer's earlier name J. ebracteatus and had seen the type, but he discarded it as misleading. He considered Liebmann's later name J. trinervis descriptive not misleading and preferable.

FIGURE 61

61 A. The distribution of Juncus ebracteatus.

61 B. The distribution of Juncus micranthus in the neotropical region.

In addition it occurs in temperate South America.

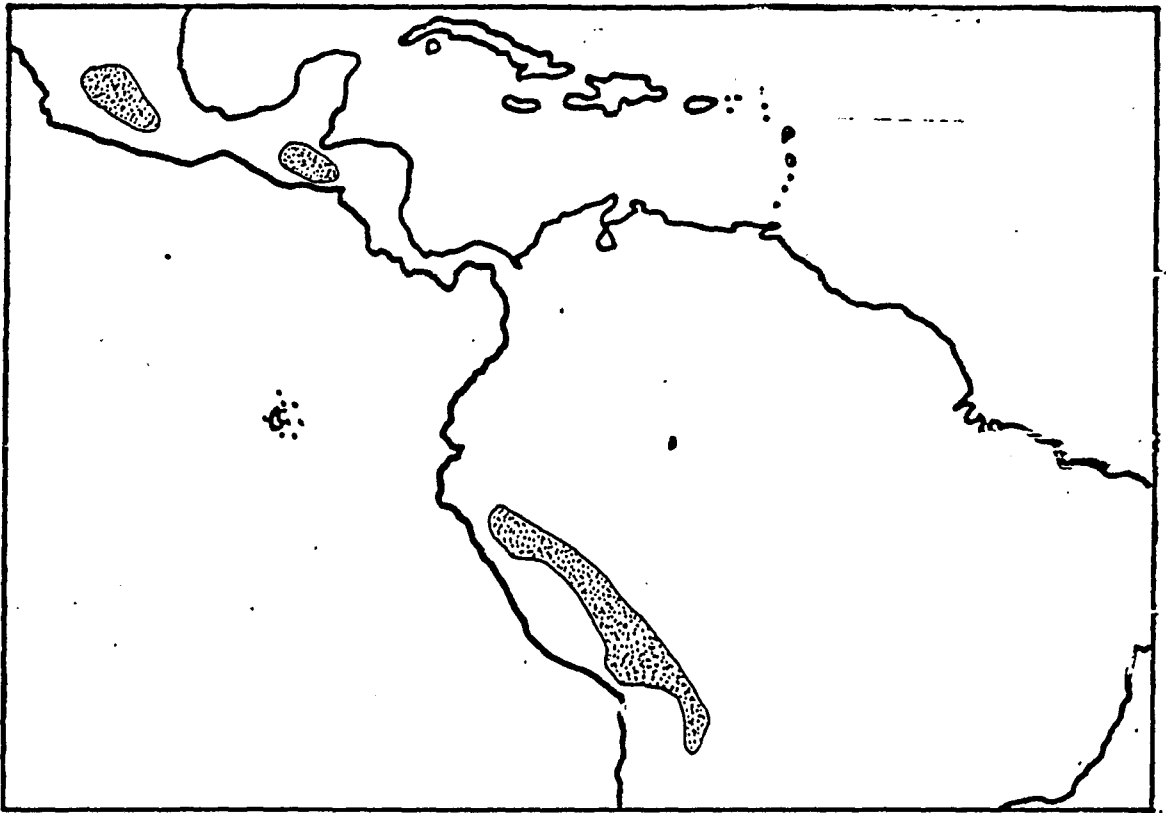


FIGURE 61 A.

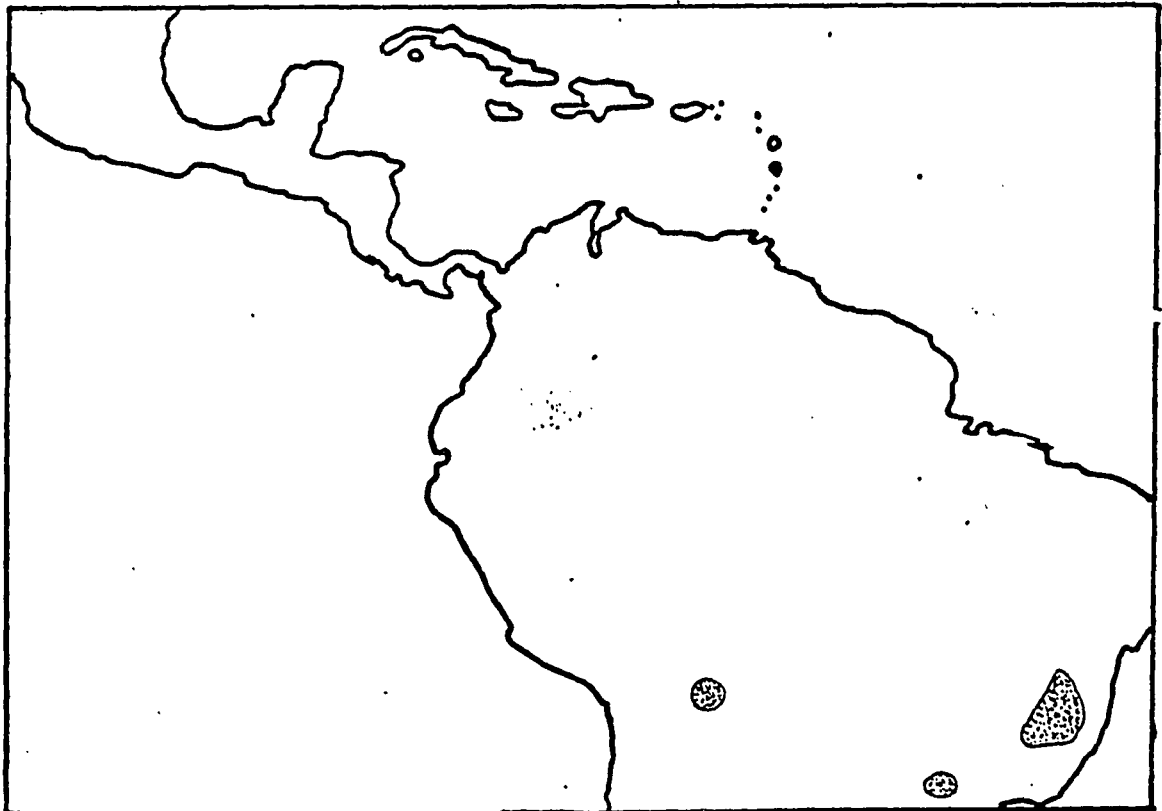


FIGURE 61 B.

31. *Juncus micranthus* Schrader ex E. Meyer, Synops. Luzularum 31. 1823.

Type. Brazil. in sabulo insularum fluv. Rio Belmonto, Prince Max Neuwind s.n. (holotype, n.v.; isotype, MO). Fig. 61 B.

Juncus scirpoides Lamarck var. *meridionalis* Buchenau, Bot. Jahrb.

Syst. 12: 324. 1890. Basionym. *Juncus micranthus* Schrader ex E. Meyer.

Juncus meridionalis (Buchenau) Herter, Estud. bot. reg. Uruguay 24: 201. 1956.

Perennial herb, 50-85 cm high. Rhizome horizontal, short-creeping, 4-9 mm diam, scales membranaceous, usually covering the surface or sometimes slightly spaced, internodes 0.5-1 cm. Culms erect, 1.2-2.5 mm diam, terete, smooth. Cataphylls 2-3 to each culm, 1-15 cm long, green, stramineous or brown, often unfolding and not densely sheathing the mature culm, rudimentary blade needle-like, 2-5 mm long. Blade bearing leaves 2-3 to each culm, all cauline and none basally inserted, lower one 20-80 cm long, sheath 5-13 cm long with membranaceous margins terminating in two rounded 1-2 mm long auricles, blade terete (0.8-)1-1.5 mm diam., hollow with transverse septa 2-8 mm apart but not always externally nodulated, upper leaf often inserted above the middle of the culm, usually short, the blade sometimes only 5 cm long. Inflorescence compound, anthelate, up to 7 x 4 cm but usually smaller and sometimes only 2.5 x 2 cm, flower heads 5-12, globose, 6-10 mm diam., 35-50 flowered, stramineous or rarely light reddish brown principal branches to 6 cm long and 1.2 mm diam. Lower inflorescence bract 2.5-6.5 cm long with 0.5-4 cm long rudimentary blade, upper bracts

progressively shorter, floral bracts membranaceous, shorter than the flowers. Tepals equal or outer ones sometimes slightly longer, 2.3-2.9 mm long, linear-lanceolate, subulate, rigid, outer ones concave, inner ones flat. Stamens 3, 1-1.5 mm long; filaments filiform; anthers oblong, 0.3-0.5 mm, much shorter than filament. Capsule ovoidal, beaked, 3-lobed, 2.2-2.9 mm (incl. beak) x 0.7-0.9 mm, usually as long as or longer than the tepals, light brown, unilocular, dehiscing laterally, the valves remaining connate at the beak. Seeds ellipsoidal, apiculate, 0.3-0.4 x 0.15-0.2 mm, reticulate, yellowish brown.

Distribution. In the highlands of southeastern Brazil from the state of Bahia, southwards into the lowlands of Paraguay, northeastern Argentina and Uruguay. Also twice collected in Bolivia. It grows in meadows and on sandy or muddy riversides as high as 1400 m altitude towards the north and as low as 200 m towards the south.

Specimens examined. BRAZIL. Bahia: Rio Brumado ca. 2 km N of Rio de Contas, 980 m, Harley et al. 15508 (NY), 20044 (K); 19.5 km SE of Morro do Chapéu, 900 m, Harley et al. 19214 (K). Minas Gerais: ca. 10 km SW of Diamantina, 1250 m, Anderson et al. 35217 (NY); ca. 18 km SW of Diamantina on Curvelo rd, 1400 m, Anderson 8485 (NY). São Paulo: São José dos Campos, 610 m, Mimura 123 (K).

BOLIVIA. Santa Cruz: Sara, Buena Vista, 450-500 m, Steinbach 5245 (F, GH, NY), 6728 (F, GH, MO, NY).

PARAGUAY. Sierra de Maracayu, Hassler 5259 (G); Tobaty, Hassler 6263 (G); Caaguagu (?), Balansa 395 (GOET); Santiago, Estancia La Soledad, Pedersen 4299 (NY); Yhú, Hassler 9487 (MO, GH, NY, S).

Juncus micranthus is most closely related to J. densiflorus.

From this species it has traditionally been said to differ in having equal long tepals and the capsule longer than these, whereas J. densiflorus has longer outer tepals and the capsule shorter than these.

In this set of characters the two species are sometimes difficult to distinguish in the southern part of their distributional areas.

Juncus micranthus is, however, a more delicate plant, smaller in all vegetative and floral dimensions, but with proportionally much thicker rhizome, which is 4-9 mm in diam. relative to a plant height of 50-85 cm, and the rhizome internodes are short, less than 1 cm, so the culms arise crowded. Juncus densiflorus in contrast is a larger plant with proportionally thinner rhizome which is 3-7 mm in diam. relative to a plant height of 65-135 cm, the rhizome internodes are more than 1.5 cm long, so the culms do not arise crowded.

32. *Juncus nodosus* Linnaeus, Sp. Pl. 2 ed., 1: 466. 1762. Type.

America septentrionali n.v. (sent to Linnaeus by Kalm, most probably from Canada, according to Engelmann, 1868, p. 472). Fig. 62 A.

Juncus rostkovii E. Meyer, Synops. Junc. 26. 1822. Basionym.

Juncus nodosus Linnaeus.

Juncus nodosus Linnaeus var. *vulgaris* Torrey, Fl. Sate New York 2: 326. 1843. Basionym. *Juncus nodosus* Linnaeus.

Juncus nodosus Linnaeus var. *genuinus* Engelmann, Trans. Acad.

Sci. St. Louis 2: 436. 1866, name only, and l.c. 2: 471. 1868, full treatment. Basionym. *Juncus nodosus* Linnaeus.

Juncus nodosus Linnaeus var. *proliferus* Lunell, Amer. Midl.

Naturalist 4: 238. 1915.. Type. USA. North Dakota: Butte.

No specimen or collector cited.

Juncus nodosus Linnaeus var. *meridianus* Hermann, J. Arnold Arbor.

25. 58. 1944. Type. México. Chihuahua: Chihuahua, 5-10 Jun 1908, Palmer 360 (holotype, US, n.v.; isotype, K, NY).

Perennial herb, 10-30 cm high. Rhizome horizontal, stoloniferous, long creeping, 0.5-1 mm diam., scales absent or few, often with bulbous thickenings at the base of the culms, internodes up to 7 cm long. Culms erect, 0.5-1.5 mm in diam., smooth. Cataphylls 0-2 to each culm, to 4 cm long, inconspicuous. Blade-bearing leaves (1-)2-4(-6) spaced along the culms or sometimes a few clustered basally, (2-)10-25 cm long; sheaths 1.5-5 cm long, with membranaceous margin terminating in two (0.5-)1-2 mm long rounded auricles; blades 0.5-1 mm diam., terete, hollow, with most often inconspicuous septa 1-5 mm apart, ad-

axially grooved almost throughout. Inflorescence compound, anthelate, up to 7.5 x 4 cm, flower heads (1-)3-5(-7), globose, 8-12 mm diam., (5-)15-25(-30) flowered, light green to stramineous or sometimes with slight red pigmentation, principal branches to 5.5 cm long and 1 mm diam. Lower inflorescence bract (1.5-)5-15 cm long, resembling cauline leaf with 0.5-1 cm long sheath, upper bracts progressively shorter. Tepals equal, 2.8-4.5 mm long, linear-lanceolate, subulate, outer ones concave, inner ones flat. Stamens 3, 1.2-1.6 mm long; filaments flat; anthers oblong to linear, 0.5-0.7 mm long, usually as long as or shorter than the filaments, before anthesis sometimes slightly longer than the filaments. Capsule narrowly ovoidal, gradually tapering into a not clearly demarcated 0.5 mm long beak, trigonous, 3-4.7 mm (incl. beak) x 0.7-1.3 mm, clearly exceeding the tepals when ripe, light to dark brown, unilocular. Seeds ellipsoidal, apiculate, 0.4-0.5 x 0.2-0.25 mm, reticulate, yellowish brown.

Distribution. A temperate North American species with main distributional area from Newfoundland southwards along the east coast to West Virginia and across the continent through northern United States and southern Canada into the Rocky Mountains, but apparently not reaching the west coast. Isolated populations occur in northern Canada, Alaska, and northern México and adjacent Texas. In México it grows in wet places near water at altitudes between 500 m and 2100 m. The 12 Mexican populations seen came from the Sierra Madre chains and the Méxican plateau.

Specimens examined. MEXICO. México: Temascaltepec, Las Mesas, 2000 m, Hinton 3726 (MO). San Luis Potosí: Characas, Whiting 634 (NY); Estación de Catorce, 1900-2000 m, Pennell 17586 (NY).

Juncus nodosus is closely related to J. torreyi and J. texanus. These three species, originally considered varieties of J. nodosus, are related through the stoloniferous rhizome with long internodes and bulbs or knobs at the base of the culms, a feature which I do not know from any other species of the genus. Juncus texanus occurs in the Texas lowland and is distinct from J. nodosus through its larger size, its long anthers which are always much longer than the filaments, instead of shorter or only slightly longer, and the long beak which makes the capsule subulate and more narrow. Juncus torreyi occurs in most of the United States and southern Canada and is even larger than J. texanus with large 40-50 flowered flower heads, which makes it easily distinguishable.

FIGURE 62

62 A. The distribution of Juncus nodosus in the neotropical region.

In addition it is widespread in temperate North America.

62 B. The distribution of Juncus densiflorus in the neotropical region.

In addition it occurs in temperate South America.

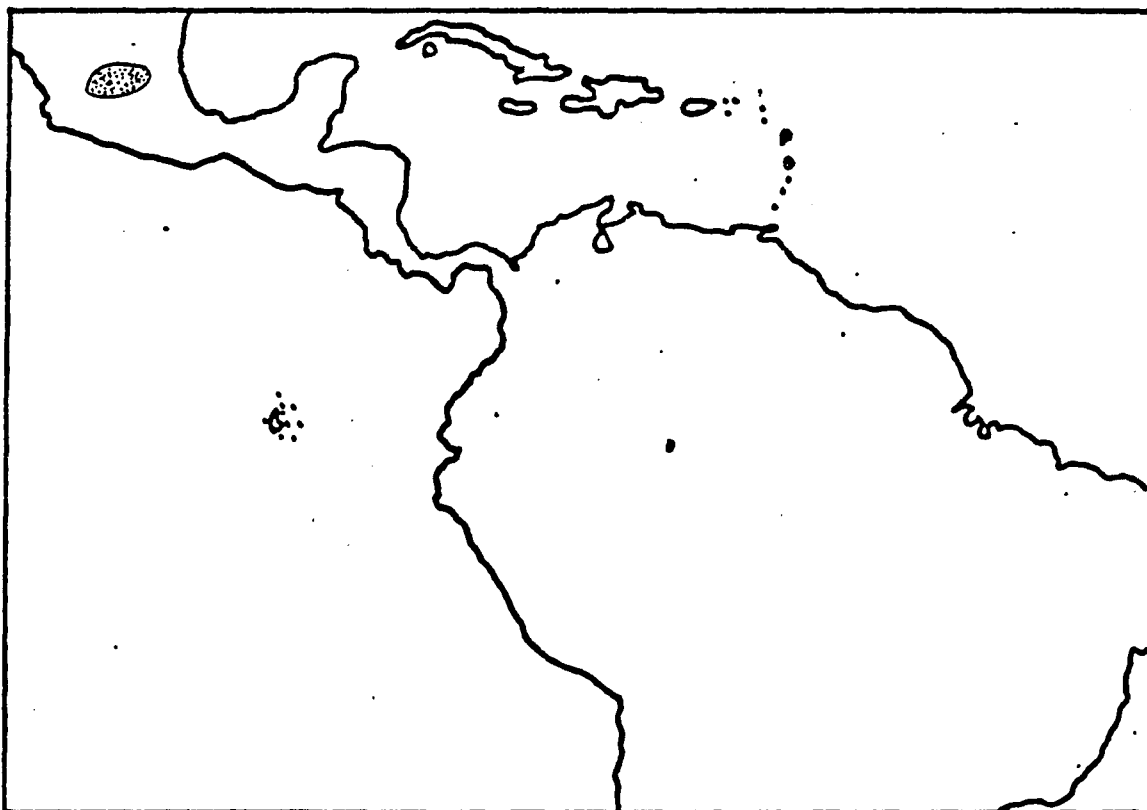


FIGURE 62 A:

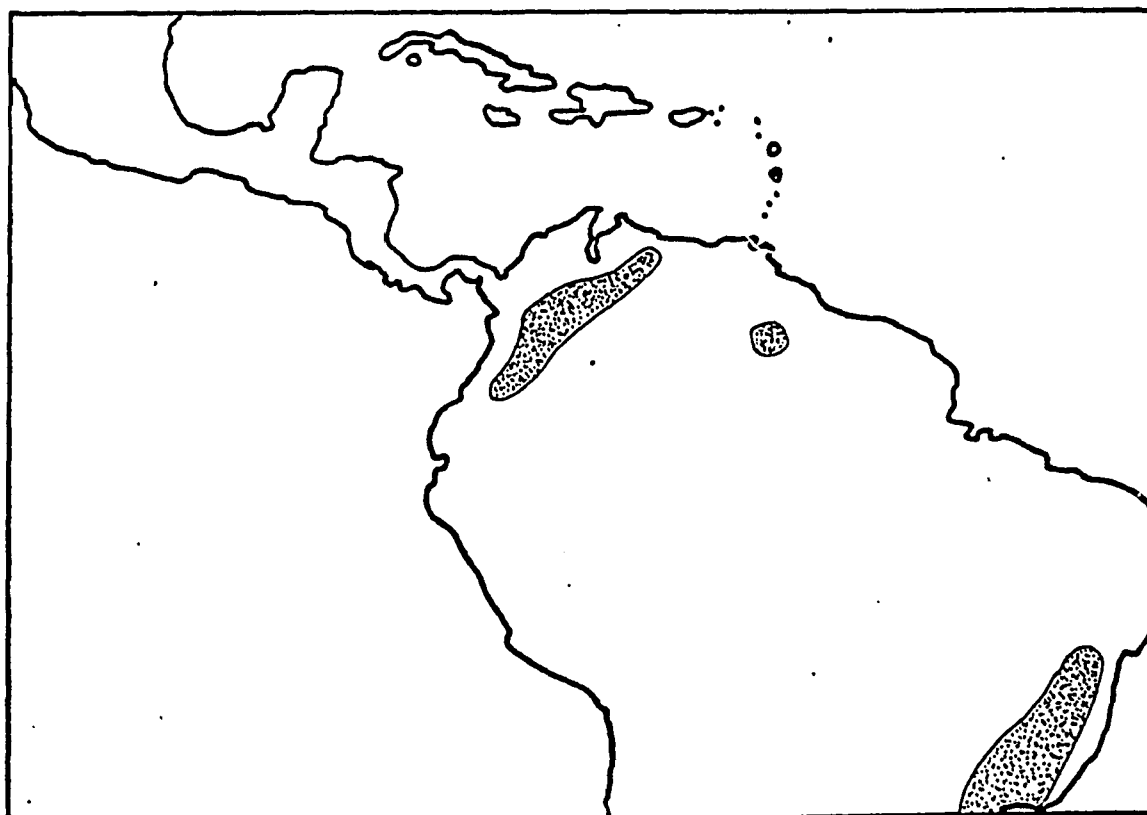


FIGURE 62 B.

33. *Juncus densiflorus* Humboldt, Bonpland & Kunth, Nov. gen. sp.

1: 238. 1816. Type. Typelocality uncertain, see discussion.

Humboldt & Bonpland s.n. (holotype, P; photo of holotype, GH; isotypes, B, P; photo of B-isotype, F, G). Fig. 62 B, 63.

Juncus cyperinus Willdenow ex Sprengel, Linnaeus Syst. veg. 16

ed. 2: 106. 1825, nom. in syn. Willdenow's herbarium name on the isotype of J. densiflorus H.B.K. at B.

Juncus polycephalus Gay ex Laharpe var. β Laharpe, Essai monogr.

jonc. 52. 1825 and in Mem. Soc. Hist. Nat. Paris 3: 140. 1827.

Basionym. Juncus densiflorus H.B.K.

Juncus pohlii Steudel, Syn. pl. glum. 2: 302. 1855. Type. Brazil.

Comargos, Pohl 5236 (holotype, W; isotype, G; isotypefragment, MO).

Juncus densiflorus Humboldt, Bonpland & Kunth var. cyperinus

(Willdenow) Buchenau, Abh. Naturwiss. Vereine Bremen 6: 397.

1879.

Juncus densiflorus Humboldt, Bonpland & Kunth var. pohlii (Steudel)

Buchenau, *ibid.* 398. 1879.

Perennial herb, 65-135 cm high. Rhizome horizontal, creeping, 3-8 mm diam., scales thin, membranaceous, not covering the rhizome, internodes 1.5-2 cm long. Culms erect, 2.5-5.5 mm diam., smooth or finely nodulated, sometimes finely longitudinally striate but never ridged. Cataphylls conspicuous, 1-3 to each culm, all basal or upper ones rarely inserted up to 20 cm from the base, stramineous to brown, lower one 1-6 cm long, upper one to 20 cm long with 4-6 mm long rudimentary needle like blade. Blade bearing leaves (1-)2(-3) spaced along

the culm, lower one 25-75 cm long, sheaths 7-16 cm long with membranaceous margins terminating in two rounded 2-4 mm long auricles, blade terete 2-4.5 mm diam., hollow with transverse septa 2-15 mm apart but not always externally nodulated, upper leaf often inserted above the middle of the culm, usually much smaller, blade sometimes only 5 cm long. Inflorescence decompound, repeatedly anthelate, up to 20 x 7 cm, or congested and sometimes only 3 x 2.5 cm, flower heads 7-45, globose, 7-15 mm diam, 20-40 flowered, stramineous, principal branches to 12 cm long and 1.5 mm in diam. Lower inflorescence bract 3-13 cm long, resembling cauline leaves with short blade or the blade rudimentary to 5 mm long, upper bracts progressively shorter, floral bracts less than half as long as the flowers. Tepals linear-lanceolate, subulate, rigid, outer ones 3-4 mm long, longer than inner ones, concave to V-shaped in cross section, inner ones 2.5-3.5 mm long, flat. Stamens 3, 1.5-2 mm long; filaments filiform; anthers oblong, 0.4-0.8 mm, distinctly shorter than the filaments. Capsule ovoidal, beaked, trigonous, 1.9-2.7 (incl. beak) x 1.1-1.2 mm, about 1/3 shorter than the tepals, light brown, unilocular, dehiscing laterally, the carpels remaining connate at the beak. Seeds ellipsoidal, apiculate, 0.4-0.5 x 0.15-0.2 mm, reticulate.

Distribution. In the Andes from Venezuela to Colombia at altitudes between 1500 m and 2700 m, and in the highlands of southeastern Brazil between 800 m and 1600 m, reaching into the lowlands of adjacent Paraguay, Argentina and Uruguay. A single collection was made on the Sororopán-tepuí. This is the only record of Juncaceae from the Guayana highlands known to me. Grows in humid places in marshes, swamps, along

FIGURE 63

Habit of Juncus densiflorus (Drawn from Irwin et al. 19960, NY).

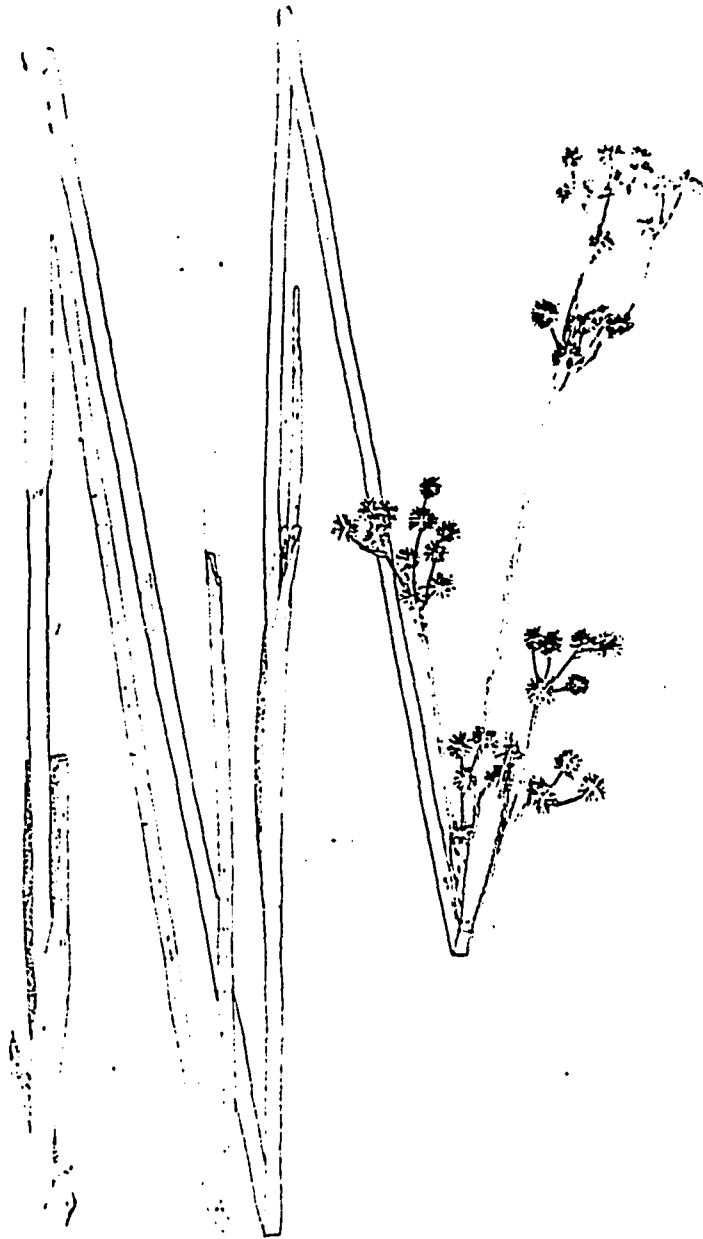


FIGURE 63

creeks and streamlets below the timberline.

Specimens examined. COLOMBIA. Antioquia: Río Teuche nr Carolina, 2000 m, Core 715 (US); San Pedro, Tomas 871 (US); La Ceja, Daniel 954A (US); E of Sonson, 2700 m, Johnson & Barkley 18C799 (US). Cauca: Chiquio, Finca Los Derrumbos, 1700 m, Asplund 10579 (S, US); El Tambo, 1700 m, von Sneider 76 (G, GH); Río Sucio-Río Piedras, W of Popayan, 1500-1700 m, Pennell & Killip 8239 (GH, NY). Cundinamarca: Sabana de Bogotá, 2600 m, Cuatrecasas 481 (F, US); Guasca, Ariste-Joseph A371 (US); Sibate, 2600-2700 m, Pennell 2511 (F, GH, MO, NY); Plateau de Bogotá, 2600 m, Triana 476 (P). Santander: Río Minero valley nr Florian, 2150 m, Fassett 25818 (US).

VENEZUELA. Bolívar: Sororopán-tepuí, 2255 m, Steysmark 60125 (F, NY). Lara: Las Sabanetas-Los Aposentos-Buenos Aires trail, 1675-2430 m, Steysmark 55419 (F, NY).

BRAZIL. Bahia: Reg. Cacaneira, Barra do Choca-Faz. Roda km 3-6, Mori et al. 11307 (NY). Goiás: without locality, Glaziou 20530 (MO, S). Minas Gerais: Caldas, Henschen 1272 (W); Vicosia State Agr. School, Irwin et al. 2661 (F, NY); Serra do Espinhaço ca. 23 km E of Diamantina, 900 m, Irwin et al. 27757 (NY); Serra do Espinhaço nr base of Serra de Piedade ca. 35 km E of Belo Horizonte, 1600 m, Irwin et al. 30360 (F, NY); Serra do Espinhaço, Serra do Itabirito ca. 45 km SE of Belo Horizonte, 1500 m, Irwin et al. 19960 (NY). Rio de Janeiro: Nova Friburgo, Glaziou 13305 (P), 18581 (P), 18981 (F); Itatiaia, Kuntze s.n. (F, NY), Brade 62250 (NY). São Paulo: Corrego Alegre, Loefgren 12415 (NY).

PARAGUAY. Misiones: Estancia La Soledad, Santiago, Pedersen 9562 (NY). San Pedro: Alto Paraguay, Primavera, Woolston 934 (NY, S).

Without department: Ingueri, Hassler 1430 (G); Villa Rica, Balansa 395a (G), Joergensen 3580 (F, MO, NY).

The typelocality of Juncus densiflorus is somewhat obscure. The protologue says 'in ripa fluminis Atabapi, juxta cataractam Guarinuma (Misiones del Alto-Orinoco)' which is on the border between Colombia and Venezuela. Four sheets of J. densiflorus collected by Humboldt and Bonpland are available. One is a sheet at P annotated as Juncus densiflorus in Kunth's hand, with the only locality indicated as 'orinoque'. The second sheet is another one at P which has two labels, one saying 'Orinoco' and the other saying 'quindiu'. The third sheet is in the Willdenow herbarium at B and has 'quindiu' as the only locality information. This third sheet is the one Humboldt sent to Willdenow for study, and the one on which Willdenow wrote the name Juncus cyperinus. The fourth sheet is a fragment at MO with the annotation 'Ex Herb Kunth...J. densiflorus Kunth'. The Orinoco locality mentioned in the protologue and on the sheets at P is a most unlikely place to find J. densiflorus. In Colombia and Venezuela this species grows above 1500 m altitude and the Atabapo tributary to the Orinoco flows through land of 200 m or less altitude. I am not aware that Humboldt and Bonpland ascended any mountain during their exploration of the Atabapo river. The mention of 'quindiu' on the sheet at B and one sheet at P suggests that the actual typelocality is Mt. Quindio in Colombia, and that a wrong label was attached to the specimen retained at P for study by Kunth, and that this error was carried on into the publication of Nova Genera et Species Plantarum. All four sheets contain the same taxon, Juncus densiflorus, as tradi-

tionally and also here circumscribed. Therefore this confusion about the typelocality does not affect the application of the correct name.

34. *Juncus echinocephalus* Balslev, Fl. Ecuador 11: 37. 1979. Type.

Ecuador. Carchi: Páramo El Angel, 3400 m, 27 Jan 1967, Sparre

14234 (holotype, S).

Figs. 64, 65 A.

Perennial herb, 30-80 cm high. Rhizome creeping, 2-5 mm in diam., scales thin membranaceous, inserted somewhat separated and not overlapping, internode 0.5-2 cm long. Culms erect, 1.2-3 mm diam., smooth or sometimes with small transverse nodules on the basal internode. Cataphylls 2-3 to each culm, lower one 1-3 cm long, upper one 5-10 cm long, conspicuous, reddish tinged when young, later light brown. Blade bearing leaves 1-2 basal and 1-2 cauline to each culm, basal one 20-50 cm long, cauline ones shorter, sometimes only 10 cm long; sheaths 4-8 cm long, first reddish tinged, turning light brown, with distinct membranaceous margins terminating in two 1.5-2.5 mm long rounded auricles; blades terete, 1-2.5 mm diam., hollow with septa 0.2-1 cm apart. Inflorescence decompound with very short principal branches, thus condensed into one or sometimes two irregularly shaped dark reddish brown, bristly heads 1-3 cm in diameter, the decompound structure sometimes indicated externally by the somewhat globular subunits of the head. Lower inflorescence bract 2-7 cm long, green, soon turning brown, sheath wide, open, rudimentary blade thin, 0.5-1.5 cm long, upper bracts progressively shorter, the ultimate ones membranaceous to 4 mm long. Tepals equal or outer ones sometimes slightly longer, 2.7-4.5 mm long, linear-lanceolate, subulate, basally pale with membranaceous margins, changing gradually to very dark brown or almost black at the apex. Stamens 6, or through abortion of the inner whorl most often 3, 1.3-1.6 mm long; anthers up to 0.7 mm long and equalling the

FIGURE 64

Habit and detail of Juncus echinocephalus (Drawn from Sparre 14234,
S; from Balslev, 1979a).

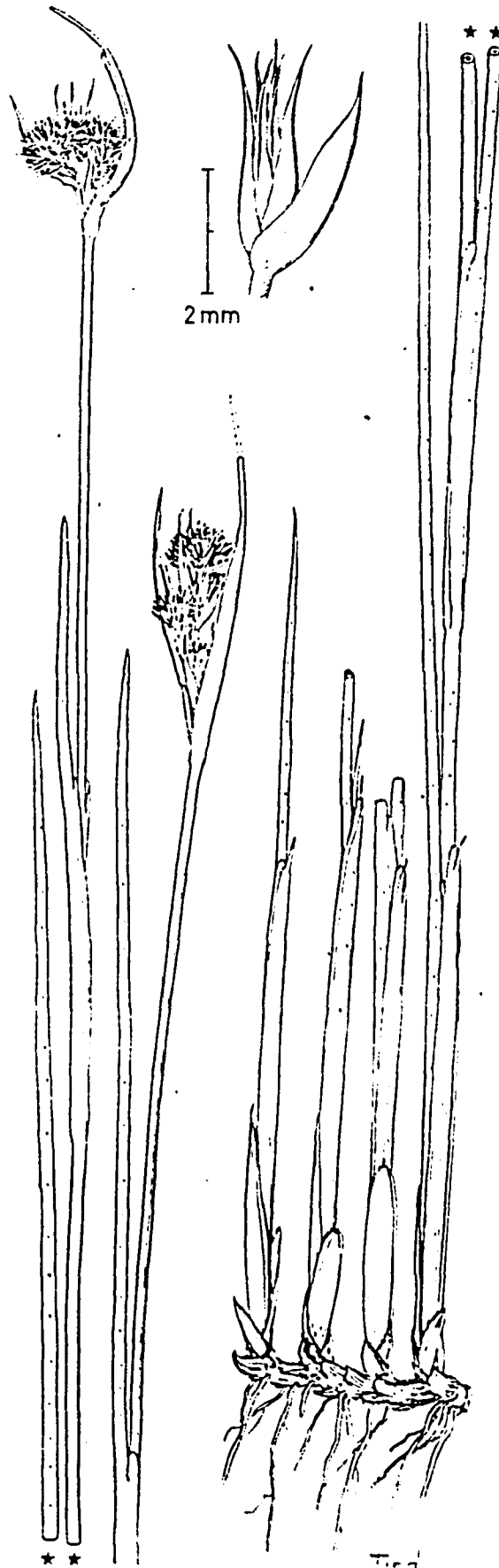


FIGURE 64

filaments, with age sometimes less than 0.3 mm long and only 1/3 as long as the filaments. Capsule ellipsoidal, beaked, trigonous to 3-lobed, 2.5-3.2 mm (incl. beak) x ca. 1 mm, shorter than tepals, gradually darker brown towards the apex, unilocular. Seeds ellipsoid apiculate, 0.4-0.5 x ca. 0.2 mm, reticulate, yellowish brown.

Distribution. In the páramos of the eastern and central cordilleras of Colombia and barely into the adjacent páramos of Ecuador (Páramo El Angel) and Venezuela (Páramo de Tamá). Grows in wet places at altitudes between 2500 m and 4200 m, most often between 2800 m and 3800 m. According to Cleef (personal communication) it is an indicator of eutrophication in the páramos and grows where cattle farming is abundant.

Specimens examined. COLOMBIA. Boyacá: Sierra Nevada del Cocuy, Valle de San José, El Playon, 3800 m, Grubb et al. 771 (COL, K); Páramo Concavo, 3770 m, Cleef 10008A (COL); Vado Hondo, 3015 m, Cleef 9540B (COL). Caldas: Río Otun, Laguna Taburetas, 3580 m, Cuatrecasas 23172 (F). Cauca: Macizo Colombiano, Valle de las Papas nr Valencia, 3100 m, Barclay & Juajibioy 5745 (US), 5802 (COL, NY), 5889 (COL, US); Letreros-Sto. Domingo, 3350 m, Idrobo et al. 3377 (P); Laguna de Cusiya-cu, 3360 m, Barclay & Juajibioy 5982 (COL, F); Llano de Paletara, 2950-3100 m, Pennell 6908 (GH, NY); Páramo Las Barbillas nr Guachocono, 3100 m, Core 966 (COL, US). Cundinamarca: 20 km SSE of S. Bernardo, 3630 m, Fosberg 20804 (COL, US); Páramo Choachi, 3700 m, Killip & Ariste-Joseph 11965 (US); Páramo de Guasca 8 km E of Guasca, 3250-3400 m, Fosberg & Valencia 21454 (US); Bogotá-Choachi rd, km 14-15, 3350 m, Cleef 2915

(P, US), 3035 (COL): Páramo de Sumapaz S of San Juan 3545 m, Cleef 8399B (COL); Usme, 3400 m, Køie 5350 (C, US). Norte de Santander: Páramo de Tamá, above la Cueva, 3100-3200 m, Cuatrecasas et al. 16623 (COL, F); Páramo de Romeral, 3800-4200 m, Killip & Smith 18627 (F, GH, NY, S, US). Santander: Páramo N of Cerrito, 3250 m, Fassett 25922 (NY). Tolima: Rosalito nr Páramo de Ruiz, 2800-3100 m, Pennell 2969 (GH, MO, NY).

VENEZUELA. Táchira: Páramo de Tamá 2 km above Betania, 2500 m, Steyermark 57222 (NY); NNE slope of Páramo de Judío, 3100-3500 m, Luteyn et al. 5953 (NY).

ECUADOR. Carchi: Tulcán-El Carmelo rd at El Frailejo, 3300 m, Harling & Anderson 12540 (GB); Nudo de Boliche, Voladero, 3900 m, Penland & Summers 917 (F, GH); E slopes of Mt Chiles above Tufiño, 3500 m, Drew E-472 (COL, US).

Juncus echinocephalus is related to J. densiflorus, J. micranthus, J. nodosus and a number of North American species. This group has creeping rhizomes, conspicuous cataphylls which is uncommon in the subgenus, beaked capsule, and rigid, long acuminate tepals that give the flower heads a bristly appearance. It is distinct among its South American allies through the congested 1-2 headed condition of the inflorescence, which is in contrast to the expanded inflorescence found in other species in which the principal inflorescence branches are well developed, clearly visible, and terminated by a globular flower head. The dark reddish brown color of the tepals also distinguishes this species from J. densiflorus, J. micranthus and J. nodosus, which all have stramineous flowers.

FIGURE 65

65 A. The distribution of Juncus echinocephalus.

65 B. The distribution of Juncus ustulatus in the neotropical region.

In addition it occurs in Paran  in southeastern Brasil.

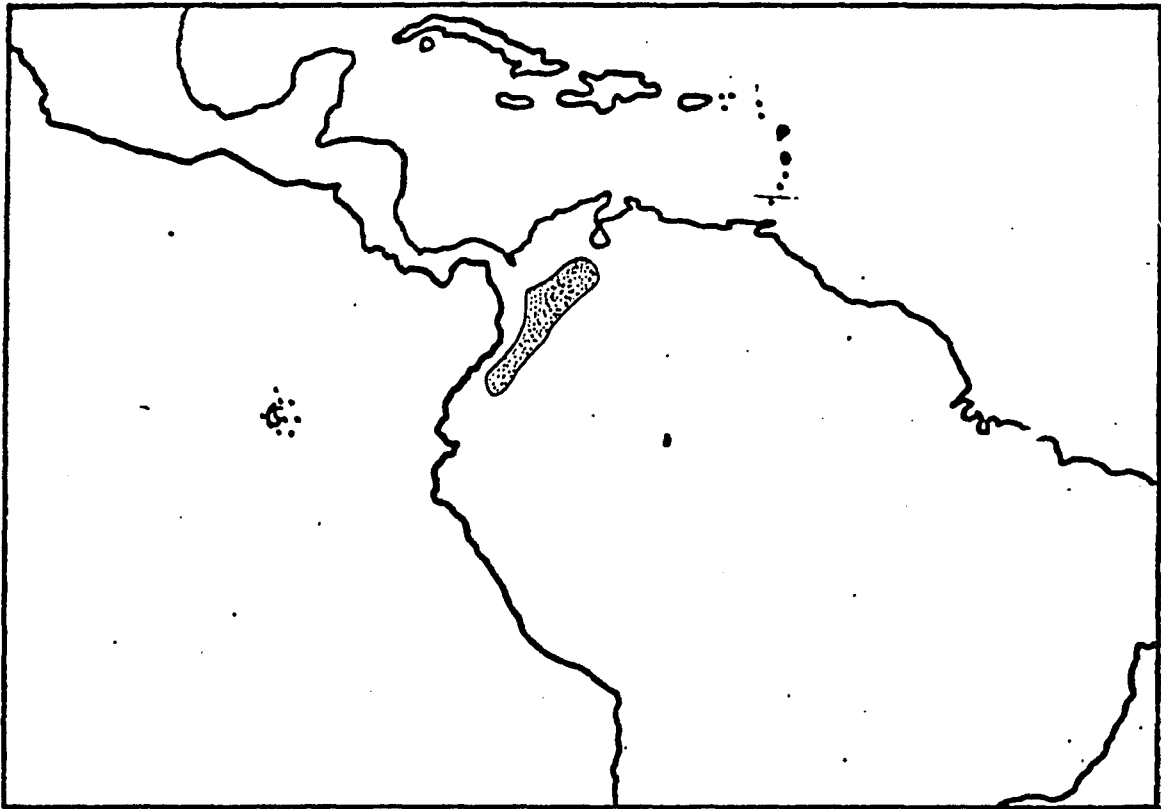


FIGURE 65 A.

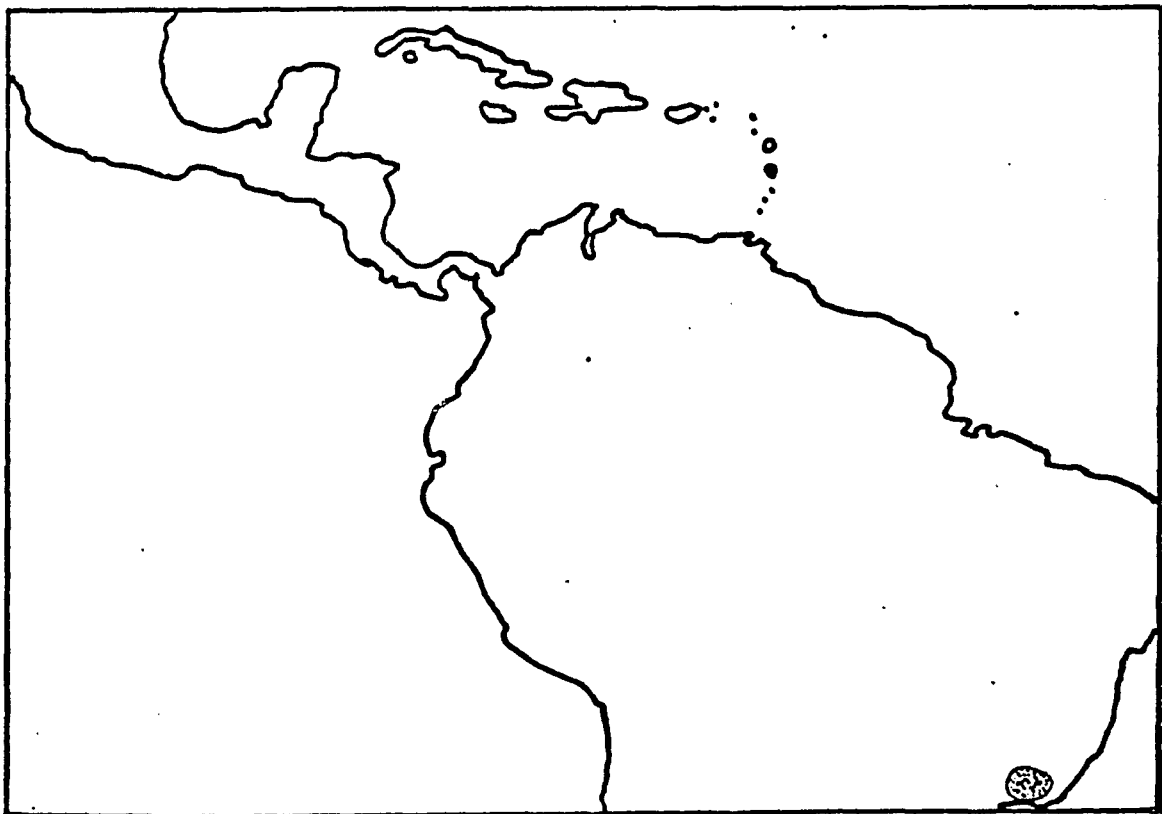


FIGURE 65 B.

35. *Juncus ustulatus* Buchenau, Abh. Naturwiss. Vereine Bremen 6: 401.

1879. Type. Brazil. Minas Gerais: Campos de Itatiaia, 23 Jan

1873, Glaziou 6752 (syntypes, C, G, K, P; photo, GH). Caldas,

Oct 1854, Lindberg 572 (syntype, S; fragment, MO). Fig. 65 B.

Perennial herb, 50-80 cm high. Rhizome horizontal, creeping, 2-4 mm diam., brown with thin membranaceous scales, internodes 0.5-1.5 cm long. Culms erect, 1.5-2.5 mm diam., terete, smooth. Cataphylls 1-3 to each culm, to 5 cm long, green and herbaceous becoming brown and sclerified with age, sometimes with glossy surface. Blade bearing leaves usually 2 cauline to each culm, the basal one inserted 5-30 cm from the base, sheath 4-6 cm long with narrow membranaceous margins terminating in two rounded 1-2 mm long auricles, blade terete, 15-35 cm long, 1-2 mm wide, upper leaf much smaller, often with the blade reduced and as short as 1 cm. Inflorescence decompose, anthelate, 3-10 x 2-7 cm, flower heads 5-50, conical to semiglobose, 6-8 mm diam., 15-50 flowered, dark castaneous. Lower inflorescence bract to 3 cm long, much shorter than the inflorescence, with herbaceous green or brown sheath and rudimentary blade, upper bracts progressively shorter, floral bracts acuminate, to 3 mm long, membranaceous. Tepals subequal, 3-3.5 mm long, linear lanceolate, subulate, rigid, outer ones slightly longer than inner ones, concave, inner ones flat. Stamens 3, ca. 1.5 mm long; filaments flat; anthers linear, ca. 0.7 mm long or slightly shorter than the filaments. Capsule ellipsoidal, beaked, trigonous to 3-lobed, 3-3.5 (incl. beak) x 0.8-1 mm, about as long as the tepals, dark brown, unilocular. Seeds ellipsoidal, apiculate, 0.6-0.7 x ca. 0.2 mm, reticulate, brown below a hyaline outer seed coat.

Distribution. Known from only three localities in southeastern Brazil. The typelocality is the historical site of Mt Itatiaia northwest of Rio de Janeiro. A syntype of Lindman has the locality 'Minas Geraes. Caldas' which I have not localized, and a more recent collection was made by Hatschbach at Teixeira Soares in Paraná, which is outside the tropical region.

Specimens examined. BRAZIL. Minas Gerais: Serra do Itatiaia, 8 Jan 1896, Ule 3767 (HBG). Paraná: Teixeira Soares, Rio das Almas, 10 Dec 1966, Hatschbach 15354 (F, K, P).

Juncus ustulatus belongs to the group of species around J. densiflorus because of its creeping rhizome, the presence of cataphylls, the long acuminate tepals and the beaked capsule. It is distinct from the other species of that group through its inflorescence which has many more, 5-50, relatively small flowerheads, 6-8 mm in diam., of dark castaneous color. Juncus echinocephalus also has dark flowers, but in that species the inflorescence is condensed to one or rarely two flower heads, which are much larger.

Juncus subg. *Ensifolii* (Snogerup) Snogerup, Bot. Not. 131: 187.

1978.

Juncus subg. *Septati* Buchenau, Abh. Naturwiss. Vereine Bremen

4: 406. 1875, pro parte.

Juncus sectio *Septati* (Buchenau) Vierhapper in Engler & Prantl,

Nat. Pflanzenfam. 2 ed. 15a: 217. 1930, pro parte.

Juncus sectio *Ensifolii* Snogerup, Bot. Not. 116: 151. 1963.

Type species. *Juncus ensifolius* Wikström.

Rhizomatous herbs to 60 cm high. Rhizome creeping, with varying internode length. Culms erect, curved, laterally compressed, the edges sharp or sometimes narrowly winged. Leaves basal and cauline, sheaths keeled, blades laterally compressed, sword likely curved, with sharp edges (ensiform, equitant, Iris like), septa incomplete. Inflorescence terminal decompound with few to many flower heads in anthelate arrangement, each head 5-50 flowered.

Distribution. Subg. *Ensifolii* is distributed in western North America from central México to Alaska, through the Aleutian Islands and along the Kuril Islands to Japan. The group is in need of revision. Almost 30 names of specific and varietal rank have been suggested, but the number of species is more likely about five in North America and one to three in Asia. Specific boundaries are not obvious in subg. *Ensifolii* and it appears to be in the process of vigorous evolution.

The ensiformed leaved Junci barely reach into our area. Specimens from central México agree well with Juncus xiphioides of southern California and adjacent areas. Juncus ensifolius Wikström var. brunnescens (Rydberg) Cronquist and var. montanus (Engelmann) C. L. Hitchcock (sensu Cronquist, 1977) reach into the northern states of México. Subg. Ensifolii is close to subg. Septati, from which I consider it derived. It possesses most of the characteristics of that subgenus, but it differs in having curved laterally compressed culms, and leaf blades with sharp or sometimes slightly winged edges and reduced septa. Lateral compression of leaf blades and culms occurs in subg. Septati also, but is then not combined with sharp or winged edges and reduced septa. The assemblage of septate species around Juncus mertensianus Bongard, J. nevadensis S. Watson, J. ebracteatus E. Meyer and J. liebmannii Macbride is probably the sister group to subg. Ensifolii. The two groups agree in seed and floral morphology.

36. *Juncus xiphioides* E. Meyer, Synops. Junc. 50. 1822. Type. USA.

California: Monterey, 1791, Haenke s.n., n.v. Fig. 66.

Juncus xiphioides E. Meyer var. *littoralis* Engelmann, Trans.

Acad. Sci. St. Louis 2: 481. 1868. Basionym. *Juncus xiphioides* E. Meyer.

Juncus xiphioides E. Meyer var. *auratus* Engelmann, Trans.

Acad. Sci. St. Louis 2: 481. 1868. Type. USA. California:
Monte Diablo nr San Francisco, Brewer in Calif. St. Surv. No.
338, n.v.

Perennial herb, 30-80 cm high. Rhizome creeping and ascending, 3-5 mm diam., with membranaceous brown to 1 cm long scales inserted up to 1 cm apart, internodes 1-4 cm long. Culms erect, 1.5-6 mm wide, often sword likely curved, laterally compressed with sharp or narrowly winged edges, smooth or longitudinally striate. Blade bearing leaves 2-6 basal to 40 cm long, and 2-5 cauline progressively shorter upwards; sheaths occupying about half or more of the entire length, sharply keeled, with papery membranaceous margins gradually disappearing or drawn out into inconspicuous auricles; blades laterally compressed, 3-8 mm wide, with sharp edges or narrowly winged (equitant, ensiform, sword-like, Iris-like), sometimes with partial cross partitions but never with septa spanning the entire width. Inflorescence compound, anthelate, up to 20 x 8 cm but usually smaller and sometimes only 4 x 2 cm, flower heads 5-50, globose to semiglobose, 6-10 mm diam., 10-50 flowered, pale stramineous or sometimes brown but never castaneous.

FIGURE 66

The distribution of Juncus xiphioides in the neotropical region.

In addition it occurs in the western United States from Oregon to California.

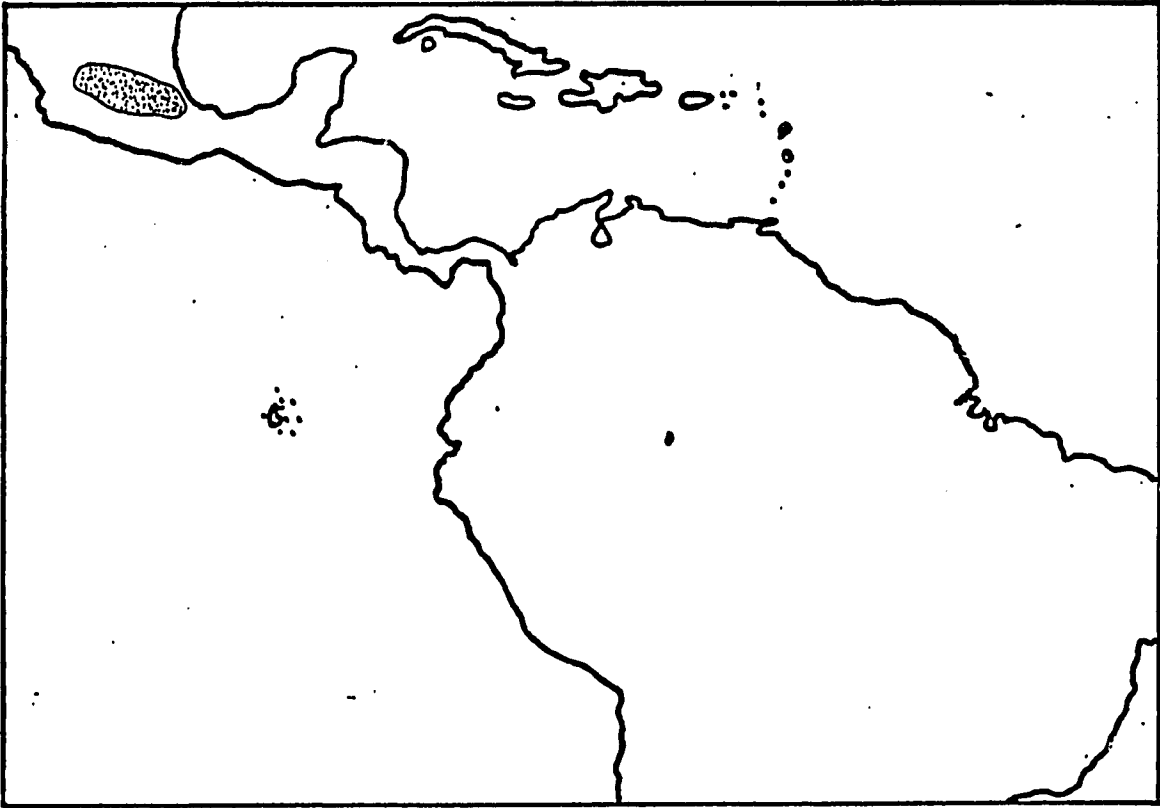


FIGURE 66

Lower inflorescence bract ensiform, usually about half as long as the inflorescence, upper bracts progressively shorter, membranaceous, floral bracts about as long as the flowers. Tepals equal or outer ones slightly longer, 2.5-3.5 mm long, linear-lanceolate, acute, outer ones concave or slightly keeled, inner ones flat. Stamens 6, 1-1.5 mm long; filaments filiform, widened at the base; anthers 0.4-0.7 mm long, shorter than the filaments. Capsule ellipsoidal, beaked, trigonous, 3-4 (incl. beak) x 0.7-0.8 mm, slightly longer than the tepals, stramineous to light brown, glossy, unilocular. Seeds ellipsoidal, apiculate, ca. 0.5 x 0.3 mm, reticulate, brown.

Distribution. Western United States from Oregon to southern California, in Baja California and central México.

Specimens examined. MEXICO. Puebla: Mt Popocatepetl, Balls et al. B5108 (K). San Luis Potosí: 22°N lat., 1850-2450 m, Parry & Palmer 897 (MO, NY); San Luis Potosí, Schaffner 220 (BREM); Morales, Schaffner 549 (K).

NUMERICAL LIST OF TAXA

1. Rostkovia

- 1-1. R. magellanica (Lam.) Hook. f.

2. Distichia .

- 2-1. D. muscoides Nees & Meyen

- 2-2. D. filamentosa Buchenau

3. Patosia

- 3-1. P. clandestina (Phil.) Buchenau

4. Oxychloe

- 4-1. O. andina Phil.

5. Luzula

- 5-1. L. gigantea Desv.

- 5-2. L. denticulata Liebm.

- 5-3a. L. campestris (L.) DC. var. multiflora (Ehr.) Cěl.

- 5-3b. L. campestris (L.) DC. var. ulei (Buchenau) Barros

- 5-4. L. caricina E. Meyer

- 5-5. L. ecuadoriensis Balslev

- 5-6. L. excelsa Buchenau

- 5-7. L. vulcanica Liebm.

- 5-8. L. racemosa Desv.

6. Juncus

- 6-1. J. acutus L. subsp. leopoldii (Parl.) Snogerup

- 6-2. J. roemerianus Scheele

- 6-3. J. maritimus Lam.

- 6-4. J. bufonius L.

Juncus (cont.)

- 6-5a. J. tenuis Willd. var. tenuis
- 6-5b. J. tenuis Willd. var. platycaulos (HBK.) Buchenau
- 6-5c. J. tenuis Willd. var. dichotomus (Ell.) Wood
- 6-6. J. imbricatus Lah.
- 6-7. J. arequipensis Balslev
- 6-8. J. capillaceus Lam.
- 6-9. J. uruguensis Griseb.
- 6-10. J. effusus L.
- 6-11. J. aemulans Liebm.
- 6-12. J. conglomeratus L.
- 6-13. J. patens E. Meyer
- 6-14. J. procerus E. Meyer
- 6-15a. J. arcticus Willd. var. mexicanus (Willd.) Balslev
- 6-15b. J. arcticus Willd. var. montanus (Engelm.) Balslev
- 6-15c. J. arcticus Willd. var. andicola (Hooker) Balslev
- 6-16. J. ramboi Barros subsp. colombianus Balslev
- 6-17. J. marginatus Rostk.
- 6-18. J. cyperoides Lah.
- 6-19. J. repens Michx.
- 6-20. J. microcephalus HBK.
- 6-21. J. pallescens Lam.
- 6-22. J. acuminatus Michx.
- 6-23. J. ecuadoriensis Balslev
- 6-24. J. breviculmis Balslev
- 6-25. J. guadeloupensis Buchenau

Juncus (cont.)

- 6-26. J. achalensis Barros
- 6-27. J. debilis A. Gray
- 6-28. J. stipulatus Nees & Meyen
- 6-29a. J. liebmannii Macbr. var. liebmannii
- 6-29b. J. liebmannii Macbr. var. quitensis (Buchenau) Balslev
- 6-30. J. ebracteatus E. Meyer
- 6-31. J. micranthus Schrader ex E. Meyer
- 6-32. J. nodosus L.
- 6-33. J. densiflorus HBK.
- 6-34. J. echinocephalus Balslev
- 6-35. J. ustulatus Buchenau
- 6-36. J. xiphioides E. Meyer

LIST OF EXSICCATAE

Abbott, R. Q., 271 (6-20).

Acleto, C., 405 (5-1)

Acosta-Solis, M., 5638 (6-4), 5639 (6-20), 5864 (6-4), 7205 (5-1),
7546 (6-15c), 7906 (6-21), 7908 (6-6), 8329 (5-1), 8391 (6-4),
8420 (5-8), 8429 (6-15c), 8779 (2-1), 8989 (6-4), 9218 (6-6),
9730 (6-15c), 10027 (6-8), 10034 (6-4), 10036 (6-6), 10082 (6-6;
6-8), 10337 (6-6), 10862 (6-4), 13214 (6-8), 13596 (6-8), 14040
(6-8), 14041 (6-6), 14419 (6-4), 14471 (6-6), 14695 (6-4), 16973
(6-4), 17669 (5-1), 17888 (6-4), 19150 (6-5a), 19177 (5-1),
19987 (5-8), 20026 (5-8), 20075 (5-1), 20268 (6-4), 20518 (6-5a)
20530 (6-14), 21167 (6-15c), 21222 (6-15c), 21223 (6-6), 21263
(6-8), 21335 (6-18), 21353 (6-18), 21355 (6-6), 21366 (6-4),
21483 (6-15c), 21503 (6-15c), 21677 (5-1).

Adams, C. D., 5733 (6-5c), 10598 (6-5a), 10687 (6-5a).

Adolfo 237g (6-8), 288 (2-1).

Adersen, H., 804 (6-21).

Aguilar, P., s.n. (2-1), 96 (6-30), 187 (6-15), 335 (6-30).

Aguirre, J. & O. Rangel, 251 (6-10).

Alboff, N., s.n. (6-1), s.n. (6-6).

Alduin, C. et al., 270 (6-5).

Alston, A. H. G., 7083 (6-5a), 7394 (6-5b), 8227 (6-5a), 8311 (6-28).

Alvarez, R., 695 (6-5c).

Amórtegui, B. G., 207 (6-10).

Anderson, W. R. (et al.), 8485 (6-31), 8885 (6-20), 35217 (6-31).

Andersson, 355 (1-1), 356 (1-1).

André, E., 624 (6-5b), 732 (6-10), 768 (6-8), 844 (6-8), 971 (5-1),
1369 (6-5b), K1430 (6-20), 2244 (5-1), 2954 (6-15c), 3111 (5-1),
3277 (5-1), 3514 (6-15c), 3982 (6-18), 4025 (6-6).

Andreas, C. H., 350 (6-18), 483 (6-8), 497 (6-18), 729 (6-18).

Apolinar-María, Bro., 165 (6-20).

Apollinaire & Arthur, 44 (6-20), 123 (5-8).

Araque, J. & F. A. Barkley, 18S722 (6-24).

Archer, W. A., 182 (6-5a), 1183 (6-10).

Arechavaleta, J., 478 (6-8).

Ariste-Joseph, Bro., A141 (6-6), A143 (6-10), A166 (6-4), A364 (6-6),
A371 (6-33), A386 (5-1), A393 (6-8), A395 (6-4), A398 (6-8),
A509 (5-1), 1905 (6-10), 1919 (6-5a).

Aristeguita, L., 940 (5-1).

Arsene, G., 2505 (6-10), 5306 (6-5c), 6361 (6-32), 6687 (6-30), 10991
(6-15a), 11726 (6-5c), 17140 (6-15b), 17632 (6-4).

Asplund, E., 54 (6-14), 66 (6-8), 522 (6-6), 658 (6-6), 688 (6-4),
807 (6-30), 808 (6-6), 819 (6-15c), 897 (4-1), 898 (2-1), 913 (6-28),
1008 (6-15c), 1039 (6-28), 1878 (4-1), 1879 (2-1), 2023 (6-30),
2298 (6-6), 2307 (6-30), 2558 (6-28), 2668 (4-1), 2768 (6-28),
2808 (6-28), 3480 (6-15a), 3546 (6-6), 3675 (6-6), 3702 (6-15),
3703 (6-6), 3704 (6-30), 3904 (2-1), 3947 (4-1), 3948 (2-1),
3984 (2-1), 3985 (4-1), 4347 (6-28), 6042 (6-6), 6227 (6-29b),
6229 (6-4), 6264 (6-15c), 6373 (5-8), 6374 (6-28), 6378 (4-1),
6396 (6-15), 6399 (5-8), 6437 (6-5a), 6493 (5-1), 6494 (5-5),
6502 (3-1), 6588 (5-8), 6896 (6-6), 6910 (6-15c), 6948 (6-29b),
6993 (6-6), 6995 (6-4), 6996 (6-6), 6997 (6-5a), 6998 (6-21),
7025 (6-10), 7102 (6-28), 7110 (6-8), 7371 (6-20), 7422 (5-8),

Asplund, E. (continued), 7496 (5-8), 7794 (5-7), 7807 (2-1), 7938 (5-8),
 8449 (5-8), 8455 (6-15c), 8768 (5-1), 9598 (6-20), 9608 (6-5a),
 9684 (5-1), 9685 (5-5), 9915 (5-1), 10579 (6-33), 11382 (5-8),
 11553 (2-1), 11629 (6-28), 11687 (5-8), 11691 (6-15c), 11705 (5-8),
 12751 (6-18), 12885 (6-4), 12887 (6-18), 13101 (6-21), 13103 (5-8),
 14879 (5-8), 16029 (6-29b), 16086 (6-20), 16151 (6-8), 16241 (6-29b),
 16248 (5-8), 16884 (6-23; 629b), 16894 (6-18), 16903 (6-10),
 17758 (6-14), 17991 (6-23), 19395 (6-4).

Baker, 4650 (6-17).

Balansa, B., 392 (6-5c; 6-6), 392a (6-5c), 392b (6-5c), 393 (6-17),
 393a (6-17), 395 (6-31), 395a (6-33).

Ballesteros, J. & C. Villamizar, 3 (6-5b), 18 (6-5), 21 (6-6), 39 (6-8).

Balls, N. et al., B4475 (5-2), B4555 (6-15a), B4641 (5-4), B4979 (5-4),
 B4981 (5-2), B5451 (6-29a), B5501 (6-29a), B5502 (6-30), B5708
 (6-36).

Balslev, H. (et al.), 803 (6-10), 827 (6-10), 892 (6-4), 895 (6-29b),
 957 (6-6), 961 (6-6), 962 (6-8), 980 (6-28), 983 (6-4), 989A (6-28),
 998 (6-15c), 1047 (6-6), 1048 (6-15c), 1053 (6-28), 1061 (6-15c),
 1077 (6-20), 1078 (2-1), 1079 (6-6), 1080A (6-15), 1082 (6-6),
 1083 (6-21), 1084 (6-15), 1085 (3-1), 1086 (6-28), 1098 (6-6),
 1105 (5-8), 1118 (6-30), 1119 (6-28), 1120 (6-28), 1122 (6-28),
 1126 (5-6), 1127 (6-4), 1128 (5-6), 1131 (5-8), 1135 (6-28),
 1137 (6-4), 1138 (6-30), 1139 (6-6), 1140 (6-15), 1141 (6-15c),
 1142 (5-8), 1145 (2-1), 1146 (2-2), 1147 (4-1), 1148 (5-8),
 1148A (5-7), 1150 (4-1), 1151 (6-28), 1152 (6-28), 1154 (2-1),
 1155 (2-1), 1163 (2-1), 1164 (2-1), 1165 (6-5a), 1166 (6-6),
 1168 (5-5), 1182 (6-15c), 1183 (5-8), 1184 (5-5), -185 (6-28),

Balslev, H. (continued), 1186 (6-15c), 1190 (6-8), 1191 (6-20),
 1192 (6-4), 1197 (6-18), 1198 (6-21), 1199 (6-4), 1202 (6-18),
 1207 (5-8), 1211 (6-4), 1212 (6-18), 1213 (6-21), 1214 (6-4),
 1216 (6-6), 1217 (6-21), 1218 (6-14), 1219 (6-20), 1220 (6-23),
 1221 (6-14), 1222 (6-4), 1233 (6-18), 1235 (6-28), 1236 (6-21),
 1237 (6-14), 1238 (6-10), 1239 (6-18), 1240 (6-20), 1247 (6-4),
 1248 (6-20), 1249 (6-20), 1250 (6-18), 1251 (6-5b), 1252 (6-5a),
 1253 (6-10), 1254 (6-15c), 1258 (6-23), 1269 (6-20), 1270 (6-5a),
 1273 (6-14), 1274 (6-10), 1283 (6-5a), 1285 (6-20), 1310 (6-4),
 1312 (6-20), 1317 (6-5a), 1318 (6-18), 1319 (6-20), 1320 (6-10),
 1347 (6-20), 1349 (6-4), 1350 (6-5a), 1351 (6-18), 1354 (6-20),
 1355 (6-21), 1358 (6-10), 1359 (6-21), 1360 (6-14), 1361 (6-10),
 1362 (6-6), 1363 (6-5a), 1364 (6-23), 1365 (5-1), 1366 (6-18),
 1368 (6-20), 1371 (5-1), 1403 (6-10), 1406 (6-23), 1407 (6-20),
 1412 (6-28), 1413 (6-6), 1416 (6-6), 1437 (6-4), 1438 (6-6),
 1440 (6-14), 1444 (2-1), 1452 (6-28), 1492 (5-8), 1509 (5-5),
 1526 (6-28), 1536 (6-14), 1540 (6-5a), 1542 (5-8), 1548 (5-8),
 1550 (6-4), 1551 (6-21), 1554 (6-18), 1565 (6-14), 1566 (6-6),
 1567 (6-18), 1569 (6-20), 1573 (5-1), 1574 (6-28), 1579 (6-4),
 1587 (6-23), 1603 (6-20), 1604 (6-5a), 1618 (5-8), 1620 (2-1),
 1621 (2-1), 1654 (6-20), 1655 (6-4), 1656 (6-5a), 1657 (6-20),
 1658 (6-21), 1677 (6-5a), 1723 (5-1), 1827 (6-4), 1924 (6-5a),
 AAU-23599 (5-8), AAU-23814 (6-4), AAU-23835 (5-1), AAU-23838 (6-10),
 AAU-23839 (6-4), AAU-23840 (6-10), AAU-23846 (6-29b), AAU-23847
 (6-23), AAU-23848 (6-15c), AAU-23896 (5-7), AAU-23898 (6-28),
 AAU-23899 (6-28), AAU-23904 (6-15c), AAU-23905 (6-28), AAU-23907
 (6-4), AAU-23911 (5-1), AAU-23950 (6-15c), AAU-24111 (5-8),

Balslev, H. (continued), AAU-24122 (6-28), AAU-24126 (5-8), AAU-24129 (6-4), AAU-24144 (5-1), AAU-24180 (6-6), AAU-24181 (6-8), AAU-24182 (6-15c), AAU-24183 (6-6), AAU-24184 (6-6), AAU-24185 (5-7), AAU-24186 (5-8), AAU-24187 (5-8), AAU-24188 (5-1), AAU-24189 (5-1), AAU-24190 (2-1).

Bang, M., s.n. (5-6), 73 (6-30), 89 (6-15c), 116 (6-6; 6-30), 1076 (6-30), 1871 (5-8), 2410 (6-10).

Barclay, A. S. & R. E. Schultes, 165 (6-28).

Barclay, H. G., 4330 (6-10), 4616 (5-1), 5218 (5-7), 5220 (2-1), 5279 (5-1).

Barclay, H. G. & P. Juajibioy, 5745 (6-34), 5802 (6-34), 5889 (6-34), 5982 (6-34), 6105 (5-8), 6208 (5-1), 6266 (6-4), 6317 (2-1), 6318 (5-7), 6323 (2-1), 6326 (5-7), 6398 (5-1), 6451 (2-1), 6458 (5-8), 6522 (6-23), 6614 (5-1), 7320 (6-5b), 7324 (2-1), 7342 (5-8), 7456 (2-1), 7590 (6-34), 8009 (5-8), 8133 (6-15c), 8163B (5-8), 8285 (6-23), 8287 (5-8), 8535 (6-18), 8786 (2-1), 8838 (5-1), 8839 (5-8), 8840 (5-1), 9146 (5-7), 9211 (5-7), 9234 (2-1), 9600 (6-24).

Barklay, F. A., 14597A (6-32), 18A024 (6-10).

Barlow, F. D., 30/138 (6-19).

Barreto, M., 8611 (6-10).

Barriga, H. G., 4881 (6-6), 10012 (6-5), 17196 (5-7).

Bartlett, H. H., 19931 (6-1), 20569 (6-1), 20701 (6-4), 20702 (6-6), 20703 (6-8), 20814 (6-5c), 21033 (6-6), 21099 (6-8), 21110 (6-8).

Beaman, J. H., 1691 (5-8), 1742 (5-8), 1780 (5-8), 1981 (5-4), 1985 (5-8), 2055 (5-8), 2065 (6-30), 2148 (5-8), 2194 (5-4), 2223 (5-8), 2225 (5-8), 2332 (5-8), 2358 (5-8), 2554 (5-7), 2786 (5-8), 2806 (5-2),

Beaman, H. H. (continued), 2851 (5-8), 2928 (5-8), 2944 (5-2),
 3076 (5-8), 3126 (6-30), 3136 (5-8), 3149 (5-8), 3179 (5-2),
 3213 (5-8), 3254 (5-2), 3257 (5-8), 3268 (5-4), 3455 (5-8),
 3484 (5-8), 3527 (5-7), 3633 (5-8), 3729 (6-5c), 3794 (5-8),
 3881 (5-4), 3898 (6-29a), 3919 (5-4), 3924 (6-15), 4040 (5-2),
 4096 (5-2), 4097 (5-8), 4180 (5-8), 4186 (6-29a), 4325 (5-4).

Beaufils, s.n. (6-15).

Beck; S. G., 331a (5-8), 1018 (6-30), 1031 (6-30), 1047 (6-15c),
 1130 (5-6), 1130A (5-6), 1268 (5-7), 1883 (6-15c), 1902 (6-30),
 1975 (4-1), 1988 (6-30), 2458 (6-15), 2468 (6-15c), 2472 (6-15c),
 2783 (5-6), 2885 (5-8), 2894 (5-8), 3897 (6-21), 3944 (5-6),
 3960 (5-8), 4172 (5-6), 4209 (5-8), 4243 (6-28), 4312A (5-8),
 4323 (5-7), 4338 (6-6), 4349 (5-8), 4442 (6-21), 4630 (5-6),
 4630A (5-6), 6024 (5-7), 6188 (5-8).

Bell, P. R., 78 (5-8), 360 (5-8), 691 (5-1).

Bena, P., s.n. (6-25).

Bennett et al., 771 (6-5b).

Benoist, M. R., 2049 (6-29b), 2651 (6-5a), 2720 (6-29b), 3655 (6-29b).

Bequaert, J., 15 (6-4).

Berlandier, 299 (6-5a), 526 (6-30), 527 (6-5a), 528 (6-5a), 744 (6-30),
 752 (6-15a).

Bernard, A., s.n. (5-1).

Bernardi, L., 16623 (5-8).

Bernoulli & Cario, 1021 (6-30).

Bertero, 347 (6-4), 1060 (6-4), 1061 (5-3; 6-18), 1070 (6-4).

Biese, W., 891 (6-15).

Birger, S., s.n. (1-1).

- Black, G. A. (& Boelcke), 46-673 (6-23), 51-11482 (6-1).
- Black, J., JB-A 80 (5-8).
- Blair, I. J., 522 (2-1).
- Boffa, P., s.n. (6-20).
- Bonner, W., 95 (1-1), 104 (1-1).
- Bonpland, s.n. (2-1).
- Borders, s.n. (6-18).
- Bornmüller, J., 395 (6-5c), 396 (6-8).
- Borscher, A., s.n. (6-14).
- Bossiere, s.n. (1-1).
- Botteri (& Sumichrast), 185 (6-10), 186 (6-10).
- Bourgeau, M., 207 (6-15a), 208 (6-30), 1147 (5-4), 1148 (6-29a),
2592 (6-10).
- Brade, A. C., 15140 (6-20), 28195 (6-20), 62250 (6-33).
- Breedlove, D. E., 6788 (6-10), 8603 (5-2), 8894 (6-27), 10881 (6-5c),
11555 (5-2), 12342 (5-2), 14446 (6-10), 14617 (6-10), 14626 (6-30),
14803 (6-17), 14806 (6-10), 14930 (6-30), 15069 (6-17),
15106 (5-4), 15252 (6-29a), 15276 (6-29a), 15321 (5-4),
19963 (6-27), 21486 (6-27), 22754 (5-2), 26722 (5-8), 29371 (5-8),
40268 (5-2).
- Breteler, F. J., 4147 (6-5b).
- Breuninger, N. B., 306 (6-6), 326 (5-1).
- Bristol, M. L., 403 (6-10), 937 (6-5).
- Britton, N. L. (et al.), 286 (6-17), 3321 (6-4), 3449 (6-4), 9677 (6-19),
10057 (6-17), 14719 (6-19), 15234 (6-17), 15686 (6-19).
- Brooke, W. M. A., 5315 (5-8), 6394 (6-15c).

Buchtien, O., 68 (5-1), 89 (6-30), 156 (6-30), 508 (6-30), 509 (6-6),
 829 (6-6), 834 (6-30), 1101 (6-14), 1240 (6-6; 4-1), 2557 (6-30),
 2558 (6-6), 2559 (6-6), 2560 (5-8), 2561 (5-8), 2600 (5-1),
 2601 (5-6), 2602 (5-8), 4543 (6-28), 8530 (6-4), 8820 (6-30),
 8821 (5-8), 8919 (5-1), 8920 (5-6), 9327 (5-7), 9359 (2-1),
 9360 (4-1).

Burchell, 4429 (6-33).

Burcò, M., 20377 (6-6).

Burger, W. C. (et al.), 5970 (5-2), 6317 (5-2), 7406 (5-2), 9454 (6-10).

Bøcher, T. et al., 85 (6-15c).

Cabrera, A. L. (et al.), 20 (6-15), 1619 (6-5c), 1677 (6-5c) 1738 (6-1),
 1892 (6-6), 2454 (6-6), 2685 (6-1), 2733 (6-21), 3836 (6-4),
 3935 (6-4), 8646 (4-1), 16465 (6-6), 21443 (2-1).

Callejas, R. et al., 976 (6-10).

Camargo, O., 57351 (6-17), 59372 (6-5c), 59407 (6-4), 59534 (6-4),
 59551 (6-8), 59747 (6-5c), 59970 (6-33), 61670 (6-33), 61774 (6-8),
 61783 (6-31), 62469 (6-4), 62642 (6-10), 62820 (6-5c).

Camp, W. H., 2748 (6-17), 2749 (6-10), E2048 (6-6), E2051 (6-14),
 E2113 (6-18), E2130 (6-20), E2290 (5-1), E2618 (6-23), E2619 (6-20),
 E2627 (6-18), E2746 (6-4), E3983a (6-4), E3983 (6-18), E4171 (6-4;
 6-5a).

Caraventa, A., s.n. (6-4).

Cárdenas, E., 128 (6-15a).

Cárdenas, M., 85 (6-15), 775 (6-8).

Cardich, A., s.n. (2-1).

Carlson, M., 4126 (5-2).

Carette, E., s.n. (6-15).

Castellanos, A., 6929 (5-3b), 16139 (3-1), 114288 (6-18), 114299 (6-15a).

Castillon, 3227 (2-1), 50610 (2-1).

Cazalet, P. C. D. et al., 5342 (5-1), 5427 (6-28), 5460 (5-1), 5585
(6-4), 5723 (5-7).

Cerrate, E., 37 (6-6), 39 (6-30), 2278 (6-15c), 2731 (6-4), 3211 (6-21),
5809 (6-4).

Cevasco, H., s.n. (6-20).

Chamisso, A. de, s.n. (6-6), s.n. (6-8).

Chavez, L., 96 (6-21).

Chavez, R., 3300 (2-1).

Chindoy, P. J., 172 (6-20).

Cisnero, R. C., 1645 (6-11).

Claude Joseph, Bro., 1104 (6-4), 3962 (6-18), 5205 (6-18).

Claussen, M., 1033 (6-20).

Clayton, W. D., 4217 (6-5c), 4374 (6-8), 4479 (6-31).

Cleef, A. M. (et al.), 129 (5-8), 543 (5-1), 595 (6-28), 617 (2-1),
871A (6-18), 992 (5-1), 1095 (5-8), 1319 (5-8), 1589 (5-1),
1630 (5-1), 1740 (5-8), 1787 (5-8), 1796 (5-8), 1922 (5-8),
1955A (5-1), 2046 (5-7), 2061 (6-24), 2113 (5-8), 2265 (5-1),
2312B (5-8), 2351 (6-28), 2418 (5-7), 2579 (5-7), 2915 (6-34),
3005 (6-23), 3035 (6-23; 6-34), 3153 (6-23), 3639 (6-28), 3852B
(5-8), 3938 (6-4), 4000 (6-23), 4183 (5-1), 4234 (5-8), 4274 (6-18),
4278A (6-18), 4285 (6-18), 4303 (5-1), 4372A (6-18), 4391A (6-18),
4406A (6-18), 4410A (6-18), 4433 (5-8), 4582 (5-8), 4621 (5-1),
4696 (5-8), 4713B (5-8), 4824B (6-18), 5134A (5-1), 5187 (6-18),
5237A (5-1), 5476 (6-18), 5537 (5-8), 5578A (6-18), 5597 (5-7),

- Cleef, A. M. (continued), 5657 (5-8), 5670 (5-8), 5680A (5-8),
 5807 (5-8), 5808 (5-8), 5926 (6-24), 5986 (2-1), 6122 (5-8),
 6301 (6-23), 6483A (5-8), 6527A (5-7), 6546 (5-7), 6690A (5-1),
 6740 (6-24), 6824B (5-8), 7136A (6-24), 7333 (5-1), 7443 (5-8),
 7931 (5-8), 8092 (5-1), 8310B (5-1), 8360A (5-1), 8399B (6-34),
 8447A (6-23), 8503 (5-8), 8524 (2-1), 8665B (5-8), 8680A (5-8),
 8731 (2-1), 8787B (5-8), 8833A (5-8), 8857B (5-8), 8914 (2-1),
 8928B (5-8), 8960A (5-8), 9018A (5-8), 9018B (2-1), 9036B (5-8),
 9045C (5-8), 9204A (5-8), 9225B (6-23), 9321A (5-8), 9406A (6-23),
 9540B (6-34), 9554 (6-23), 9619A (5-1), 9828 (5-8), 10008A (6-34).
- Cochrane, T. et al., 8557 (5-2), 8561 (5-4).
- Colaris, W. J. J., 1385 (6-30).
- Comber, H. F., 297 (3-1), 421 (6-18).
- Conrad, J. et al., 1979 (6-31), 2731 (6-21).
- Conzatti, C., 215 (6-30), 419 (5-2).
- Cook, O. F. et al., 1834 (5-1).
- Coore, E. L., 415 (5-1), 608 (6-4), 711 (6-20), 715 (6-33), 908 (5-1),
 966 (6-34), 985 (6-23), 1004 (6-23), 1590 (5-1).
- Correll, D. S. et al., 20173 (6-15a), 23173 (5-4).
- Costa Sacco, J. da, 423 (6-33), 427 (6-4), 434 (6-5c), 667 (6-4).
- Coulter, 1584 (6-30).
- Couthouy, J. P., s.n. (5-1).
- Cristóbal, C. L., 16302 (6-4).
- Croat, T. B., 32871 (6-10), 40469 (6-30), 44120 (6-15a), 46199 (6-11),
 47735 (6-17).
- Cronquist, A. et al., 8859 (5-2).

Cruz, N. D. da et al., 6376 (6-20), 6394 (6-10), 6395 (6-20).

Cuatrecasas, J. (et al.), 376 (5-1), 436 (6-10), 436A (6-23),

475 (6-5), 477 (6-10), 479 (6-20), 481 (6-33), 1367 (5-1),

1469 (5-8), 1487^{bis} (5-8), 1516D (2-1), 1518 (2-1), 1557 (6-24),

2062 (6-10), 2064 (6-4), 2212 (6-10), 5437 (6-16), 5523 (6-10;

6-23), 9305 (2-1), 9344C (2-1), 9438 (5-1), 9488 (6-23),

9876 (6-23), 10067 (6-20), 11808 (6-10), 11872 (6-34), 11896 (5-1),

12115 (6-5), 12250 (6-10), 12623 (6-34), 12717 (5-1), 13509 (6-24),

14720 (5-1), 14728 (2-1), 19458 (6-18), 20644 (6-5b), 20651 (6-5),

20674 (6-5), 20674A (6-6), 20697 (6-8), 20543 (6-5a), 23172 (6-34),

23209 (5-8), 23220 (2-1), 23232 (2-1), 24580 (5-8), 25089 (5-1),

25100 (6-10), 25591 (5-1), 25595 (6-34), 26907 (5-1), 27697 (5-1).

Curran, H. M., 2132 (6-10).

Curtiss, A. H., s.n. (6-19).

Daniel, Bro., 954A (6-33), 3306 (6-20), 3430 (6-10).

D'Arcy, W. G., 10178 (5-2).

Davidse, G. (et al.), 861 (6-4), 893 (6-20), 1133 (5-2), 1167 (5-2),

1182 (5-3a), 1183 (5-3a), 2112 (6-5a), 2232 (6-20), 2241 (6-17),

2242 (6-27), 8220 (6-4), 10245 (5-2), 10562 (6-33), 10901A (6-20),

10919 (6-20), 11350A (6-5c), 11514 (6-20).

Davidson, C., 3351 (2-1).

Dawson, G., 1004 (6-4).

Dayton, W. A., 3142 (5-2).

Degener, O., 20354A (6-5a).

Diaz, A., s.n. (6-21).

Dickerman, R. W., 1036 (6-10).

- Didrichsen, 3324 (6-18).
- Diguet, M. L., s.n. (6-17).
- Diguet, L., s.n. (6-17).
- Dombrowski, L., 1634 (6-5c).
- Donat, A., 46 (6-15a), 498 (1-1), 557 (6-4).
- Drew, E., E106 (6-29b), E232 (2-1), E471 (6-29b), E472 (6-34), E475a (6-23).
- Duarte, A. P., 5682 (6-20).
- Dudley, T. R. et al., 1459 (1-1).
- Dunn, D. B. et al., 18792 (5-8), 20415 (5-8), 21888 (5-8).
- Dusén, P., 40 (5-3b), 2357 (6-33), 5521 (6-4), 6100 (1-1), 6251A (6-6), 7780 (6-33), 10804 (6-10), 10930 (6-20), 11521 (6-17), 14406 (6-31), 15172 (6-5c), 16938 (6-5c).
- Duss, P., 3996 (6-25), 4622 (6-25).
- Dwyer, J. D., 10754 (6-17).
- Edwards, P. J., 31 (5-1).
- Eggler, W. A., 434 (5-2), (1950)44 (5-2).
- Eiten, G. et al., 2325 (6-10), 2514 (6-20), 6996 (6-20).
- Ekman, E. L., s.n. (6-17), 1986 (6-5c), 1987 (6-20), 1988 (6-20), 1989 (6-33), 8963 (6-2), 9511 (6-10), 10733 (6-19), 10782 (6-17), 10808 (6-19), 10833 (6-17), 17109 (6-17), 17931 (6-17).
- Ellenberg, H., 230 (6-6), 277 (5-8), 311 (6-6), 443 (5-8), 444 (6-30), 482 (6-30), 516 (6-30), 525 (6-30), 542 (5-8), 559 (6-15c), 597 (5-8), 623 (5-8), 655 (5-8), 1047 (6-15a), 1048a (6-15a), 1699 (6-8), 1720 (5-8), 1848a (5-8), 1855 (6-20), 1856 (6-18), 1857 (6-30), 1870 (6-8), 1942 (6-6), 1973 (5-8), 2186 (5-8),

Ellenberg, H. (continued), 2982 (6-26), 3235 (5-7), 4122 (5-8),

4204 (6-15), 4241 (4-1), 4772 (5-1), 5012 (5-8).

Elliot, S., 133 (6-8), 151 (6-18).

Ern, H., 153 (5-8), 304 (5-2).

Espinosa, R., 899 (6-20), 1633 (6-21), 2166 (6-6), 2192 (6-10),

3075 (6-10), 3082 (5-1).

Evangelista, M., s.n. (5-8).

Ewan, J. A., 15576 (6-5a), 15631 (6-8), 15719 (6-5a), 16134 (6-15c),

16297 (6-10), 16298 (6-29b), 16363 (6-34), 16369 (6-10).

Eyerdam, W. J. (et al.), 10137 (6-18), 10140 (6-18), 10189 (6-14),

10306 (6-18), 10634 (6-4), 10723 (6-8), 22332 (6-4),

22801 (6-5c), 23053 (6-6), 23272 (6-8), 23280 (6-4), 23358 (6-6),

24108 (6-28), 24445 (6-4), 24997 (6-9), 25037 (6-6), 25110 (5-6),

25113 (6-4).

Fabris, H. A. (et al.), 7936 (6-4).

Fagerlind, F. & G. Wibom, s.n. (5-1), 753 (6-18), 816 (6-15c),

817 (6-15c), 818 (6-6), 819 (6-15c), 858 (6-6), 1020 (6-15c),

1021 (6-4), 1299 (6-21), 1405 (5-1), 1405^{II} (5-1).

Fassett, N. C., 22769 (6-15b), 25021 (6-10), 25142 (6-10), 25150 (6-5a),

25176 (6-5a), 25641 (6-4), 25647 (6-20), 25648 (6-20), 25814 (6-10),

25818 (6-33), 25900 (6-20), 25922 (6-34), 25925 (6-34),

25927 (6-23), 25942 (6-4), 25946 (6-23), 25962 (6-20), 25995 (6-23),

25999 (6-24), 26037 (6-4), 28462 (6-15c), 28481 (6-10),

29077 (6-15a), 29078 (6-15a), 29083 (6-15b), 29084 (6-15a),

29095 (6-15a).

- Fendler, A., 1570 (6-4), 1580 (6-10), 1581 (6-10), 2183 (6-20).
- Fernandez, A. & L. E. Mora, 1234 (6-18).
- Ferreyra, R., s.n. (6-18), 1282 (2-1), 5212 (6-15c), 5615 (6-30),
8544 (5-1), 12910 (6-6), 14328 (2-1), 16790 (5-6).
- Fiebrig, K., 2323 (6-5c), 2640 (6-30), 2884 (6-20), 2922 (5-6),
3304 (5-8).
- Firmin, G., 126 (6-6), 132 (6-6), 139 (6-15c), 213 (6-4), 318 (6-6).
- Firmin, L. H., s.n. (1-1).
- Fischer, G. L., s.n. (6-30), 35218 (5-4).
- Fischer, W., 177 (6-15a).
- Flyr, D., 1195 (6-5a).
- Folsom, J. P. & R. B. Channell, 7203 (6-20).
- Forero, E. et al., 3630 (2-1).
- Fortuna, J., s.n. (6-1), 47 (6-15).
- Fosberg, F. R. (et al.), 20243 (6-23), 20681 (5-1), 20804 (6-34),
21362 (6-4), 21452 (5-1), 21454 (6-34), 21464 (6-23), 21864 (6-10),
22227 (6-10), 22444 (6-29b), 22533 (6-5a), 22850 (5-1).
- Fries, R. E., s.n. (6-21), 725 (2-1), 1023 (5-8), 1259a (6-20),
1263 (6-5c), 1268 (6-5c), 1269 (6-30).
- Fröderström & Hultén, 376 (5-8).
- Fruchard, 987 (6-8).
- Funck & Schlim, 52 (6-25).
- Galen Smith, S. (et al.), 1094 (6-10), 1317 (6-4), 1342 (6-8), 1370
(6-23), 1371 (6-10), 1373 (6-16).
- Galeotti, M., 5764 (5-2), 5817 (6-10), 5845 (6-15a; 6-30).
- Gallinal, J. P., 117 (6-9), 189 (6-9), 218 (6-8), 345 (6-9),
407 (6-8), PE1159 (6-9), 1337 (6-8), 1580 (6-9), 1778 (6-8),

- Gallinal, J. P. (continued), 1870 (6-8), 2484 (6-8), 3056 (6-9),
 PE5130 (6-6), 5898 (6-33).
- Garcia, M., 67 (6-5).
- Garcia, J., 175 (5-8).
- Garcia-Barriga, H., 17197B (6-18).
- Gargantea-Fabrega, M. de, s.n. (6-18).
- Gaudichaud, C., 108 (6-5c), 265 (6-33).
- Gay, C., 73 (6-18), 278 (6-18).
- Gehrt, A., 3386 (6-20), 12895 (6-10).
- Gentry, A. et al., 23295 (2-1).
- Gentry, H.S., 6301 (6-10).
- Ghiesbrecht, M., s.n. (5-2), s.n. (6-15a).
- Gibbs, P. E. et al., 3271 (6-20), 3425 (6-10).
- Gillet, J. M. & R. Jaramillo, 16533 (6-10).
- Gines, Bro., 1674 (6-24).
- Glassman, S. F., 1672 (6-10).
- Glaziou, M. A., II288 (6-10), III1272 (6-33), 1858a (6-33), 6423 (6-20),
 6429 (5-3b), 6439 (6-10), 6770 (6-5c), 9042 (5-3b), 11630 (6-33),
 13305 (6-33), 15514 (6-33), 17835 (6-20), 18581 (6-33),
 18981 (6-33), 20529 (6-20), 20530 (6-33).
- Godet, 110 (2-1).
- Godfrey, R. K., 66672 (6-5), 66708 (6-4), 67180 (6-4).
- Gomez-Pompa, A., 1809 (6-10).
- Gonzales Mas, A., s.n. (6-5a).
- Gonzales, S., 21990 (6-5a).
- Goodall, N., 441 (1-1), 576 (6-5), 594 (1-1), 793 (1-1), 4205 (1-1).

- Goudot, M. J., s.n. (5-1).
- Grabrandt, R. A. J. & J. M. Idrobo, 137 (5-1).
- Graf, K., 286 (4-1), 356 (6-30), 471 (4-1).
- Grandjot, C., s.n. (3-1).
- Grant, V., 7350 (6-10).
- Greene, S. W., 444 (1-1), 802 (1-1), 1492 (1-1), 1631 (1-1), 1984 (1-1),
2356 (1-1), 2889 (1-1), 3057 (1-1).
- Gregg, Dr., 720 (6-15a).
- Gregory, D. P. & G. Eiten, 299 (5-8).
- Grubb, P. J. et al., 137 (5-8), 275 (5-8), 293 (5-8), 310 (2-1),
321 (5-1), 549 (2-1), 590 (5-8), 693 (5-1), 771 (6-34), 791 (6-4).
- Guarin, R. & M. Villareal, 952 (6-4), 960 (6-4).
- Guillou, M. le, 112 (1-1).
- Guiñazu, J. R., 236 (1-1).
- Gunckel, H., 51 (6-14), 1465 (6-18), 1996 (6-8), 14654 (6-18).
- Gusinde, M., 609 (6-14), 610 (6-18).
- Gussfeldt, P. s.n. (3-1).
- Hahn, M., 1035^{bis} (5-4).
- Hammarlund, C., 150 (6-30), 314 (6-6), 420 (6-30).
- Hammel, B., 2756 (5-2).
- Hariot, M. P., s.n. (1-1).
- Harley, R. M. et al., 15508 (6-31), 19214 (6-31), 20044 (6-31).
- Harling, G. (et al.), 652 (6-6), 653 (6-21), 774 (6-4), 775 (6-6),
798 (6-8), 877 (6-23), 878 (6-23), 1160 (6-18), 1293 (6-10),
1294 (6-20), 1295 (6-20), 1337 (6-10), 1375 (6-20), 1377 (6-10),
1424 (5-8), 1466 (6-15c), 1470 (5-8), 1604 (6-5a), 1616 (6-10),

- Harling, G. (continued), 1625 (6-5a), 1628 (6-5a), 4392 (5-8),
 6587 (6-4), 6603 (6-6), 6937 (5-8), 8215 (6-23), 8329 (5-7),
 8385 (6-18), 8753 (6-23), 8900 (5-1), 8979 (5-8), 10408 (6-20),
 10409 (6-5a), 12122 (5-8), 12531 (5-1), 12540 (6-34),
 15040 (5-1).
- Harmon, W. E. (et al.), 3140 (6-10), 3586 (5-2).
- Harris, W. (et al.), 10532 (6-4), 10898 (6-4), 10905 (6-5c),
 11421 (6-5c), 11573 (6-4), 11842 (6-5c), 12493 (6-4), 12494 (6-5c),
 12497 (6-5a).
- Harrison, A. K., s.n. (6-30).
- Harteman, F., 68 (6-4), 77 (5-8).
- Hartweg, 1169 (2-1), 1444 (5-8).
- Hassler, E., 1430 (6-33), 2122 (6-20), 5259 (6-31), 6263 (6-31),
 9847 (6-31).
- Hastings, G. T., 479 (6-15).
- Hatch, W. R., 171 (5-2).
- Hatcher, J. B., s.n. (1-1), s.n. (6-15a).
- Hatschbach, G., 8342 (6-10), 12289 (6-20), 12307 (6-31), 13756 (6-20),
 14882 (6-20), 14877 (6-20), 15354 (6-35), 15389 (6-20),
 16397 (6-10).
- Hauman, L., s.n. (3-1), 46 (6-18).
- Hauthal, R., 382 (6-28).
- Hawkes, J. G. et al., 1880 (6-30), 1913 (5-2), 3898 (2-1).
- Hazlett, D., 1481 (6-17).
- Hedge, W. H., 6938 (6-5a).
- Heinrichs, E., 41 (6-6), 701 (5-8).

- Heithaus, R., 257A (5-2).
- Henschen, S. E., 1272 (6-33).
- Herbst, R., 1199 (6-31).
- Hermann, F. J., 11342 (6-10).
- Hernandez, E., s.n. (5-8).
- Hertel, R., 1587 (6-20).
- Herter, G., 0536 (6-21), 26607 (6-6), 50403 (6-9), 50404 (6-4),
 68064 (6-8), 68128 (6-6), 71404 (6-1), 76133 (6-6), 76184 (6-4),
 76325 (6-8), 79524 (6-20), 79536 (6-6), 79571 (6-6), 80031 (6-21),
 80067 (6-8), 81392 (6-1), 81569 (6-20), 81569 (6-20), 81571 (6-5c),
 81809 (6-1), 88776 (6-17), 99868 (6-17).
- Herter, W. G., 349f (6-20), 1150a (6-17), 1738 (6-3), 1876a (6-33),
 2128 (6-20), 4380 (6-5c), 50510 (6-9).
- Herzog, T., 2439 (2-1), 2440 (2-1).
- Hidalgo, M. S., 12 (6-10).
- Hieronymus, G. (et al.), 9 (6-1), 117 (6-1), 120 (6-5c), 252 (6-6),
 529 (6-6), 654 (6-5c), 735 (5-6), 755 (6-5a), 892 (6-6).
- Hill, A. W., 482 (6-30), 483 (6-4), 487 (2-2).
- Hill, S. R., 1738 (6-30).
- Hinton, G. B., 1307 (5-2), 1332 (6-30), 1386 (6-30), 1564 (6-29a),
 3379 (6-10), 3487 (6-10), 3525 (6-4), 3702 (6-4), 3726 (6-22; 6-32),
 3905 (6-22), 4055 (6-30), 5601 (6-22), 14452 (5-4), 15363 (6-10),
 15647 (5-2).
- Hitchcock, A. S., 20852 (5-8), 20854 (5-1), 21047 (5-8).
- Hoehne, F. C., 4717 (6-20), 18696 (6-20), 20302 (6-20), 24459 (6-1),
 29865 (6-20).

Hollermayer, P. A., s.n. (6-18), 58 (6-18), 111a (6-18), 361 (6-5c).

Holm, R. W. & H. H. Iltis, 474 (5-2), 485 (5-2), 616 (6-4), 618 (6-4).

Holm-Nielsen, L. B. (et al.), 260 (6-5a), 1168 (6-4), 1468 (5-1),
 1537 (6-4), 3540 (6-23), 4697 (6-18), 4792 (6-23), 5067 (6-20),
 5082 (6-23), 5106 (6-20), 5257 (6-29b), 5317 (6-29b), 5371 (5-1),
 5554 (5-1), 5555 (6-4), 5812 (6-28), 6664 (6-15c), 6732 (2-1),
 6779 (6-4), 6943 (6-20), 7127 (6-4), 23584 (6-20), 23585 (6-29b),
 23586 (6-4), 23634 (6-4), 23635 (6-5b), 23636 (6-6), 23637 (6-5a),
 23638 (6-8), 23680 (5-1), 23682 (6-28), 23683 (5-7), 23684 (5-7),
 23685 (2-1), 23686 (5-8), 23687 (5-7; 5-8), 23707 (5-1),
 23708 (6-28), 23709 (6-15c), 23710 (6-4), 23771 (5-7), 23778 (6-28),
 24038 (5-7).

Holmgren, I., 661 (5-1).

Holton, I. F., s.n. (6-10).

Holway, E. W. D. & M. M., 355 (6-30), 551 (5-6), 619 (5-6).

Huertas, G. & L. A. Camargo, 5009 (6-10), 6202 (6-10), 6646 (6-4).

Huidobu, R., 1260 (6-6).

Humbert, H. (et al.), 21256 (6-1), 21295 (6-4), 26315 (6-24), 26402
 (5-1), 27076 (2-1).

Hunewell, F. W., 15902 (6-30).

Hunziker, A. T. (et al.), 1308 (6-15), 4120 (4-1), 6462 (6-6).

Husnot, 46 (6-25).

Hutchinson, P. C. (et al.), 238 (6-18), 4254 (5-7), 4287 (6-4),
 4294 (6-30), 5697 (6-20).

Hyades, M. le, 466 (1-1).

Ibarrola, T., 785 (6-21), 1067 (6-33), 1192 (6-17), 1335 (6-17),
 1342 (6-20), 1825 (6-17), 2614 (6-6).

Idinoel, H., s.n. (6-4), 6 (6-5b), 20 (6-20).

Idrobo, J. M. (et al.), 315 (6-10), 336 (6-10), 431 (6-23),
2245 (6-34), 3377 (6-34).

Illin, N., 87 (6-14), 23774 (6-18).

Iltis, H. H. (et al.), 16 (2-1), 154 (5-8), 205 (6-5b), 248 (5-4),
415a (6-30), 430 (2-1), 509 (2-1; 4-1), 510 (2-1), 513 (2-1),
681 (6-6), 682 (6-6), 6-4), 957 (6-15a), 1005 (5-8), 1151 (6-30),
1284A (2-1), 1285 (2-1), 1305 (6-15a), 1315 (5-8), 1708 (5-8),
1716 (5-8), E459 (6-15c), E534a (6-4), G209 (6-5a),
G211 (5-8), G258 (5-8).

Infantes, J., 2438 (5-7).

Irwin, H. S. (et al.), 2661 (6-33), 5224 (6-20), 8099 (6-20), 9457
(6-20), 9458 (6-20), 9749 (6-20), 19960 (6-33), 27742 (6-20),
29580 (6-5c), 29620 (6-20), 30360 (6-33), 31012 (6-20).

Jaffuel, F. (et al.), 2948 (6-18), 3057 (6-18), 3238 (6-18).

Jameson, W., 5 (5-1), 50 (5-8), 51 (6-15c), 98 (5-8), 127 (1-1),
150 (5-8), 188 (5-1), 263 (6-29b), 405 (5-1), 470 (6-15c),
602 (2-1), 749 (6-6), 880 (6-29b), 887 (6-15c).

Jaramillo, J. M. D., 2775 (6-33), 2775A (6-10).

Jeffrey, C. et al., 2225 (6-10), 2232 (6-10).

Jimenez, A., 896 (5-2), 2230 (5-2).

Jimenez, O., 950 (6-4).

Job, M. M., 1365 (6-4).

Johnson, W. M. & F. A. Barkley, 18C799 (6-33).

Johnston, I. M. (et al.), 1203 (6-32), 4825 (4-1), 4925 (3-1),
5126 (6-1), 5460 (6-4), 6052 (4-1), 6304 (6-1), 7431 (6-15a).

Johnston, J. R., 898 (5-2).

Jones, G. N., 22671 (6-15a).

Jordan, E., 116 (5-8).

Joergensen, P., 1350 (5-6), 1443 (6-5a), 1564 (5-6), 1565 (5-6),
1592 (6-10), 2626 (6-33), 3169 (6-33), 3578 (6-17), 3580 (6-33).

Julio, Bro., 48 (6-30).

Junge, C., 156 (6-18), 2099 (6-4).

Jürgens, C., 8 (6-17; 6-20), 8a (6-5c), 29 (6-33), 47 (6-17), 71 (6-33),
114 (6-5c), 115 (6-8), 126 (6-31).

Karsten, H., s.n. (5-8).

Kausel, 4222 (6-18).

Keck, C., 431 (6-17).

Keel, S. K., K411 (6-30), K434A (6-6), K434B (6-15a), K437 (6-15a),
K458 (6-15a).

Kenoyer, L. A. (et al.), 1623 (6-30), 1673 (6-30), 1864 (6-22; 6-32),
2147 (6-15a), 2761 (6-32), 2936 (6-15a).

Killip, E. P. (et al.), 6864 (6-10), 8955 (6-10), 11921 (5-1),
11965 (6-34), 15173 (6-20), 15639 (5-8), 16709 (6-10), 17576 (2-1),
18483 (6-5b), 18627 (6-34), 18904 (6-10), 19687 (6-8), 19698 (6-4),
19883 (6-10; 6-20), 19889 (6-4), 21146 (5-8), 21614 (5-8),
21995 (6-6), 22050 (2-1), 22066 (5-8), 34208 (5-8), 34538 (6-4),
34605 (5-1).

King, R. E. & T. R. Soderstrom, 5121 (6-10).

Kirkbride, J. H. & H. Chamba, 4137 (6-20).

Klevens, J. & F. A. Barkley, 18A189 (6-10).

Knoth, C. E., 3183 (6-10), 4005 (6-18).

Koch, S. D., 76186 (6-5b).

- Koyama, T. et al., 13790 (6-31), 13829 (6-17), 14112 (5-6).
- Kral, R., 25189 (6-30).
- Krapovickas, A. (et al.), 5671 (4-1), 16302 (6-4), 16729 (6-33),
20304 (6-6), 20306 (6-33).
- Kuntze, O., 57 (6-1), 61 (3-1), 2288 (6-5a).
- Kurtz, F., 5838 (3-1), 6252 (3-1), 6688 (6-6), 6710 (6-21), 11128 (3-1).
- Køie, M., 5350 (6-34).
- Langenheim J. H. (et al.), 3373 (6-10), 3503 (6-23), 3620 (6-10),
3644 (6-16), 3682 (5-1), 3687 (5-1).
- Lankester, C. H., 226 (6-4), 227 (6-5c).
- Lara, R. & K. Parker, 21K (5-8), 24b (6-15c), 24d (6-30), 38B (6-30),
39c (6-15a), 39i (6-6), 41B (5-8).
- Larsen, C. A., s.n. (1-1).
- Lazor, R. L. & M. D. Correa, 2826 (6-20).
- Leavenworth, W. M. C. (et al.), 158 (6-32), 1130a (5-2), 1139 (5-2),
1158 (5-8).
- Lechler, W., 111 (1-1), 111a (1-1), 325 (6-18), 701 (6-4), 1380 (6-18),
1749 (6-30), 1954 (2-1).
- LeDoux, D. et al., 1933 (6-5b).
- Legrand, C. D., 1196 (6-6), 1250 (6-21), 1379 (6-8).
- Lehmann, F. C., 1576 (6-29a), 3144 (5-1), 5258 (5-1), 8473 (6-18).
- Leibold, 2832 (6-8), 2976 (6-18).
- Leitao, H. F. et al., 3131 (6-20).
- Leite, J. E., 450 (6-5c), 452 (6-17), 477 (6-4), 480 (6-4), 2005 (6-4),
2850 (6-20), 2885 (6-4), 3643 (6-10).
- Lems, K., s.n. (5-2), 650130-01 (6-20).

- Lent, R. W., 716 (5-2), 1060 (6-4), 2180 (6-10), 3902 (6-10).
- León, J. (et al.), 3366 (6-4), 5881 (6-17), 9696 (6-17), 15385 (6-19).
- Lesueur, H., 1100 (6-29a), 1102 (6-17), 1112 (6-32), 1117A (6-5a),
1121 (6-10), 1121A (6-15a), 1123 (6-22), 1126 (6-29a).
- Lindberg, 572 (6-35).
- Lindeman, J. C. (et al.), 457 (6-10), 2725 (6-10), 3686 (6-17),
3705 (6-5c), 8560 (5-3b), 8152 (6-4), 9171 (6-4).
- Linden, J., s.n. (6-10), 92 (5-4), 1130 (5-1).
- Linden, M., 412 (5-1).
- Lindig, 1401 (6-20), 1402 (6-4), 1403 (5-1), 1404 (5-8).
- Lindman, C. A. M., A617 (6-8), A621 (6-5c), A693 (6-5c), A857 (6-17).
- Liogier, A. et al., 28913 (6-5a), 28960 (6-5a).
- Llano, M. de, 70 (2-1).
- Llanos, G., s.n. (2-1).
- Loefgren, A., 270 (6-10), 12415 (6-33), 12419 (6-5c), 12425 (6-5c),
12427 (6-20).
- Lopez Miranda, A. (et al.), 1104 (6-21), 1468 (6-6), 1469 (6-21),
1481 (6-15c), 1482 (6-4), 1483 (6-18), 5287 (6-10), 6724 (6-10),
7993 (6-4), 8036 (6-21), 8330 (6-15c), 8331 (6-30).
- Lorentz, P. G. (et al.), 59a (6-20), 94 (6-5a), 443 (6-6), 463 (6-6),
500 (6-6), 609 (6-5a), 770 (6-33), 829 (2-1), 892 (6-6), 1188 (6-6),
1788 (6-6).
- Lot, A., 592 (6-10).
- Lourteig, A., 2674 (6-33).
- Lumer, C., 1174 (6-10).

Luteyn, J. L. (et al.), 5146 (6-5a), 5484 (6-15c), 5878 (6-20),
 5953 (6-34), 5954 (6-23), 5955 (6-10), 6602 (6-10), 6605 (6-20),
 6608 (6-4), 7072 (6-10).

Lyonnet, E., 40 (5-4), 42 (6-15a), 43 (5-4), 263 (5-8), 265 (5-2).

Løjtnant, B. (et al.), 11182 (5-8), 11183 (5-8), 11184 (5-1),
 11394 (6-4), 11570 (2-1), 11571 (5-8), 11580 (5-7), 11908 (6-20),
 12128 (6-23), 12129 (6-29b), 12139 (6-15c), 12405 (6-29b),
 12422 (6-18), 12440 (6-29b), 12441 (6-10), 12446 (6-18),
 12450 (6-20), 12497 (6-4), 12561 (5-1), 13706 (5-1), 13736 (5-8),
 14249 (6-20), 14258 (6-28), 14379 (5-8), 14749 (6-23),
 14855 (6-4), 15014 (6-21), 15053 (6-20), 15387 (5-8),
 15390 (6-28), 15394 (5-7).

Macbride, J. F. (et al.), 616 (5-8), 626 (5-8), 899 (2-1), 1030 (6-21),
 1132 (5-8), 1276 (6-6), 1450 (6-21), 1451 (6-5b), 2272 (6-15c),
 2306 (6-15c), 2484 (2-1), 3009 (5-8), 3319 (6-18), 3367 (5-1),
 4388 (5-1), 4389 (5-1; 5-7).

Madison, M. T., 1001 (6-30), 1003 (6-21), 6779 (5-1).

Magalhaes, M., 3327 (6-20).

Magens, O., 1787 (6-15a).

McGill, L. & D. Keil, 8345 (6-30).

Maguire, B., 39421 (5-8), 39428 (6-24).

Maldonado, R., 225 (6-18).

Malme, G., 13 (6-5c), 14 (6-21), 202 (6-8), 206 (6-8), 206B (6-8),
 1211 (6-5c).

Mandon, G., 1417 (6-28), 1423 (5-1), 1435 (6-6), 1436 (6-30),
 1437 (6-28), 1439 (6-15c), 1440 (6-28), 1441 (6-4), 1442 (4-1),

- Mandon, G. (continued), 1444 (2-1), 1445 (5-8), 1446 (5-7; 5-8),
1447 (5-6; 5-8), 1449 (5-6), 1450 (5-7), 1451 (5-8), 1452 (5-7),
1453 (5-8).
- Manning, W. E. & M. S., 53122 (6-30), 531227d (6-5b).
- Marcks, B. & C., 1132a (6-30), 1132b (6-5a), 1141 (6-30), 1267 (6-5b).
- Marks, L., 6 (5-1).
- Marticorena et al., 267 (2-1), 586 (4-1).
- Matthews, M., s.n. (6-10), s.n. (6-18).
- Matudea, E. (et al.), 2355 (5-8), 19141 (6-11), 19203 (6-15a),
19243 (6-15a), 19391 (6-30), 25606 (6-15), 25863 (6-15a),
26095 (6-10), 26156 (6-15a), 26425 (6-4), 26430 (6-10),
26560 (6-10), 26603 (5-8), 26919 (6-30).
- McDaniel, S., 6705 (6-4).
- McGill, L. A. (et al.), 1007 (6-10), 1059 (6-8), 8345 (6-30).
- McKee, H. S., 10412 (6-10), 10414 (6-8), 11213 (6-10).
- McPherson, G., 1044 (6-15a), 1050 (6-15a).
- McVaugh, R., 13819 (5-8).
- Mergens, C., 119 (6-17).
- Merxmüller, H., 22861 (5-1), 22890 (5-1).
- Metcalf, R. D., 30415 (6-30).
- Meyer, F. G., 9555 (6-6), 9556 (6-4), 9581 (6-14), 9582 (6-8),
9630 (6-8), 9852 (6-8).
- Meyer, T. (et al.), 4081 (6-1), 4175 (6-1), 15289 (6-20), 33293 (6-15a).
- Mexia, Y., 5374 (6-10), 7651 (5-8), 7882 (6-18).
- Mick, G. & K. Roe, 84 (6-5b), 172 (5-4).
- Mille, A., 356 (5-1), 357 (6-4), 358 (6-29b), 372 (6-4), 373 (6-4).

Mimura, I., 123 (6-31).

Mitastein, M., 108 (6-20).

Molina, A. (et al.), 476 (6-20), 1023 (6-10), 1033 (6-10), 1099 (6-20),
 6260 (6-22), 6283 (6-10), 6317 (6-5a), 6470 (6-10), 7717 (6-10),
 7847 (6-22), 7882 (6-22), 8287 (6-17), 10106 (6-5a), 11152 (6-17),
 11245 (6-5a), 12215 (6-10), 12553 (6-5a; 6-5b), 12797 (6-20),
 12821 (6-17), 13847 (6-5a), 13994 (6-22), 14018 (6-10), 14025 (6-22),
 17016 (6-10), 18362 (6-4), 18499 (6-5c), 18563 (6-17; 6-20),
 21240 (6-5a), 21464 (6-20), 21484 (6-5a), 22214 (6-5a),
 22255 (6-20), 22257 (6-5a), 22346 (6-5a), 24247 (6-17),
 24247 (6-17), 24313 (6-10), 24412 (6-22), 24416 (6-17),
 25447 (6-20), 25566 (6-10), 30888 (6-5), 31184 (6-10).

Montalvo, E. A., 4784 (6-5).

Montero, G., 225 (6-4), 757 (6-14), 3041 (6-18), 3364 (6-6), 3537 (6-14).

Moore, D. M., 713 (1-1), 870 (1-1), 1114 (1-1), 1587 (1-1), 1752 (1-1),
 2425 (1-1).

Moore, H. E. Jr. (et al.), 1245 (5-8), 1368 (6-15b), 1937 (6-10),
 2059 (6-22), 2066 (5-4), 2351 (6-22), 3081 (6-15a), 3234 (6-5b),
 3328 (6-10), 3331 (6-30), 3364 (6-30), 3474 (6-22), 3708 (6-29a),
 4862 (6-15a).

Mora, L. E., 858 (6-8), 883 (5-1), 955 (6-18), 1229 (6-4).

Moreno, F. P. (et al.), 264 (6-15a), 400 (6-4), 401 (6-15), 779 (6-15a).

Mori, S. (et al.), 7389 (6-20), 7447 (5-2), 11307 (6-33).

Morong, T., 1243 (6-1).

Morrison, J. L. (et al.), 17040 (6-18), 17198 (4-1), 17618 (6-18),
 17644 (6-4), 17649 (6-18).

Mosén, H., 771 (6-10), 3502 (6-2), 4445 (6-10).

Mosthaff, 26 (1-1).

Mueller, 1954 (6-30).

Muenschner, W. C., 12043 (6-10).

Muller, C. H., 3521 (6-30)

Müller, F., 1348 (6-5a), 1953 (6-10), 1955 (6-30), 2000 (6-18),
7955 (6-30).

Muñoz, R., 1016 (6-18).

Mutis, D. E., 67 (6-10).

Mutis, J. C., 2638 (6-10), 3736 (6-5a), 5221 (6-33; 6-34), 5307 (6-10),
5312 (6-8), 5321 (5-8), 6181 (6-20), 6182 (6-20), 6183 (6-20),
6186 (6-20), 6187 (6-16), 6189 (6-33), 6190 (6-16), 6191 (6-5a).

Nelson, E. W., 4878 (5-4).

Nichols, G. E., 103 (6-4).

Nicolas, s.n. (6-20), s.n. (6-15a).

Niederlin, G., s.n. (6-6).

Niguez, E., 97 (6-4).

Novaez, C., 12421 (6-20).

Oberwinhkler, B. & F., 12359 (6-20), 12360 (6-23), 12756 (5-1),
13551 (5-1).

Ochoa, C., 6-4 (2-1), 1014 (5-8), 1017 (5-1), 2014 (5-8).

Ochseniüs, C., s.n. (6-14), 1 (6-18), 1a-b (6-6).

O'Donnell, C. A., 1459 (6-1), 2050 (3-1), 2327 (6-18).

Olea, D., 51 (6-6), 166 (6-5a), 277 (6-10).

Ortega, J. G., 5542 (6-22).

Osten, C., 3072 (6-4), 4534 (6-5c), 5151 (6-33), 6908 (6-21),
14293 (6-6), 21671 (6-8), 21788 (6-2), 21788b (6-2), 21789 (6-21),
21813a (6-2), 21907 (6-33).

Pabst, G. & A. Abendroth, 7164 (6-20).

Padilla, I., 98 (5-1), 1117 (6-21).

Paillardelly, E., s.n. (2-1).

Palmer, E., 13 (6-17), 33 (6-15b), 52 (6-32), 93 (6-4), 98 (6-32),
201 (6-15a), 241 (6-30; 6-32), 253 (6-5c), 263 (6-4), 264 (6-32),
360 (6-32), 391 (6-30), 711 (6-4).

Parodi, L. R., 11790 (6-18), 12027 (6-33), 12047 (6-17).

Parry, C. C. & E. Palmer, 893 (6-22), 894 (6-4; 6-5c), 895 (6-22),
895¹/₂ (6-15a), 896 (6-4), 897 (6-36).

Pastore, A. I., 1189 (6-8), 1231 (6-8), 1232 (6-6).

Patrick, L. A., 229 (6-5c).

Pavon, s.n. (5-1).

Pearson, O. P. & A., 96 (4-1).

Pedersen, T. M., 502 (6-33), 787 (6-5c), 1060 (6-8), 1340 (6-17),
1459 (6-4), 2991 (6-6), 2999 (6-31), 4299 (6-31), 9562 (6-33).

Penland, C. W. & R. H. Summers, 424 (6-15c), 567 (5-5; 5-8),
917 (6-34), 928 (2-1), 1026 (6-14), 1028 (6-20).

Pennell, F. W. (et al.), 2049 (6-23), 2079 (5-1), 2133 (6-10), 2134
(6-20), 2166 (6-5a), 2167 (6-5a; 6-5b), 2167A (6-20), 2511 (6-33),
2512 (6-20), 2557 (6-4), 2558 (6-5b), 2969 (6-34), 3028 (5-8),
3105 (5-1), 6531 (5-1), 6543 (6-28), 6547 (6-18), 6908 (6-34),
6909 (6-23), 7126 (6-10), 8239 (6-33), 8879 (6-5a), 9858 (5-7),
9860 (2-1), 9862 (2-1), 9900 (5-1), 9901 (5-1), 9959 (5-7).

Pennell, F. W. (continued), 9963 (6-28), 12309 (3-1), 12393 (6-15),
 12540 (6-4), 12628 (6-14), 12650 (6-18), 12961 (6-18),
 13379 (6-15a), 13383 (5-8), 13492 (2-1), 13619 (6-30),
 14677 (5-8), 14693 (2-1), 16801 (6-32), 17586 (6-32), 17713 (6-30),
 17886 (6-5b), 18367 (6-30), 18376 (6-5c).

Pereira, E., 6539 (6-4).

Perez-Arbelaez, E., 2370 (6-5), 3204 (6-8).

Philippi, R. A., 39 (6-18), 43 (6-14), 104 (6-6), 133 (6-6; 6-8),
 138 (6-14), 766 (3-1), 1147 (1-1).

Pierotti, J. A., 1380 (6-6).

Pinto, P. E., 683 (6-33).

Pircher, A., 13 (5-8).

Pires, S. M. & G. A. Black, 3291 (6-33).

Pirion, A., 776 (6-18), 3477 (6-18).

Pisano, E., 2447 (1-1), 2532 (1-1), 2588 (1-1).

Pittier, H., 14125 (5-2).

Planella, J., 210 (6-8).

Plowman, T., 1965 (5-1).

Poeppig, 24 (6-4), 114 (6-18).

Pombo, F., s.n. (6-16).

Prance, G. T., 6911 (6-20), 59078 (6-20).

Prescott, G. W., 116 (6-29b), 127 (6-15c), 170 (2-1), 280 (6-29b),
 330 (5-1), 333 (5-8), 538 (2-1), 580 (5-1), 587 (5-8), 628 (-23),
 683 (2-1), 685 (1-1), 694 (6-10), 695 (6-15c), 779 (6-18), 781
 (6-21), 912 (2-1), 981 (2-1), 1404 (2-1).

Pring, G. H., 54 (6-10).

Pringle, C. G., 1116 (5-4), 1388 (6-29a), 3131 (6-20), 4216 (5-2; 5-4; 5-8), 4216a (5-2), 4853 (5-4), 5951 (5-2), 6494 (6-22), 6509 (6-20), 6652 (6-30), 7517 (6-15a), 7518 (6-10), 8123 (6-17), 9464 (6-22), 10011 (6-29a), 11721 (6-20), 13226 (6-22).

Proctor, G. R., 6824 (6-4).

Puga, 30 (6-4).

Purdie, s.n. (2-1).

Purpus, C. A., 1608 (5-8).

Rambo, B., s.n. (6-4), 29214 (6-8), 316_5 (6-20), 32172 (6-17), 34621 (6-33), 34623 (6-5c; 6-17), 36674 (5-3b; 6-20), 37679 (5-3b), 37929 (5-3b), 39987 (6-8), 38098 (6-8), 38512 (6-31), 38550 (6-4), 38743 (6-33), 39925 (6-31), 51473 (6-10), 52912 (6-17), 53098 (6-33), 53144 (6-17; 6-20), 53387 (6-33), 54676 (6-33), 53721 (6-20), 55992 (6-8), 56356 (6-33), 57059 (5-3b), 57153 (6-5c), 57157 (6-17), 57464 (5-3b), 60083 (6-5c), 60169 (6-10), 60583 (6-4).

Rauh, P263 (5-7), 1120 (6-6), 1121 (6-30), 1122 (6-15).

Reed, s.n. (6-18).

Regnell, A. F., II287 (6-20).

Reiche, C., s.n. (3-1), s.n. (4-1).

Reineck & Czermak, 23 (6-20).

Reiss, R., 1104 (6-20).

Reitz, P. R. (et al.), C121 (6-20), C1319 (6-20), 2466 (6-17), 2981 (6-10), 3370 (5-3b), 3410 (6-5), 3428 (5-3b), 6107 (6-31), 7904 (6-5c), 10593 (6-33), 14171 (6-20), 17823 (6-20).

Renvoize, S. A. (et al.), 2892A (6-4), 3568 (6-33).

Richard, P. W., 6004 (6-4).

Ridley, H. N., s.n. (6-4).

Riedel, 689 (6-20).

Rimbach, A., 120 (5-8), 530 (5-8).

Rocha, H. da, 03 (6-33).

Rodriguez, D., 1402 (4-1).

Rodriguez, L., 4800 (6-4).

Rodriguez, V., 393 (6-6), 590 (6-33), 764 (6-6).

Roe, K. (et al.), 1177 (6-10), 1179 (6-20), 1513 (6-30), 1942 (6-5a),
1970 (6-5b), 1976 (5-2).

Rohweder, O., 914 (6-5a), 915 (6-5a), 920 (6-5a).

Roiivainen, H., 1963 (1-1).

Rosas, M. R., 385 (6-10).

Rose, J. N. (et al.), 3037 (6-5b), 4309 (6-22), 5425 (6-10),
5426 (6-30), 5427 (6-5b), 5480 (6-30), 5591 (5-4), 5736 (5-8),
5747 (5-2), 5984 (5-8), 5984a (5-8), 6242 (6-15a), 7930 (6-29a),
7984 (5-8), 8377 (6-15b), 12392 (6-4), 15109 (6-4), 18825 (6-15c),
19076 (6-15a), 19271 (6-4), 19314 (6-4), 19434 (6-15),
22779 (6-14), 22922 (6-6), 22935 (6-14), 23073 (6-8), 23074 (6-5b;
6-20), 23117 (6-20), 23125 (6-23).

Rosen, S. von, s.n. (2-1).

Rosengurtt, B., B448 (6-9), B453 (6-8), B1762 (6-33), B2455 (6-33),
2618 (6-17).

Rubio, A., 53 (6-10), 81 (6-5).

Rusby, H. H. (et al.), 57 (5-8), 58 (5-1), 59 (5-8), 60 (5-8),
61 (6-30), 180 (6-26), 181 (6-6), 182 (5-8), 738 (6-10),
771 (6-10), 2520 (2-1).

Ruthsatz, B., XVIII16 (6-15), 249 (5-8), 283 (5-8), 462 (5-8), 566
(5-8), 1049 (5-8), 1130 (5-8), 1133 (5-8).

Rzedowski, J., 22372 (5-2), 23499 (5-2), 23877 (5-8).

Sagástegui, A. (et al.), 6357 (6-4), 6361 (6-21), 6418 (5-8), 6479
(6-21), 7485 (5-1), 8021 (6-21), 9019 (6-6), 9104 (5-8), 9440
(6-15c), 9584 (6-8).

Santiago Diaz, P., 1670 (6-10), 1678A (6-5), 2070 (6-10).

Saint-Hilaire, A. de, 297 (6-33), 1877 (6-4).

Salaverry, E., 39 (6-6).

Sandeman, C., 3841 (4-1), 4176 (6-10).

Sastre, C. (et al.), 2830 (6-25), 2836 (6-10), 6087 (6-25),
6843 (6-10), 6948 (6-25).

Saunders, S. G. E., 471 (6-15c), 472 (6-15c), 748 (5-1), 1152 (2-1).

Savatier, L., 164 (1-1), 287 (6-18), 1937 (1-1).

Scala, A. C., s.n. (6-33), 69 (6-5c).

Schaffner, J. G., 4 (6-4), 211 (6-4), 214 (6-5c), 216 (6-15a),
217 (6-22), 218 (6-30), 219 (6-17), 220 (6-36), 223 (6-4),
549 (6-36), 550 (6-17), 551 (6-30), 552 (6-20), 553 (6-22),
554 (6-15a), 555 (6-5c), 556 (6-4).

Schaffner, W., 106 (6-10), 107 (6-10), 523 (6-15b; 6-15a), 524 (6-15a),
525 (6-22), 526 (6-30), 530 (6-15c), 532 (6-29a), 533 (6-10),
534 (6-10).

Sharp, A. J., 44113 (6-15a).

Schiede, s.n. (6-15a), s.n. (5-2), 964 (5-8).

Schinni, A. et al., 18351 (6-4), 19084 (6-17).

Schmitz, A., 816 (5-4).

Schreiter, 6126 (2-1; 4-1), 7022 (2-1).

Schultes, R. E. (et al.), 7839 (6-10), 21167 (5-1).

Schulz, A. G., 5561 (6-6), 6127 (6-1).

- Schulz, J. P., 740 (6-23).
- Schunke, J., 9330 (6-4).
- Schwabe, G. H., 21 (6-18), 112 (6-14).
- Schwaike, s.n. (6-5c).
- Scolnik, R., 490 (6-14).
- Segadas-Vianna, F. et al., I1489 (6-20).
- Sellow, s.n. ((6-6), s.n. (6-10), 1627 (6-33).
- Sergeant, R., 21 (6-23).
- Sharp, A. J., 44113 (6-15a), 44294 (6-4), 44295 (6-30), 44806 (6-6).
- Shepard, R. S., 56 (5-8), 62 (5-7).
- Skottsberg, C. (et al.), 4 (1-1), 18 (6-8), 93 (6-14), 108 (6-6),
111 (1-1), 201 (6-8), 242 (6-21), 312 (1-14), 399 (6-6), 838 (6-14),
I292 (1-1).
- Skutch, A. F., 421 (5-2), 424 (6-4), 1044 (6-15c), 1207 (5-8), 3703
(6-20).
- Skvortzov, B., 2 (6-5c), 13 (6-5c), 15 (6-20), 40 (6-5c), 149 (6-20),
233 (6-20).
- Sleumer, H., 437 (6-15a), 551 (6-15a), 574 (6-28), 1942 (2-1).
- Smith, C., 932 (5-2).
- Smith, C. E. et al., 3675 (6-1).
- Smith, C. L., 1121 (5-17).
- Smith, D. N., 279 (5-8), 396 (5-8).
- Smith, H. M., 124 (6-4).
- Smith, L. B. (et al.), 1453 (6-20), 1568 (6-5c), 1613 (6-20),
7943 (6-10), 8409 (6-33), 9954 (6-17), 10314 (6-10), 13479 (6-20),
13687 (6-20), 13735 (6-5c), 13860 (6-33), 13998 (6-5c), 14026
(6-5c), 14759 (6-20), 14761 (6-33), 14761 (6-31).

Sneidern, K. von, s.n. (6-5a), s.n. (6-28), 76 (6-33), 1739 (2-1),
 1740 (5-1), 1741 (5-1), 2080 (6-18), 2081 (6-28), 2082 (5-1),
 2083 (5-1), 3054 (6-10), 3132 (6-5a), 5860 (6-10), A375 (5-1),
 A417^{bis} (6-15c), A431 (6-23).

Sodiro, A., s.n. (2-1), 186/2 (6-29b), 186/6 (6-18), 335 (5-8).

Soejarto, D. D. (et al.), 1162 (6-10), 3023 (6-10), 3029 (6-33).

Solbrig, O. T. et al., 3787 (6-8).

Solomon, J. C., 2517 (6-10), 2542 (5-2), 4758 (6-4), 4817 (6-15c),
 4901 (5-6), 4964 (5-8), 5297 (6-30).

Soukup, J., 58 (6-30), 361 (6-15), 408 (6-6), 725 (6-15a; 6-21; 6-30),
 850 (5-8), 1884 (6-6), 3229 (6-30), 3745 (2-1), 3973 (6-30).

Soule, O. H., 2206 (6-17).

Sparre, B., 164 (6-8), 178 (6-21), 258 (6-21), 277 (6-6), 594 (6-6),
 692 (6-6), 807 (6-5c), 932 (5-6), 1061 (6-6), 1770 (6-18),
 1843 (6-5a), 1850 (6-14), 1912 (6-4), 3139 (6-4), 13476 (5-1),
 13513 (6-4), 14004 (6-5a), 14176 (5-1), 14231 (6-29b),
 14234 (6-34), 14239 (6-15c), 15080 (6-21), 15606 (5-8),
 15678 (6-6), 15746 (5-8), 15830 (6-8), 15928 (6-20), 16511 (6-18),
 16513 (6-4), 16534 (6-20), 16567 (6-20), 16656 (6-10),
 16737 (6-5a), 16850 (6-4), 16853 (6-6), 17809 (6-15c),
 18360 (6-15c), 18528 (6-15c), 18744 (6-20), 18799 (5-1),
 18802 (6-23), 18850 (6-23), 18851 (6-23).

Spruce, R., 5432 (6-15c), 5565 (6-15c), 5755 (6-6), 5765 (5-8),
 5804 (6-28), 5876 (5-1), 5942 (6-29b), 6030 (6-18).

Stafford, D., 472 (6-6), 568 (6-15c), 629 (6-30), 648 (2-1), 691 (2-1),
 736 (4-1), 1279 (5-7), 1310 (6-28).

Standley, P. C., 27681 (6-20), 34608 (6-4), 34619 (6-4), 35273 (6-4),
 35020 (6-4), 38433 (6-4), 60998 (5-2), 61864 (5-2), 62420 (6-10),
 65098 (5-2), 67684 (5-2), 67733 (5-2), 67752 (5-2), 69633 (6-10),
 71065 (6-17), 82235 (6-20), 85381 (5-2), 90176 (6-20), 91169 (6-10),
 92445 (6-17), 92803 (6-17), 92844 (6-17).

Stanford, et al., 2475 (6-5c), 2479 (6-32), 2671 (6-15a).

Stearn, W. T., 130 (6-5a).

Stehlé, H., 669 (6-4), 682 (6-25), 1132 (6-25).

Steinbach, J., 5245 (6-31), 6014 (6-21; 6-30), 6728 (6-31),
 8709 (6-5c), 8814 (6-30), 8815 (6-30), 9352^{bis} (6-8), 9542 (6-8).

Steinbach, R. F., 254 (6-4), 578 (6-4), 611 (5-1).

Stevens, W. D., 3145 (6-17).

Steyermark, J. A., 34151 (5-2), 34923 (5-2), 43111 (5-1), 43212 (5-17),
 49770 (6-29a), 49880 (6-30), 49884 (5-4), 50165 (5-4), 50215 (5-4),
 53100 (5-7), 53204 (2-1), 54287 (6-20), 55418 (6-20), 55419 (6-33),
 55835 (5-8), 57071 (6-8), 57222 (6-34), 57274 (6-5a), 57495 (5-1),
 57496 (5-1), 60125 (6-33), 62700 (6-17), 62722 (6-20), 63010 (6-10),
 96793 (6-4), 96971 (5-1), 101156 (6-20), 101220 (6-4), 104792
 (6-20).

St. John, H., 20777 (5-8).

Stordy, R. J., 8 (2-1), 22 (6-6).

Stork, H. E. (et al.), 2908 (6-10), 10233 (6-30), 10849 (5-8).

Straw, R. M., 2486 (2-1).

Stübel, s.n. (2-1).

Stuckert, T., 15523 (6-6), 15864 (6-17), 16053 (6-6), 18497 (6-20),
 20864 (6-6), 21011 (6-6).

Sucre, P., 338 (6-20).

Tanduz, A., 4217 (5-2), 11722 (6-10).

Tate, G. H. H., 16 (5-8), 78 (5-8), 131 (5-6), 136 (5-8).

Taylor, J. & C., 11329 (6-10), 11735 (5-2), 11783 (6-4), 11805 (6-10),
17701 (6-10).

Taylor, R. J., 4331 (5-2), 4463 (6-4).

Terry, 1317 (5-2).

Thomasson, K., s.n. (6-10), s.n. (6-18).

Thorne, R. F., 32060 (6-4).

Thurber, G., 343 (6-22).

Tillett, S. S., 747-1008 (6-10).

Tomas, Bro., 871 (6-33).

Ton, A. S., 828 (6-10; 6-11), 915 (6-10), 946 (6-5c), 948 (5-4),
964 (6-4), 974 (6-29a), 1087 (6-30), 1294 (6-5c), 2295 (6-17),
2360 (6-11), 2517 (6-10), 2915 (6-5c).

Torregrosa, C. & F. A. Barkley, 18A166 (6-10).

Tovar, O., 1933 (6-4), 2417 (2-1), 3501 (6-6), 5099 (2-1).

Triana, J., 473 (6-5a), 474 (6-4), 476 (6-10; 6-33), 478 (6-29b),
1049 (6-29b).

Troll, 429 (6-5c), 1425 (6-30), 1877 (2-1), 2353 (6-30), 2900 (2-1).

Tucker, J. M., 1022 (6-5a; 6-5c), 1161 (6-10), 1192 (6-5a).

Tückerheim, H. von, 1295 (6-5a), 3796 (6-17).

Ule, E., 1387 (6-17), 1622 (6-33), 1920 (6-20), 3767 (6-35).

Urville, J. Dumont-D', s.n. (1-1), s.n. (6-8), s.n. (6-18).

Valencia, J., s.n. (6-6; 6-8).

Valentin, E., s.n. (1-1).

Vareschi, 2147 (5-1), 2233 (5-1).

Vargas, C., 252 (6-30), 542 (5-8), 544 (5-8), 676 (6-15a), 785 (6-30),
1070 (5-8), 2446 (6-15c), 2768 (5-1), 2785 (6-15c), 2807 (6-15c),
7200 (6-4), 7261 (5-1), 12253 (2-1), 13827 (6-4).

Ventania, P., 457 (6-6).

Venturi, S., 98 (6-8), 509 (6-21), 2999 (6-10), 3053 (5-6), 3075 (5-6),
4003 (6-5a), 4369 (6-1), 4584 (6-10), 4712 (5-6), 4768 (6-18),
4813 (5-6), 6528 (4-1), 6529 (4-1), 6530 (4-1), 6544 (2-1),
6545 (2-1), 6546 (2-1), 6547 (2-1), 7278 (2-1), 7280 (4-1),
7281 (4-1), 7726 (6-5a), 8658 (4-1), 9446 (6-18), 9673 (6-21),
9863 (6-5a; 6-6), 10166 (6-1).

Vervoorst, F. B., 3234 (4-1), 4632 (1-1).

Villeda, M. E., 158 (6-5).

Volleman, 27 (6-18).

Walter, H. & E., 38 (6-6), 105 (6-1), 299 (5-8).

Weaver, J. N., 799 (6-15a), 853 (6-15a), 859 (6-15a), 864 (6-15a).

Weberbauer, A., 948 (2-1), 987 (4-1), 1367 (6-15), 2449 (5-8),
2700 (6-30), 3283 (6-15c), 6475 (5-8), 6623 (5-8), 7089 (2-1),
7493 (5-8), 7585 (5-1).

Weberling, 5870 (2-1).

Webster, G. L. (et al.), 2820 (6-30), 11799 (6-30), 12315 (5-2),

Weddell, M. H. A., 3727 (5-6), 3815 (6-6), 4752 (4-1), 4755 (2-1).

Werderman, E., 453 (4-1), 574 (6-18), 937 (4-1), 972 (6-15a),
1286 (6-15a).

West, J., 3685 (6-6), 4973 (6-18).

West. R. C., F28 (6-6), I5 (6-6), K3 (6-30), K9 (6-15a).

Weston, A. S., 5839 (5-2).

Weydahl, E., 184 (5-8), 317 (5-8), 356 (6-4), 357 (5-8).

White, S. (et al.), 123 (6-28), 521 (5-8).

White, S. S., 2089 (6-32), 2268 (6-32), 2278 (6-15b).

Whiting, A. J., 634 (6-32).

Whitmore, J. L., 43 (5-2).

Wiggins, I. L. (et al.), 100 (6-4), 4859 (6-15a), 9828 (6-4).

Wilbur, L. R., 20307 (5-2).

Wilczek, E., 9 (2-1; 3-1), 75 (3-1), 576 (6-4).

Wilkes, Capt., s.n. (1-1), s.n. (2-1).

Will, s.n. (1-1).

Williams, L. O. (et al.), s.n. (6-33), 11245 (6-5a), 12766 (6-10),
 13286 (6-20), 13674 (6-20), 13928 (5-2), 15848 (6-17), 21990 (6-5a),
 22532 (6-5b), 22666 (6-11), 22855 (6-5a), 22864 (6-30),
 25368 (6-5a), 25459 (6-30), 25926 (5-2), 27332 (6-30),
 28179 (6-5a), 28272 (6-4).

Williams, R. S., 2497 (6-6).

Wilson, 491 (6-5c).

Woerner, R., s.n. (6-14).

Woodbury, R., s.n. (6-5a).

Woodson, R. E. (et al.), 432 (5-2), 1094 (5-2).

Woolston, A. L., 602 (6-20), 928 (6-20), 928 (6-17), 934 (6-33),
 1361 (6-20), 1361 (6-17).

Worth, C. R. (et al.), 8882 (6-4), 16378 (6-18).

Wright, C., s.n. (6-19), 86 (6-19), 1720 (6-15b), 3243 (6-19).

Wynd, F. L. & C. H. Mueller, 561 (6-5a).

Yepes-Agreto, S., 3263 (6-10).

Young, G. & M. Sierra, 142 (6-5).

Xolocotzi, E. H., X2136 (6-15a).

Xuarez, G., 15541 (6-8).

Zimny, Z., s.n. (2-1).

Zudzuki, F., 442 (2-1).

Zöllner, O., 8730B (6-18).

Øllgaard, B. & H. Balslev, 8206 (6-28), 8435 (2-1), 8536A (6-28),
8552 (6-15c), 8778 (6-28), 8850 (2-1), 8890 (5-8), 8916 (5-8),
8930 (6-15c), 9322 (6-10), 9547 (5-1), 9661 (5-1), 9891 (5-7),
9905 (2-1), 9988 (5-8), 10051 (5-8), 10121 (2-1).

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AUTOBIOGRAPHICAL STATEMENT

BY

HENRIK BALSLEV

I was born on the 4th of January 1951 in Ndolage near the village of Kamachumu about 50 miles from the town of Bukoba in the West Lake Region of Tanganyika, where my danish parents worked as doctor and nurse at the mission hospital. My first six years I spent at Ndolage. At age seven I went to Bukoba to attend boarding school. In 1961 my family and I returned to Denmark to live in the village of Bindslev in northern Jylland. I attended fourth through seventh grade at Bindslev Central Skole, and eight through 12th grade at Hjørring Gymnasium from which I graduated with highschool diploma in 1970. From 1970 to 1971 I attended the Royal Danish School of Architecture. In the fall of 1971 I entered the University of Aarhus to persue my interest in Biology. I was introduced to botany through several courses at the Institute of Botany, and also through several fieldtrips to the Norwegian mountains, the Pyrrenees, the Canary Islands and other places. An initial plan to study East African arborescent Euphorbia brought me to the Kew Gardens in 1974 and 1975 for two short visits, and on a five month expedition to Kenya and Tanzania from September 1975 to January 1975. As a member of the Third Danish Botanical Expedition to Ecuador in 1976 my interest was turned towards the neotropical flora, and as a thesis topic for my Cand. Scient. degree I chose

to work on the family Juncaceae for the Flora of Ecuador. On the 21st of August 1978 I finished my Cand. Scient. degree, and on the 2nd of September 1978 I started as a Graduate Fellow at The New York Botanical Garden, and as a Graduate Student at the City University of New York, working half time in the herbarium, and dedicating the other half on my time to Ph. D. studies and thesis research. In May of 1980 I spent one month doing fieldwork in Ecuador and Colombia. In February of 1980 I visited the herbaria of the Harvard University in Boston, the Field Museum in Chicago, the Missouri Botanical Garden in St. Louis, and the United States National Herbarium in Washington, D.C. November of 1980 through February 1981 I spent travelling in the Andes from Bolivia to Ecuador collecting material for my thesis, and in May and June 1981 I visited a number of European herbaria in Germany, Austria, Switzerland, France and England. From September of 1981 I have been professor of botany at the Pontificia Universidad Catolica del Ecuador in Quito, Ecuador.