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A RE-EVALUATION OF THE JUNCUS TRIFORMIS COMPLEX (JUNCACEAE)

City University of New York

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A RE-EVALUATION OF THE <u>JUNCUS</u> <u>TRIFORMIS</u> COMPLEX (JUNCACEAE)

by

BARBARA ERTTER

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

1983

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

22 April 1983
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ABSTRACT

A RE-EVALUATION OF THE JUNCUS TRIFORMIS COMPLEX (JUNCACEAE)

by Barbara Ertter
Advisor: Dr. Arthur Cronquist
The New York Botanical Garden
The City University of New York

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. 1983.

The *Juncus triformis* complex is a small group of dwarf annual rushes in western North America. All have narrow basal leaves, inconspicuous bracts, solitary terminal heads or flowers, 2-3 stamens, and completely plurilocular capsules. The complex illustrates a progressive adaptation to seasonally moist habitats, involving development of an annual habit, reduction in size of plant to only 2 cm, reduction in number of flowers to only 1, loss of bracts and inner stamens, transition from trimery to dimery, and transition from out-crossing to selfing as the primary mode of pollination. Chromosome numbers display an aneuploid reduction series from n = 19 to n = 16.

The complex was last revised in 1948 by Hermann, who recognized nine species. The present revision recognizes nine species and two additional varieties, a total of 11 taxa, arranged into four informal groups. Changes from Hermann's revision are the segregation of two new species (J. **luciensis** and J. **tiehmii**) from *J. kelloggii*, the discovery of a new variety (J. **leiospermus** var. **ahartii**), the reduction of *J. abjectus* to a variety of J. hemiendytus, and the inclusion of J. megaspermus within J. triformis.

A combination of scanning electron microscopy of seed coat patterns and morphological data indicate that the closest relatives of the J. triformis complex are either a group of Southern Hemisphere perennials, the New World perennials J. marginatus and J. filipendulus, or the South African annuals, all in subg. Graminifolii. The association of the J. triformis complex with the South African annuals and J. capitatus as a segregate subg. Juncinella is rejected.

Acknowledgments

First and foremost, I would like to acknowledge the continual encouragement and constructive criticism of my major advisor, Arthur Cronquist, of the New York Botanical Garden. His unfailing interest and open door policy supplied much that is essential to a quality graduate program but is so often lacking.

My thanks also go out to the members of my committee, who generously gave of their time to evaluate my dissertation and attend my examinations: Noel H. Holmgren of the New York Botanical Garden, James L. Reveal of the University of Maryland, Thomas Jensen of Lehman College, Peter Nelson of Brooklyn College, and Andrew Greller of Queens College. I would also like to thank Janice C. Coffey of St. Mary's College in North Carolina, who shared her knowledge of Juncaceae by acting as my outside reader.

I am also deeply appreciative of the willingness of the staff of the New York Botanical Garden to lend their expertise. In particular I wish to acknowledge Rupert Barneby for his mastery of the intricacies of English, Latin, and the rules of nomenclature; Noel Holmgren for his editorial and graphics standards; and Patricia K. Holmgren for her efforts in procuring loans. The friendship offered by these people, who welcomed me into their homes, is worth more than I can express.

Various other members of the New York Botanical Garden have also contributed to this dissertation. Bobbi Angell provided most of the marvelously executed line drawings. The lab technicians, Don Black and Alenka Remec O'Connor, gave technical advice and kept the

laboratory and darkroom in working condition. Chester Chambers, greenhouse manager, was always willing to supply potting material and suggestions for growing recalcitrant dwarf rushes. The librarians were invaluable when it came to locating pertinent literature. The secretaries, especially Linda Marschner and Lucy Kluska, typed my labels and loan requests, lent me their typewriters, and handled my correspondence while I was away.

The faculty and staff of Lehman College also deserve recognition. In particular I would like to express my deepest appreciation to Mike Baxter, who spent many hours introducing me to the SEM and keeping it in working condition. The ready access to the SEM and related equipment provided by him and by Thomas Jensen was invaluable to this aspect of my research.

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I must also firmly acknowledge the cooperation of scientists at other institutions, who freely shared their invaluable knowledge of Juncus around the world. Frederick J. Hermann dredged his mind for memories of one of his projects of 35 years ago. John Thomas Howell made sure that I saw the collections of dwarf rushes he had accumulated for his Sierran flora. Elizabeth Edgar of Christchurch sent me seeds and specimens of New Zealand rushes. A. A. (Obermeyer) Mauve of Pretoria generously made her manuscript of the South African rushes available, along with SEM's of the seeds. Tim Spira of the White Mountain Research Station in California, David Wagner of the University of Oregon, and Robert Holland of Orangevale, California, all sent me specimens representing populations of which I would not otherwise have been aware. Without their input my study would have been decidedly handicapped.

My knowledge of populations in the field and of distributions would have been much more limited were it not for the eager cooperation of numerous non- and semi-professional botanists, who took me into the field and made available unicate collections from their private herbaria. Foremost among these are Lowell Ahart of Honcut, California; Arnold (Jerry) Tiehm of Reno, Nevada; and Margaret and Loring Williams, also of Reno. Mr. Ahart and his family kindly allowed me to stay on their ranch for several days and showed me populations of both varieties of J. leiospermus, which I would otherwise never have seen. Mr. Tiehm and the Williams, all active members of the Northern Nevada Native Plant Society, helped get me started on my field work and subsequently sent me specimens from across northern Nevada, where the complex had previously been all but unknown.

Words of appreciation are in order for the following people as well: Billie Lee Turner, director of the University of Texas at Austin herbarium, who provided encouragement and the leeway necessary to finish my dissertation; the curators and staffs of the herbaria from which I borrowed specimens; Larry Dorr, for providing some last-minute scanning electron micrographs; and the Forest Service and

Bureau of Land Management botanists who helped rather than hindered my search for rushes on public lands.

Last, but certainly not least, I would like to acknowledge some of the earlier and more lasting influences on my career:
Patricia L. Packard, my first botany professor at the College of Idaho, whose inspiration and friendship have remained with me;
Jeffrey L. Strachan, who took many of my best photographs and pressed wee plants with me until the wee hours of the morning more times than I care to remember;
and my parents, Larry and Zelda Ertter, who may have never understood exactly what I was doing, let alone why, but who nevertheless unfailingly provided their love and support at all times.

To all of you, my love and deepest appreciation.

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Introduction

The Juncus triformis complex is a small group of highly reduced annual rushes found in vernally moist areas of western North America, centered in California. Although the complex was revised as recently as 1948, two aspects deserve further investigation.

First is the exact circumscription of taxa within the complex. Engelmann (1866, 1868) introduced the complex by describing J. triformis, consisting of three varieties, and J. kelloggii. Hermann (1948) recognized nine species, six of which he proposed as new. Although Hermann's circumscription has been widely accepted, it was based exclusively on morphology and contained little or no discussion of the individual taxa to support his conclusions. The potential for disagreement is exemplified by Cronquist's (1977) reduction of all the Intermountain members of the complex under J. kelloggii.

The second aspect is the placement and origin of the complex within the genus. On the one hand the J. triformis complex may be associated with the numerous perennial North American species of subg. Graminifolii Buchenau. Alternatively the J. triformis complex, the Mediterranean J. capitatus Weig., and some South African endemics have been treated as as a natural group of annuals separate from the perennial species of subg. Graminifolii (e.g., Buchenau, 1880; Weimarck, 1946). While the first arrangement would indicate an origin of the complex from perennial species in situ, the second would derive it instead from a far-flung assemblage of annuals.

The present re-evaluation of the J. triformis complex is based primarily on a morphological examination of a wide selection of herbarium specimens, four summers of field work (1978-1981), scanning electron microscopy of seed coat patterns, chromosomal studies, and observations of cultivated specimens. As a result of these studies, 11 taxa are recognized, representing nine species and two additional varieties. Furthermore, the closest relatives of the complex are apparently neither the western North American perennials nor the South African annuals, but rather the Southern Hemisphere perennials.

Unless otherwise specified, the following may be assumed:

1) References to Engelmann and Hermann are to their 1868 and 1948 works respectively.
2) Subgenus *Graminifolii* includes both annuals and perennials. A synopsis of the subgenera of *Juncus* forms Appendix I.
3) For the most part, counties and other place names are in California.
4) References to *J. bufonius* L. are sensu lato.
5) Locations of duplicates of my collections are based on records of their distribution to different herbaria.

In addition, the following abbreviations have been used:

1) ICBN -- International Code of Botanical Nomenclature [Leningrad Congress] (Stafleu et al., 1978).
2) *Herb. Norm.* -- *Herbarium Juncorum Boreali-Americanorum Normale*, a set of exsiccatae distributed by Engelmann.
3) Herbarium acronyms are those specified in *Index Herbariorum I*, 7th edition (Holmgren et al., 1981)

To avoid confusion as to place of publication, Latin descriptions of new taxa have been omitted from this dissertation. No new species, varieties, or combinations are to be considered effectively published in this work, though eventual valid publication is intended.

History

The Juncus triformis complex was initiated by George Engelmann, in "A revision of the North American species of the genus Juncus". Although the first half of this work was published in 1866, the last 40 pages were not published until 1868, allowing the integration of new material arriving from California.

In the 1866 portion of his work Engelmann referred in several places to a new subgenus, Juncellus, which he planned to establish containing as its sole species J. saginoides from California. Neither subgenus nor species were actually described, and by 1868 Engelmann, having studied additional specimens sent by Bolander, dropped the new subgenus and specific epithet. He described instead J. triformis and J. kelloggii, the former consisting of the three varieties α stylosus, β brachystylus, and γ uniflorus. The last-named variety was to replace the provisional name J. saginoides. Both subg. Juncellus and J. saginoides have appeared in subsequent synonymies and publications (e.g., Heller, 1898, 1900, 1909), but always without descriptions. They are therefore not validly published.

When describing J. triformis, Engelmann explained his changed decision as follows:

> Only the small dimerous form was known to me when the first part of this paper went to press, and was then considered as the type of a distinct subgenus, Juncellus, allied through its single-flowered stems to Rostkovia, and distinguished by its dimerism from any other known Juncus (see pp. 426, 428 & 436). Mr. Bolander, however, has since discovered other forms of the plant which bear trimerous flowers, thus assimilating it to the ordinary form of Junci and more particularly to the European J.

> capitatus, and destroying the subgenus Juncellus. I am now convinced that it must be placed with its European ally near J. marginatus, in the section Graminei, the dimerous variety constituting an anomaly not otherwise observed in this genus, but again found among the allied Restiaceae and Eriocauloneae, where dimerism and trimerism occur in the same genus--whether in the same species, is unknown to me.

Collections of the Juncus triformis complex that formed the basis of Engelmann's decisions were collected in conjunction with the State Geological Survey of California, established by an act of the California State Legislature on April 21, 1860, and headed by Josiah D. Whitney as Director and Geologist-in-Chief. Although concerned primarily with geology (particularly auriferous), the legislative act also specified a "full and scientific description of its botanical productions" (Whitney, 1876). William Henry Brewer was designated State Botanist; he resigned after four years and was succeeded by Henry Nicholas Bolander. Unfortunately the Survey suffered from lack of support, both popular and financial, and was denied further funding by the 1873-1874 State Legislature. The two most complete sets of the botanical collections resulting from the survey were the one kept by the State and the one sent to Asa Gray; these sets are now at UC and GH.

Undoubtedly the "small dimerous form" available to Engelmann in 1866 was a lone Hillebrand collection cited among several of Bolander's in the 1868 protologue, as several other Hillebrand collections were cited elsewhere in the first half of the revision. Wilhelm Hillebrand, author of Flora of Hawaii, visited California from Honolulu in 1863. He collected with Brewer for the Survey that year, mostly around Yosemite Valley, Big Tree Grove, and Mount Dana (Ewan, 1955). During this expedition he made a collection of depauperate J. capillaris. The plants are dimerous and for the most part one-flowered, though a few stems bear very young second flowers. Apparently Engelmann had actually considered recognizing the plant as a new genus, as the MO sheet has a pencilled herbarium name referring to the dimerous condition.

The Bolander collections cited by Engelmann were all made in 1866, when Bolander collected for the Survey around the state. Bolander's strong interest in mosses gained from an early exposure to Lesquereux probably preadapted him for spotting inconspicuous plants.

Knowledge of Bolander's itinerary is critical in determining the localities of types based on his collections. Unfortunately his fieldbook at GH provides only a vague picture of his travels, as entries are not made in strict order of collection, and dates are infrequently given. As a general outline, he made two major collecting trips in 1866, the first to Mendocino County in April and May, and the second to the Sierra Nevada from June to September. He first travelled north through Petaluma and collected around Ukiah April 14-19. From here he continued north to the Russian River Valley, Sherwood Valley, Long Valley, and Cahto, eventually reaching Round Valley in northern Mendocino County by the 29th. He then travelled to the coast by an unspecified route, arriving in Mendocino City by May 8. He collected in the general vicinity of Mendocino (Fort Bragg, Noyo, Big and Little rivers, Anderson Valley) for at least two weeks before returning to San Francisco.

For the second trip he was attached to an exploration of Yosemite and the Sierra Nevada under the command of Clarence King. Starting mid-June the group proceeded from Mariposa up the old Yosemite trail, passing near the present-day Wawona entrance of Yosemite National Park. After spending some time in Yosemite Valley and the Big Trees, they followed the upper Tuolumne River to Tuolumne Meadows before crossing the Sierra Nevada to reach Mono Lake by mid-September.

Bolander made several large collections of members of the J. triformis complex, responding to Engelmann's request for exsiccatae to distribute as part of his Herbarium Juncorum Boreali-Americanorum Normale (abbreviated as Herb. Norm. or Hb.N.). Engelmann (1866) intended that these exsiccatae would "stand in place of expensive plates, and . . . be far preferable to them". It is my belief that these collections, chosen and widely distributed by Engelmann to represent his concept of the species, should be given preference when designating lectotypes of species described in his revision.

While Hillebrand's and Bolander's collections formed the basis for the three varieties of J. triformis, the other species, J. kelloggii, was based on a single 1866 collection from San Francisco made by Albert Kellogg, the premier resident botanist of California. These early collections were followed by a multitude of others, so that by the end of the century the group had been found throughout California as well as in Nevada, Oregon, Washington, and Baja California, Mexico. One early collection was used by Greene (1890) as the type of a new species, J. uncialis. Others are the only collections of the complex from Washington, the only ones from Nevada for over 100 years, and the only record for J. capillaris outside of the Sierra Nevada. A list of collections before 1900 is given in Appendix II.

Several of these collections were available for study by the German expert on the morphology and taxonomy of Juncaceae, Franz Georg Philipp Buchenau. In his Monographia Juncacearum (1890), Buchenau generally accepted Engelmann's evaluation of the J. triformis complex, although he included var. uniflorus within var. brachystylus. In his 1906 revision of Juncaceae in Engler's Pflanzenreich (which contained the first illustrations of the group), Buchenau included within var. brachystylus not only var. uniflorus but also J. uncialis, though he did mention that Leiberg 375 might qualify as a distinct species [see J. hemiendytus var. abjectus]. More significant was his decision that J. kelloggii was nothing more than an aberrant form of J. bufonius var. pumilo Griseb, resulting in the consignment of J. kelloggii to limbo for many years.

Both Engelmann and Buchenau were ambivalent about the degree of distinctiveness among the components of the J. triformis complex, as neither person had access to enough material to determine if the differences were of taxonomic significance. Engelmann (1868) distinguished the varieties by a combination of style length and flower number. He felt that these differences were insufficient for specific recognition; instead he placed more importance on "the similarity of the whole appearance of the plants and of most of their parts, and, above all, the absolute identity of the well-marked seeds". He further believed that "eventually intermediate forms will dispel all doubts".

Buchenau (1890) maintained var. brachystylus as distinct from var. stylosus with the following commentary:

> Ob die beiden als Varietäten aufgefuhrten Pflanzen (var. stylosus und brachystylus) als Varietäten, als Arten, oder als heterostyle Formen aufzufassen sind, können nur Beobachtungen in der freien Natur lehren. -- Die Verschiedenheiten in Baue der Geschlectsorgane sind sehr gross; doch finden sich ähnliche Verschiedenheiten bei höher entwickelten, entomophilen Blüten ja nicht selten. -- Mittelformen zwischen beiden scheinen nicht vorzukommen.

> [Whether the two plants presented here as varieties (var. stylosus and brachystylus) are to be interpreted as varieties, as species, or as heterostylous forms can only be learned from observations in the field. The differences in structure of the reproductive organs are very great; however, comparable differences are not uncommon among the more highly developed entomophilous flowers. Intermediate forms between the two do not appear to occur.]

Buchenau therefore did not share Engelmann's expectations of forthcoming intermediates.

Subsequent floras varied in their treatment of the three varieties. Some, such as Watson (1880), Howell (1903), Jepson (1922, 1923), and Smiley (1921) followed Engelmann in treating all three as separate varieties of J. triformis. In contrast Piper (1906) recognized the three taxa at the specific level, proposing J. brachystylus and treating var. uniflorus as a synonym of J. uncialis. Piper's arrangement was followed by Rydberg (1917), Abrams and Coville (1923), and Davis (1952). Peck (1941) had an intermediate treatment; he recognized two species, J. triformis and J. brachystylus, with var. uniflorus a variety of the second. Munz (1935) apparently submerged var. brachystylus into J. triformis without a trace, treating only var. uniflorus as a separate variety.

Engelmann's other species in the complex, J. kelloggii, was in essence forgotten until Frederick J. Hermann by chance ran across an isotype at US filed under J. bufonius as per Buchenau. Hermann's realization that this specimen was decidedly not J. bufonius led him to examine the entire complex more closely.

Hermann's revision, published in 1948, recognized nine distinct species in the complex, six of which were proposed as new. Engelmann's J. triformis var. stylosus was divided into J. triformis s.s., *J. megaspermus*, and *J. leiospermus*. *Juncus kelloggii* and *J. triformis* var. *brachystylus* were merged at the specific rank, *J. uncialis* was retained but restricted in application, and *J. triformis* var. *uniflorus* was split into *J. bryoides*, *J. capillaris*, *J. hemiendytus*, and *J. abjectus*. The treatment contained excellent keys and descriptions, but no illustrations and practically no discussions of the different species.

Hermann's work was "greatly abetted by the painstaking efforts of John Thomas Howell to search out their retreats in all his field work during the past ten years" (Hermann, 1948). Howell, the first person since Bolander to actively seek out these diminutive plants, made his collections in conjunction with his own on-going study of the flora of the Sierra Nevada. Some of the flavor of his expeditions is recorded in *Base Camp Botany*, a series of unpublished annotated checklists by Howell. In the initial 1940 checklist, under the entry for *Juncus brachystylus* (*Howell 15904*, actually *J. capillaris*), we read:

> Probably Peter Friedricksen will remember this rush as the ridiculously tiny plant which made the botanist so vociferously enthusiastic that he (Peter) retraced his steps fully 25 feet to look at the cause of the uproar. But what botanist wouldn't have shouted for joy to discover this dwarf rush flourishing near timberline at almost 11000 ft. where heretofore it has been known no higher than middle elevations in the main forest belt and never so far south!

This range extension was later published by Howell (1941).

The 1941 checklist also made reference to collections of *J. brachystylus*, but the 1942 checklist reported additional collections only as *Juncus* spp. with the comment, "According to Dr. F. J. Hermann the material represents three unpublished species, so we cannot use his manuscript names yet; but aren't we gratified that all of them aren't the same thing although they looked superficially alike!" The new names finally appeared in the 1948 checklist, the same year Hermann's revision was published.

Hermann's arrangement was promptly and almost unanimously accepted by subsequent authors (e.g., Munz, 1959; Peck, 1961; Howitt & Howell, 1964; Hitchcock, 1969; Smith, 1976). The noteworthy exceptions have been Hoover (1970) and Cronquist (1977). Hoover, in his flora of Santa Barbara County, restricted J. kelloggii to the type collection and resurrected the name J. brachystylus for the rest. In his treatment of the Juncaceae for the Intermountain Flora, Cronquist lumped all but J. triformis, J. megaspermus, and J. leiospermus (which do not occur in the Intermountain region and were therefore not treated) in an all-inclusive J. kelloggii, with the comment:

> The several segregate species proposed by Hermann appear to be mere technical variants, often locally constant as in self-pollinated groups in other genera, but with widely overlapping ranges and similar habitat requirements.

In the present re-evaluation of the J. triformis complex, I recognize nine species and two additional varieties, a total of 11 taxa, arranged into four informal groups. The archaic "triformis" group contains J. triformis and J. leiospermus with two varieties: var. leiospermus and var. ahartii. The ridge-seeded "kelloggii" group consists of the four species J. kelloggii (including J. triformis var. brachystylus), J. luciensis, J. tiehmii, and J. capillaris. Juncus bryoides stands isolated in the third group, while the "uncialis" group comprises J. uncialis and J. hemiendytus, the latter consisting of var.

hemiendytus and var. abjectus.

A comparison of Engelmann's, Hermann's and my treatments is given as Fig. 1.

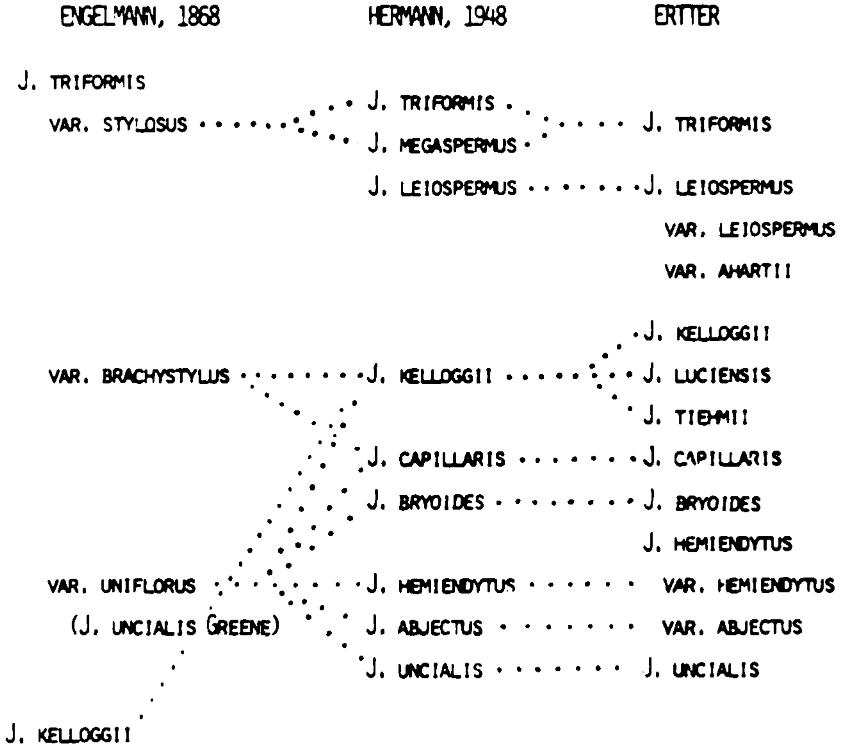

Fig. 1. Comparison of taxonomic treatments by Engelmann, Hermann, and Ertter.

Morphology

Methods:

Morphological observations and measurements were made primarily on dried specimens from various herbaria and my own collections. The latter were mainly collected from 1978 to 1981 in California, Idaho, Nevada, and Oregon. About 130 numbers were collected and significant range extensions were located in all four states. The field work not only resulted in the collection of large enough samples to study intrapopulational variation, but also allowed observation of colors, forms, flowering behavior, microhabitat preferences, and other features best studied on living plants. Chromosomal material and viable seeds were also collected.

Herbarium specimens of the *J. triformis* complex were examined from the following institutions: A, BKL, CAS, CHSC, CIC, DAV, DS, F, FSC, GH, HSC, ISC, JEPS, LA, LL, MICH, MO, NA, NDG, NESH, NY, OBI, ORE, OSC, PH, POM, RENO, RM, RSA, SACT, SBBG, SD, SFSU, TEX, UC, UCSB, US, UTC, WILLU, WS, WTU. The loan from CAS was by far the largest, as the first set of Howell's collections is there. In all, about 450 collections besides my own were studied. A large percentage of these represented mixed populations, thereby furthering comparison of the component taxa. The holdings of NY, TEX-LL, and GH-A were used for examination of other species in the genus.

Supplemental observations were obtained from preserved chromosomal material, made easier by the fact that entire plants were sometimes fixed, and from plants grown from seed.

Results and Discussion:

Members of the J. triformis complex are small caespitose annuals having basal leaves and solitary terminal heads or flowers. Annual species have arisen elsewhere in the genus: in the eprophyllate subgenera Graminifolii[1] (J. capitatus Weigel, South African annuals) and Septati (J. pygmaeus Rich.), and the prophyllate subgenus Poiophylla (J. bufonius). In addition, several perennials are capable of flowering the first year, such as J. planifolius R. Br. and J. caespiticus E. Mey. (subg. Graminifolii), and J. bulbosus L. (subg. Septati). The reduced size is also not unusual and has developed in some perennials, for example J. antarcticus Hook. (subg. Graminifolii), J. minimus Buch. (subg. Alpini), and J. duranii Ewan (subg. Septati). Because of the capacity for further depauperization under adverse conditions, maximum sizes and numbers of parts are of considerably greater importance than are minimums in the J. triformis complex.

Like other species in the genus, members of the J. triformis complex are glabrous and often suffused with an orange to reddish pigment, perhaps glycosides of luteolinidin (Fregda et al., 1978), especially in the capsules, tepals, and leaf bases. The degree of pigmentation is genetically determined to a certain extent, but it is also a function of maturity and environmental exposure. Whether the plant dries stramineous or reddish is of some systematic significance.

The leaves are strictly basal and so crowded that the internodes are usually not discernible. The main exception involves plants growing in moss mats, as is frequently the case with J. capillaris. Here a distinct

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[1] For synopsis of infrageneric categories see Appendix I.

axis or stem several millimeters long is often visible between the uppermost lateral root and the lowermost leaves. This feature is strongly environmentally dependent and is therefore of limited taxonomic importance.

From the cluster of leaves a number of stems or culms arise, each bearing a solitary terminal head or single flower. Culms, branches, and new leaves arise within the sheaths of older leaves. A well-developed plant on bare ground forms a complete hemisphere, with leaves and culms pushing out in all directions, while a young or depauperate plant may consist of a single culm and leaf.

ROOTS--Roots of the J. triformis complex are even smaller, weaker, and more inconspicuous than are those of J. bufonius, to the extent that the two can be told apart by the amount of effort needed to pull them up. Other than that I have not found the morphology of the roots to be of taxonomic significance.

LEAVES--Except for slight differences in length, the leaf is uniform within the complex. It consists of an ill-defined blade and sheath. The filiform to linear, terete to canaliculate blade terminates in a usually darkly pigmented apex tipped with an acute to acuminate inconspicuous callosity. The lower third or fourth of the leaf is flattened with broad membranous margins which enwrap the culm. Neither auricles (which are important taxonomically in some perennials, including many North American members of subg. Graminifolii) nor ligules occur at the juncture of blade and sheath. Reduced scale-like leaves called "cataphylls" at the base of the culm are also lacking.

CULMS--Because of the highly reduced nature of the plants in the _J. triformis_ complex, it is difficult to ascertain whether "stem", "culm", or "peduncle" should be applied to the axis that bears the inflorescence. Although both Engelmann and Hermann used the term "peduncle", according to Coffey (pers. comm.), "culm" would be more in line with the standard terminology presently in use for the family as a whole.

The culms vary within and between species in the complex in number, length, width, and color. The maximum number is dependent in large part on environmental conditions, as plants will continue producing new culms as long as adequate water, light, space, and nutrients are available. There is some genetic component as well, however, in that uniflorous species more often have large numbers of culms than do species with several flowers per head.

The length, especially maximum length, is of greater systematic significance, though here too environmental factors can be influential. This is especially noticeable in _J. triformis_, where culms of plants growing in the center of dense stands can be several times longer than those of isolated plants at the edges of the same stands. In general, the culms are at least twice the length of the leaves. The most noteworthy exception is the type of _J. kelloggii_, in which the culms hardly developed at all, so that the flowers nestle in a clump of leaves. I have not found this extreme in any other collections of the "kelloggii" group, though it occurs in occasional specimens of _J. bryoides_ and populations of both varieties of _J. hemiendytus_ at higher elevations in the Sierra Nevada.

Thickness of culm can vary as much in a single plant as between species. Nevertheless, this character is of some systematic significance in that most of the culms of a species are within a certain range, and maximum width is also useful. For example, J. tiehmii tends to have more consistently narrow culms than does J. capillaris, to the extent that this character can aid in sorting plants from mixed populations.

Color of culm generally matches that of the plant as a whole. In J. capillaris sections of the culm will often turn dark red or black, perhaps due to damage, insects, disease, or normal aging. Whatever the cause it can aid in distinguishing J. capillaris from J. tiehmii.

INFLORESCENCE--The structure of the inflorescence is of fundamental importance in Juncus systematics. Buchenau, in several papers (e.g., 1865, 1871), emphasized the dichotomy between those subgenera (e.g., Poiophylli, Genuini) characterized by single flowers, each subtended by two bracts called "Hüllblätter" or "prophylls", arranged cymosely in drepania; and those subgenera (e.g., Graminifolii, Septati) with eprophyllate flowers clustered into centripetal indeterminate heads. Both groups have additional bracts ("Zwischenblätter" or "hypsophylls") which subtend each pedicel and branch or head of the inflorescence.

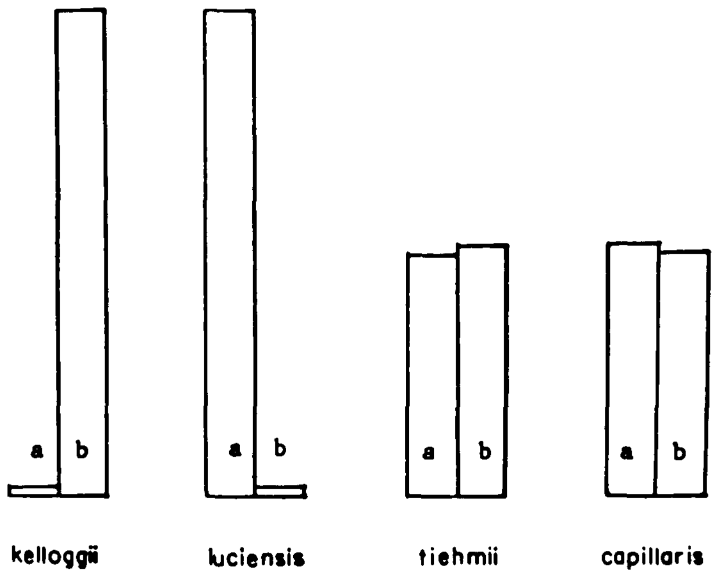
As befits its placement in subg. Graminifolii s.l., the J. triformis complex falls clearly in the latter subdivision of the genus. One of the most distinctive trends within the complex, however, is the reduction of the typical branched many-headed inflorescence, so that even the most archaic species in the complex have strictly solitary terminal heads. This simplification is not unknown elsewhere among the eprophyllate rushes, both annual and perennial, and in fact characterizes the entire subg. Alpini and some species in subg. Septati, such as J. chlorocephalus Engelm. and J. mertensianus Bong. in the western

United States. In subg. Graminifolii reduced specimens of J. planifolius from Chile with only 1-3 heads have been named var. demissus (Steud.) Buch. Among the other annuals in this subgenus, solitary heads predominate in J. scabriusculus Kunth., J. obliquus Adams., and J. capitatus. Other annual and perennial species that normally have several heads per inflorescence will often have solitary heads on depauperate plants. In contrast I have seen auxiliary heads in the J. triformis complex extremely rarely, only on a few exceptionally vigorous plants of J. triformis (Ertter & Strachan 3070, NY) and J. tiehmii (Ertter & Strachan 2987, NY).

A further reduction, the loss of flowers in the head until a solitary flower remains, is well-illustrated independently by the three main lineages in the J. triformis complex. Indeed, were it not for their capitate relatives it would be difficult to determine if the solitary-flowered species were derived from capitate eprophyllate species or single-flowered prophyllate species, perhaps even J. bufonius. In fact Buchenau (1906) associated the type of J. kelloggii with this ubiquitous species, although he had earlier (1890) concluded that Kellogg's specimen was a member of subg. Graminifolii because of its few-flowered heads.

Unlike monocephaly, uniflory is rare in the eprophyllate subgenera except on depauperate plants. Apparently only the J. triformis complex has species that are strictly solitary-flowered; it was in fact partly this character which led Engelmann (1866) to propose a new subgenus. Even the most reduced South African species have two or three flowers as often as one (e.g., J. parvulus E.Mey. & Buch., J. polytrichus E.Mey. & Buch.), and Mauve (pers. comm., 1981) treats these as depauperate versions of other more floriferous species. Similarly both Buchenau (1890, 1906) and Snogerup (1980) considered the predominantly one-flowered J. capitatus var. physcomitrioides Baen. to be nothing more than the depauperate extreme of the species. Among eprophyllate perennials the only species with a similar reduction is J. pelocarpus E. Mey., a member of subg. Septati of eastern North America, which is also unusual in that the single or paired flowers are in an arrangement otherwise characteristic of the prophyllate subgenera.

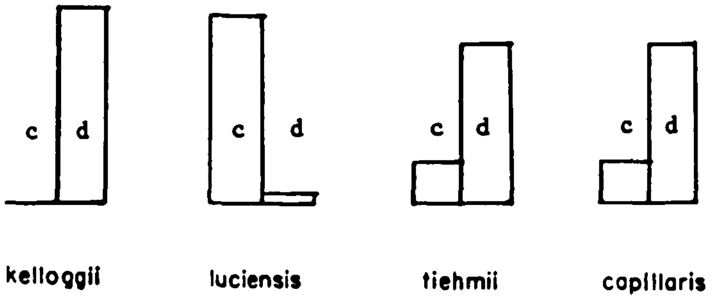
Because of the limited material available to them, both Engelmann (1868) and Buchenau (1890, 1906) were uncertain of the exact significance of uniflory in the J. triformis complex. Engelmann assigned all solitary-flowered plants to var. uniflorus, which Buchenau did not recognize at all but which Hermann (1948) split into several distinct species. The main difficulty with uniflory as a taxonomic character is that even in many-flowered species the culms are initially one-flowered and may remain so on depauperate plants. The question is whether additional flowers will develop under favorable conditions. Fortunately most collections of the complex contain a large enough sample to answer this question. Figure 2 is based on a sample of 100 plants (5 plants randomly selected from each of 20 different populations as represented by herbarium collections) from each of the four species in the "kelloggii" group. In 2a, the first column represents the number of plants with strictly solitary flowers, while the second is the number of plants with at least one culm bearing two or more flowers. In 2b, the populations in which all 5 sample plants were strictly uniflorous are contrasted with those in which at least one culm on one



a = plants with only solitary flowers

b = plants with at least one culm bearing more than one flower

2a



c = samples in which all 5 plants had only solitary flowers

d = samples in which at least one plant had at least one culm with more than one flower

2b

Fig. 2. Uniflory in the "kelloggii" group. a, based on 100 plants from each species. b, based on 5-plant samples from 20 populations of each species.

of the five sample plants had more than one flower.

Even with such an apparently tenuous distinction, the difference between *J. kelloggii* and *J. luciensis* is undeniable. The results are less conclusive for *J. tiehmii* and *J. capillaris*, but at least some plants in the majority of populations have some several-flowered culms. This would have been more pronounced if a larger sample had been taken from each population. What is important here is the almost total lack of multiple flowers in *J. luciensis*, even on plants with over 100 culms. It is worth noting that in the few exceptions only a couple of culms at best had paired flowers, and these came from populations mixed with *J. tiehmii*, possibly indicating a low level of gene flow.

The fact that absence of multiple flowers was one of the characters used to assign collections to *J. luciensis* admittedly makes the difference somewhat less cogent, but it is nevertheless only one of several characters that support the recognition of four geographically defined species distinguished by a suite of correlated morphological characters.

In contrast, the uniflory of *J. leiospermus* var. *ahartii* is not as consistent as that of *J. luciensis*, nor is it correlated with as many characters. This is why I treat the former as only a variety.

The uniflory of *J. bryoides* and the "uncialis" group is so fixed that out of all the specimens I examined I found only a few fascicled and one normal culm of *J. hemiendytus* bearing paired flowers. A single plant in an otherwise normal population of *J. triformis* from San Diego County (*Gander 3392*, SD) is almost completely single flowered, even though it possesses a large number of culms. I accept this merely as an indication of the inherent diversity within the species.

PEDICELS--The only pedicel characters which proved useful in the complex were orientation and length, measured from the subtending bract to the base of the tepals. Juncus hemiendytus var. abjectus, not having a subtending bract, was not considered to have a pedicel. In the "triformis" group the pedicel is at least visible, though still only a few millimeters long, and in more derived species the pedicel is even shorter. The pedicels on the horizontal culms are sometimes bent, thereby supporting the flowers in an erect position. This is most noticeable in J. tiehmii.

FLOWERS--The typical Juncus flower is trimerous and perfect, with three outer and three inner tepals, six stamens opposite the tepals, and a tricarpellate multi-ovulate ovary bearing a single style with three long-papillate stigmas. As one variation, gynodioecy is known in J. roemerianus Scheele (Buchenau, 1906; Eleuterius, 1978). I have observed flowers with undeveloped anthers on cultivated specimens of J. leiospermus, especially on young depauperate plants, but I do not know if such also occurs in the wild.

A more common variation is the loss of the anthers opposite the inner tepals. Except for occasional monstrosities, all members of the J. triformis complex display the reduced number of anthers. This character is common in Juncus and can be present or absent in different populations or individuals of J. ensifolius Wikst. s.l. (subg. Ensifolii) and the annual J. pygmaeus (subg. Septati). Even the normally six-anthered J. bufonius has been reported to occasionally have only three anthers (Buchenau, 1871). In subg. Graminifolii, J. marginatus Rostk. s.l., J. filipendulus Buckl., J. planifolius, J.

antarcticus, and occasionally J. dregeanus Kunth. have only three anthers; otherwise the perennial species have six. The annual species J. capitatus and J. obliquus are also three-anthered, but the rest of the South African annuals are six-anthered.

A strong dichotomy exists in the complex between those species with flowers modified for anemophily and those which are instead modified for self-pollination. The flowers of the former open widely at anthesis and have long styles, long stigmas, large anthers, and short filaments. The flowers of the latter do not open as widely at anthesis and have short styles, short stigmas, small anthers, and long filaments. Only a few populations of J. leiospermus and J. triformis have styles and anthers of intermediate length (one of these, Ertter & Strachan 3060, may represent introgression from J. capillaris). Further discussion is postponed for the Flowering Behavior section.

The phenomenon that Buchenau found most interesting in the J. triformis complex was the frequent occurrence of dimery, to the extent that he devoted a section of one of his numerous papers to the subject (Buchenau, 1871). He reported dimerous flowers on depauperate plants of J. bufonius, usually at the tips of the inflorescence branches. Dimery is also known on the depauperate specimens of J. capitatus that have been named var. physcomitrioides, but Snogerup (1963) noted that seeds from these plants can give rise to normal offspring. I know of no reports of dimery in the South African annuals. Even those species capable of producing dimerous flowers do not come close to the condition found in some members of the J. triformis complex, in which dimery can be the normal condition. Even the typically trimerous species display a greater proportion of dimerous flowers than is found outside of the complex.

One might think that the transition from trimery to dimery would be an example of a discrete evolutionary change; a species would have to be either dimerous or trimerous. In reality the situation is more complex. For one thing, there is a continuum involving the percentage of dimerous flowers on a plant and in a population. Apparently the phenomenon first appears as an option for depauperate plants of normally trimerous species, as in the case of J. bufonius and J. capitatus. This sporadic dimery is not uncommon in the J. triformis complex, where it most often is expressed in depauperate or very young plants. The frequency of dimery can then increase, so that whole plants and entire populations are predominantly dimerous. Examples of the latter are three populations of the normally trimerous J. triformis from Butte County (Jokerst 0830), Kern County (Hardham 3680A), and San Diego County (Ertter & Strachan 3521). Ultimately dimery reaches the level found in J. tiehmii and J. hemiendytus, where it is consistently associated with a cohort of other features, morphological and otherwise.

Another aspect of the non-discrete nature of the transition from trimery to dimery is that not all cycles of the flower are reduced lock-step. For example, although flowers of J. uncialis usually have six tepals, they often have only two anthers, and I have found several flowers of J. hemiendytus with four tepals surrounding a trilocular capsule. In addition, five-tepaled flowers occur sporadically in most species. In such cases it is difficult to say if the flower is dimerous or trimerous.

Figure 3 illustrates the relative occurrence of different degrees of dimery in the short-styled members of the complex, based on the number of flowers having four, five, and six or more tepals out of a total of 100 flowers selected from approximately 20 populations of each taxon. In most species there is a clear dominance of either trimery or dimery, thus justifying its use as a diagnostic character. The obvious exception is J. capillaris, which may therefore be an example of a species caught in the middle of the transition. Note that in all species at least a few flowers vary in tepal number from the norm.

The segments at the top of the six-tepal column in J. bryoides and J. uncialis represent flowers with seven or eight tepals. This "hypermery" is most often encountered in J. leiospermus, in which I found a few flowers with as many as ten tepals, but none with only four or five. Pentamerous flowers have been reported elsewhere in Juncaceae in Luzula campestris (L.) DC. (Buchenau, 1871).

TEPALS--The tepals of the perianth (called sepals of the calyx in some treatments) provide an abundance of potential taxonomic characters, but many of these deal with shape, color pattern, texture, and other features which are subject to a range of variation and difficult to communicate effectively. In general:

1) Inner and outer tepals are of similar size, shape, color, and texture. If they are not equal, the inner are more likely to be longer, especially if the flowers are not fully developed. This is particularly noticeable in J. capillaris, J. triformis, and J. leiospermus. On the other hand, some populations of J. luciensis (e.g., Pollard s.n.), have long-acuminate outer tepals. In J. capitatus the inner tepals are much shorter, thinner, and

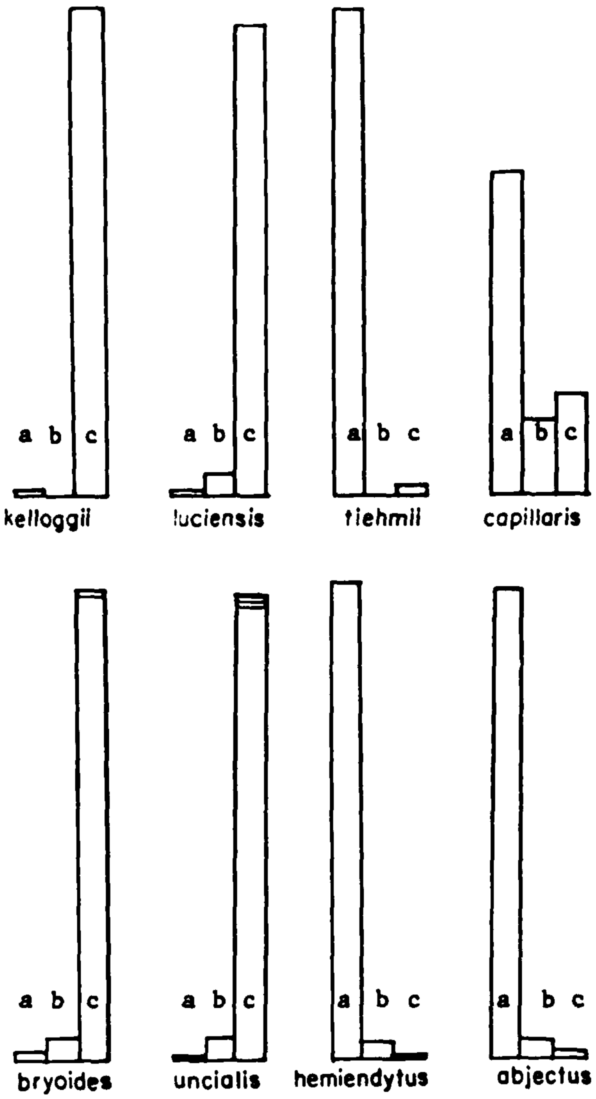


Fig. 3. Dimery in the short-styled members of the J. triformis complex, based on 100 flowers from each species.
a = flowers with 4 tepals. b = flowers with 5 tepals.
c = flowers with 6 tepals (segments at top represent flowers with 7 or 8 tepals).

differently shaped.

2) The shape varies from almost linear to nearly ovate, with the apex obtuse to attentuate. Much of this variation can occur between species, within species, or even on the same plant. _Juncus triformis_ in particular is highly variable in this regard. Obtuse to acute tepals are most characteristic of the "uncialis" group, while those of _J. capillaris_ are the most attenuate. Typically the tepals are straight or somewhat recurved, but in _J. bryoides_ they usually curve inwardly, almost concealing the capsule.

3) Tepals consist of a herbaceous central band and membranous margins, which are clearly delimited in most but not all species. The central band may have nearly parallel sides, as in the "uncialis" group, or it may taper evenly. In _J. bryoides_ it is sometimes greatly reduced or even absent so that the entire tepal is membranous. Most frequently each margin is about as wide as the central band, which extends beyond the margins at the apex. However, especially on the inner tepals, the margins may surpass the central band, running the length of the tepal and meeting at the apex.

4) The tepals are thin and delicate, similar to those of some South African annuals and quite unlike the firm ones of _J. capillaris_ and most perennials. They also lack the longitudinal ridges that tend to develop on the firmer tepals of many species, including _J. bufonius_. Hitchcock (1969) referred to the "minutely roughened tips" of the tepals of _J. capillaris_, but I have not found this to be particularly noticeable. They are certainly a far cry from the distinctive papillate tepals that characterize most western North

American perennial representatives of subg. *Graminifolii*.

5) The color pattern has certain drawbacks, which prevents its use as a primary character. It varies within a species, reddens with maturity, fades with age, and is difficult to describe exactly. Nevertheless, each species in the complex has a color pattern characteristic enough to be used as an important secondary character. The pattern involves the pigmentation of and contrast between central band, margins, and capsule. When young the central band is dark olive-green except for the darkly pigmented tip. Later it often becomes suffused with a light or dark reddish pigmentation, especially at the top and bottom. The central bands of the tepals of *J. tiehmii* are further distinctive in that they usually have pinkish edges bordering the light green middle.

The time of development of the reddish pigmentation is somewhat significant. The central bands of the tepals of *J. kelloggii* usually become strongly suffused by the time of anthesis, while those of *J. luciensis* usually remain light yellow-green until the capsule is nearly mature.

The membranous margins of most species in the "kelloggii" and "uncialis" groups are usually unpigmented and clearly demarcated from the herbaceous central band. This is not always the case in *J. capillaris*, *J. bryoides*, and the "triformis" group. In these species the inner part of the margin may be darkly pigmented and merge with the central band without a distinct break. I believe that this condition, best exemplified by *J. leiospermus* and *J. bryoides*, is the primitive tepal pattern in the complex.

The contrast between central band and margins can give the flowers a striped appearance, most noticeable in J. bryoides and to a lesser extent J. tiehmii. In J. capillaris most of the distal part of the tepal is usually black or at least darkly pigmented and contrasts strongly with the largely unpigmented light green capsule. In the other species, however, the tepals and capsules are similar enough in shade to have a uniform cast to the naked eye, although closer inspection will reveal the patterns described above.

ANTHERS--As previously mentioned, members of the J. triformis complex normally have three (two in the dimerous species) anthers, which are relatively large (1-2 mm) or relatively small (ca 0.5 mm). The large anthers are linear and become distinctly twisted after dehiscing. They are sometimes sagittate at the base with flaring lobes. The small anthers are oval and only insignificantly twisted. Both kinds are yellow, basifixed, and laterally dehiscent. I found an interesting aberration in some cytological material of J. triformis (Ertter & Strachan 3942), in which one side of the anther was sterile and tepaloid.

PISTIL--The main taxonomic characters of the pistil at anthesis are the length of the style and stigmas, both absolute and relative to the anthers and tepals. At one extreme the style is over 3 mm long so that the equally long stigmas are well-exserted even before the tepals spread. At the other extreme the style is essentially lacking and the short stigmas are situated just above the small anthers. Both extremes and intermediates are found throughout the genus and can vary even within the same species (e.g., J. scirpoides Engelm., J. capitatus).

Buchenau (1906) rejected the idea that the long- and short-styled species in the *J. triformis* complex might be only heterostylic forms of a single species.

There is also some variation in stigmatic coloration, ranging from white to pink. This is best observed on living plants, which limits its taxonomic utility.

CAPSULE--The mature capsule of *Juncus* supplies a great number of diagnostic characters involving size, shape, color, texture, and placentation. In the *J. triformis* complex the capsules may be longer or shorter than the tepals and range from almost round to obovate to narrowly oblong in outline. The apex is uniformly blunt, either rounded or retuse; no species in the complex has the tapering beak found in some other members of the genus. The style may or may not be persistent. As a broad generality the color at maturity tends to be comparable to that of the tepals, with the apex often darker or more intensely pigmented. The most conspicuous exception is *J. capillaris*, as previously mentioned.

The capsules are thin-walled, and the valves can be almost torulose, most notably in the long capsules of *J. tiehmii*. Within subg. *Graminifolii* some South African annuals have comparably delicate capsules, but *J. planifolius*, which otherwise has many similarities with the *J. triformis* complex, has hard, shiny, thick-walled capsules.

The placentation is of considerable interest, as this is a character that is both relatively constant within a species and also different between species or species-groups. The capsules range from completely plurilocular with axial placentation to fully unilocular with parietal placentation. Within the _J_. _triformis_ complex the capsules are fairly uniform in being fully plurilocular with the placentae fused proximally. At dehiscence the upper valves above the area of fusion spread wide open, sometimes nearly at right angles. The valves of the long dimerous capsules of _J_. _tiehmii_ and _J_. _hemiendytus_ may even become recurved. I know of no other species of _Juncus_ with comparable dehiscence, though it appears that the Southern Hemisphere representatives of subg. _Graminifolii_ come closest. In contrast, most North American eprophyllate perennials are imperfectly triseptate at best (i.e., the septa are not fused at the center), and many are completely unilocular.

For the most part one to several indistinct rows of two to 12 seeds occur in each locule. The maximum numbers of rows and seeds can be taxonomically useful, though like almost all other characters they are limited by the vigor of the plant and the individual flower. The rows are not well-defined, but from total counts of seeds per capsule compared to seeds per row the "kelloggii" group tends to have only two rows per locule while the "uncialis" group has four. The same comparison holds between _J_. _triformis_ and _J_. _leiospermus_, emphasizing the connection between the long-styled and short-styled members of the ridged- and smooth-seeded lineages respectively.

SEEDS--The seeds range from 0.3 to 0.8 mm long. In general seed size makes a good supplementary character, but in _J_. _triformis_ almost the entire range occurs, even within the same capsule. Salisbury (1974) found that seeds from a single population of _J_. _tenuis_ showed great variation in required dormancy period; perhaps the diversity of seed size in J. triformis is also related to dormancy. It is worth noting that in both the "kelloggii" and "uncialis" groups the taxa with the largest seeds (J. capillaris and J. hemiendytus var. abjectus) grow mainly at high elevations with short growing seasons and harsh winters.

The shape can be characteristic but is easily distorted by adjacent seeds. It ranges from nearly globose to oblong-ellipsoid. There is often a distinct umbo at the chalazal end and/or a smaller apiculus at the micropylar end, so that a seed may be umbonulate (Fig. 6a), apiculate (Fig. 8h), or both (Fig. 7e).

A thick outer layer is found on the seeds of many species of Juncus, including most North American and South African members of subg. Graminifolii. In some species this coat has been attenuated into tails, a feature that appears to have arisen independently several times within the genus. In contrast, the seeds of many other species, including those in the J. triformis complex, have an exceptionally thin outer layer. This may explain why the seeds of the complex do not become noticeably mucilaginous when wet, as reported in some species such as J. tenuis (Salisbury, 1974).

In species where it is not completely obscured by the thick outer layer, the pattern of the seed coat has proven to be one of the most reliable taxonomic characters. However, it is difficult to appreciate fully except at high magnifications (the details of the seed coat pattern as observed using scanning electron microscopy form a separate section). Nevertheless, even at 10x the seeds of some species in the J. triformis complex display distinct longitudinal ridges while those of others appear to be essentially smooth.

Buchenau (1867, 1906) described the color of the seeds in great detail, but Engelmann discounted the importance of this character. In the *J. triformis* complex, seed color ranges from golden brown to very dark brown and has a certain specific constancy. I noted white seeds on one plant from an otherwise normal population of *J. kelloggii* from Marin County (*Howell 21980*, NY).

Flowering Behavior

Buchenau (1892) devoted an article to flowering behavior in Juncaceae. He had no living members of the _J_. _triformis_ complex to study, but my own observations of plants in the field and in cultivation show that the flowering behavior of the group is consistent with that described by Buchenau.

The most noteworthy phenomenon in the _J_. _triformis_ complex is the occurrence of two classes of style length, which can be labelled simply "long" (1-3 mm) and "short" (0-0.5 mm). Flowers with long styles have relatively large anthers (1-3 mm), while short-styled flowers have small anthers (0.2--0.5 mm). Intermediates do occur, as in depauperate representatives of long-styled species, but the great majority of plants in the complex can be assigned unequivocally to the long-styled or short-styled categories. Outside of the complex both long-styled and short-styled extremes occur, along with a number of species with medium length styles. Buchenau (1906) illustrated both long-styled and short-styled forms of _J_. _capitatus_, although this phenomenon has not been mentioned in modern floras (e.g., Snogerup, 1980).

Neither Engelmann nor Buchenau was certain of the relation between the long-styled and short-styled members of the _J_. _triformis_ complex. Engelmann assigned the phenomenon varietal significance, while according to Buchenau (1890):

> Heterostylie scheint bei den Juncaceen nicht vorzukommen; die sehr verschiedene Länge des Griffels bei _J_. _triformis_, _Luz_. _campestris_ u. a. Arten beruht vielmehr wohl auf Variabilität und dient, soweit wir bis jetzt wissen, nicht zur Herbeiführung der Kreuzbefruchtung.

> [Heterostyly does not appear to occur in Juncaceae; the large difference in style lengths found in _J_. _triformis_, _L_. _campestris_ and other species is probably indicative more of variability and does not, as far as we presently know, serve to bring about cross-fertilization.]

Hermann treated the differences in style length at the specific level; the present study supports such an arrangement.

Flowers of _Juncus_ are uniformly protogynous and usually open in the morning. This is easily observed in the long-styled representatives of the _J_. _triformis_ complex, which are clearly chasmogamous and primarily out-crossing. The stigmas are well-exserted and are available for cross-pollination for about a day before the tepals spread and the anthers dehisce. The tepals spread at about 90 degrees, giving the flower an attractive if inconspicuous star-like appearance (Fig. 4a), and remain open for about a day or so. Some flowers in cultivation never did open, or else possessed rudimentary anthers. I do not know if this phenomenon occurs under natural growing conditions. No insect visitation was observed, so anemophily is probably the primary mode of pollination in the long-styled species.

In contrast, the short-styled species are clearly primarily autogamous, as the short stigmas rest directly upon the small anthers, which dehisce only an hour or so after the flowers open (Fig. 4b). The tepals do not spread as widely as in the long-styled species, and the flowers remain open for only a few hours. Buchenau (1906) called

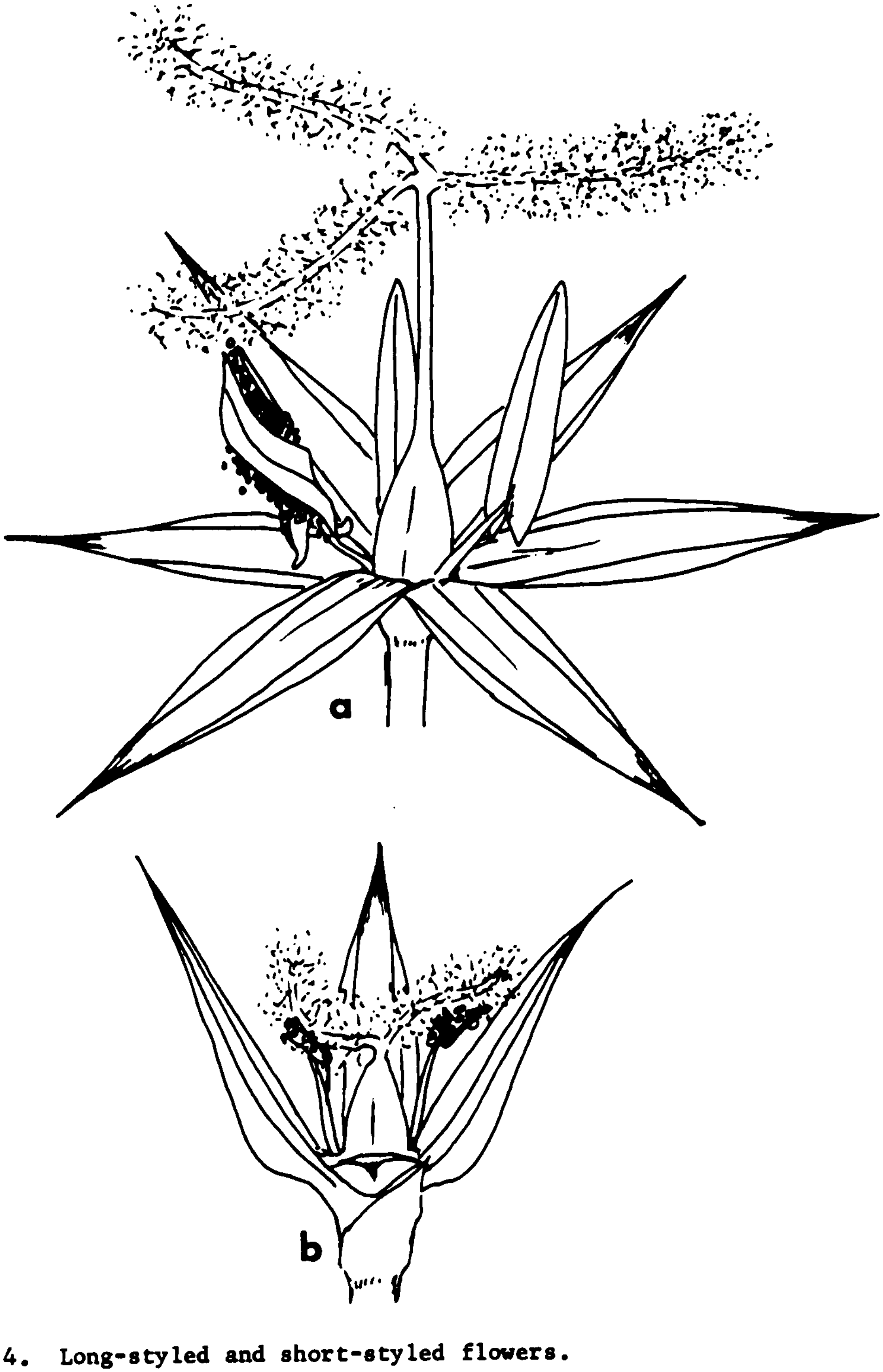


Fig. 4. Long-styled and short-styled flowers.
a, *J. triformis*. b, *J. tiehmii*

the short-styled extreme of J. capitatus cleistogamous and applied the term to several other species as well, including J. repens in subg. Graminifolii. I have observed flowers that have opened, if only slightly, in some short-styled species: J. tiehmii, J. luciensis, J. bryoides, J. uncialis, and J. hemiendytus. It is likely that flowers in the other short-styled species also open under proper conditions. I do not, however, know if some flowers set seed without ever opening; i.e., if they are truly cleistogamous.

Hybrids are well-documented in Juncus; examples would be those listed by Moore and Edgar (1976) in New Zealand, and the one described by Reinking (1981) as J. x stuckeyi. I believe that hybridization experiments could prove highly relevant for evaluating the relationship of J. leiospermus var. leiospermus, var. ahartii, J. uncialis, and J. luciensis; or of J. triformis and J. capillaris. The long-styled species, especially plants in which the anthers fail to develop, are well-suited for hybridization experiments, and I did in fact place some J. luciensis pollen on a male-sterile J. leiospermus flower in the course of my cultivation experiments. (The experiment was unfortunately prematurely terminated by voracious pigeons).

SEM of Seed Coat Patterns

Features of the seed have long been incorporated into the taxonomy of Juncus, due perhaps to the limited number of reliable characters otherwise available. Probably the most useful character has been the pattern of the seed coat, commented on by both Engelmann (1866) and Buchenau (1867) and included in their descriptions.

According to Engelmann (1866), "The seeds, when perfectly ripe, furnish some of the most interesting and constant characters". In those seeds where the pattern was not obscured by a thick coat, he noted 8 to 40 or more longitudinal lines connected by transverse ones. If both longitudinal and transverse lines were equally faint he referred to the seeds as "semina transverse lineolata". Seeds with prominent longitudinal ribs (costae) connected by numerous delicate cross-lines (lineolae) he called "semina costata". He applied the term "semina reticulata" to seeds with prominent ribs and equally prominent cross-bars. The rectangular mesh of this last pattern often contained numerous delicate transverse lines. Engelmann divided each of these three main types into a total of eight categories:

I. SEMINA RETICULATA, vix seu distincte apiculata.
   1. Semina levissime irregulariter reticulata seu laeviuscula, non costata nec lineolata.
   2. Semina regulariter reticulata, areis laevibus seu levissime longitudinaliter lineolatis.
   3. Semina regulariter reticulata, areis tenuiter transverse lineolatis.

II. SEMINA TRANSVERSE LINEOLATA, levisseme costata; vix seu distincte apiculata seu breviter caudata.
   1. Semina areis latioribus fere transverse reticulata.
   2. Semina areis angustissimis transverse lineolata.

III. SEMINA COSTATA, plus minus caudata.

1. Semina inter costas plerumque pauciores conspicuas lineolata; apiculata seu breviter caudata.
2. Semina inter costas plures distincte reticulata; apiculata seu plus minus caudata.
3. Semina inter costas numerosissimas tenues seu tenuissimas transverse lineolata seu laevia; caudata.

Engelmann (1866) placed J. saginoides in his category II-2 with both prophyllate and eprophyllate species representing almost every subgenus. In 1868 he specified that J. kelloggii belonged near J. marginatus (subg. Graminifolii) in category III-1, a group otherwise composed of J. longistylus Torr., J. filipendulus (both subg. Graminifolii), J. roemerianus, J. maritimus Lam., and J. acutus L. (all subg. Thalassii). According to Engelmann the seeds of J. kelloggii were "similar to the seeds of the last species [J. triformis], but with much more prominent dark ribs". He did not assign J. triformis to any category, so presumably it would take the place of its nomenclatural predecessor, J. saginoides. Apparently he felt that the "prominent dark ribs" were different enough to warrant placing the two closely related species far apart in his seed pattern classification.

In an article on seed coat patterns of German Juncaceae, Buchenau (1867) independently confirmed most of Engelmann's observations, though he emphasized the honeycomb-like nature of the pattern. He also introduced the term "transtilla" for the prominent cross-bars of the "semina reticulata". His 1906 treatment contains detailed drawings of the seeds of many species of Juncaceae, including some of the J. triformis complex.

Critical to Engelmann's treatment of his three varieties of J. triformis as one species was "the absolute identity of the well-marked seeds". When Greene (1890) discovered similar plants whose seeds were not prominently ridged, he described them as a new species, J.

uncialis. Starting with Brandegee (1893), subsequent workers paid little attention to seed differences in the J. triformis complex, attributing them simply to degree of maturity. Only with Hermann's revision was their importance re-emphasized and used to help delimit new species. Hermann (pers. comm.) would have liked to include drawings of the seeds in his revision but was prevented from doing so for a number of reasons.

The taxonomic significance of seed coat patterns in Juncus has also been discussed by other workers (e.g., Satake, 1933), but these are at best peripheral to the J. triformis complex and are not discussed further in this paper.

Engelmann and Buchenau illuminated the seeds with strong incident light and magnified them 50 to 75 times. Greene and Hermann also relied on light microscopy. More recently scanning electron microscopy (SEM) has allowed a sharper view showing greater and more exact detail. I am aware of the application of SEM to seeds of the European J. bufonius aggregate (Cope & Stace, 1978), the Minnesota Junci (Clemants, 1979), the neotropical Juncaceae (Balslev, 1982), the Australian Juncaceae (Coffey, pers. comm.), and the South African Juncaceae (Mauve, pers. comm.). A concordance of all these micrographs could be extremely illuminating, not only for their present systematic value but for paleoecological studies as well.

Because seed coat pattern has proven to be a good character for Juncus in general and the J. triformis complex in particular, I investigated SEM of seeds as an aid both for determination of taxa within the complex and for comparisons with potentially related groups.

Methods:

Engelmann (1866) stated, "It may not be useless to caution botanists not to be deceived by seeds loosely lying about with the specimens, as they very often will be found mixed". This is particularly relevant to the *J. triformis* complex, as single collections often represent mixed populations. Seeds were therefore preferentially taken directly from capsules.

Seeds were examined from several collections of all members of the *J. triformis* complex, as well as from 32 other eprophyllate and 12 prophyllate species, representing almost all subgenera. Most were taken from my own collections and pre-existing herbarium specimens at NY, supplemented by loans from other institutions. If only a few seeds were present they were returned to the sheets after being examined. A print was mounted on the sheet of certain critical collections (e.g., the type of *J. kelloggii*).

Air-dried seeds were coated with a 200 nm layer of gold using a Technics Humer II. They were examined with a JEOL-U3 scanning electron microscope and photographed using Polaroid Type 55 positive/negative film. No attempt was made to remove outer seed layers, though in some instances layers were incidentally removed during preparation. The inner layers thus exposed were also examined.

Results:

I confirmed that two major seed patterns do indeed occur in the *J. triformis* complex. The first, a faint more or less transversely elongated honeycomb (Figs. 5a, 6, 7), characterizes *J. leiospermus*, *J.*

bryoides, and the "uncialis" group. At the ends of the seeds longitudinal ridges may develop, but otherwise the pattern is of low relief, so that the seeds appear smooth under low magnification. In contrast, seeds with the second pattern (Figs. 5b, 8, 9) possess prominent long ridges the entire length of the seed, apparently formed by the thickening of the vertical edges of the transversely elongate honeycomb. The fainter transverse lines connecting the ridges are more closely spaced than in the first type. This second pattern characterizes J. triformis and the "kelloggii" group, though it is often faint in J. capillaris. Both patterns are usually overlain with a network of finer lines (see Fig. 7d, 8b), and yet another system of underlying faint ridges can be seen at high magnifications on some seeds (e.g., Fig. 7f). An additional peculiar feature on some seeds, in particular those of J. bryoides and J. hemiendytus, is the occurrence of nodules such as those in Fig. 6e and Fig. 6f. I do not know if these nodules are an integral part of the seed coat pattern or represent an infection of some kind.

Elsewhere in the genus a diversity of other patterns occurs. The first (Figs. 5c, 10h, 11i) is essentially a smaller more compact version of the honeycomb pattern with deeper relief. This pattern, often much less regular than drawn, is common throughout the genus. More complicated is the pattern (Figs. 5d, 11a,d,g,h) that prevails in the eprophyllate subgenera Septati, Ensifolii, and some Graminifolii. In this pattern prominent longitudinal ridges are connected by widely spaced prominent cross-bars. The ridges are often more or less beaded, and the areoles frequently contain numerous fine transverse lines. A variety of intricate patterns (Fig. 11b,c), mostly in subg. Graminifolii, are in my understanding derived from this last pattern. I also observed several other patterns in the genus, but as these were mostly from prophyllate species they are not pertinent to the present study. It should be mentioned that the basic patterns blend one into the other, although the pattern is relatively stable within and characteristic of a given species.

In many species a thick outer layer obscures the underlying pattern, which could only be observed on seeds where the layer was partially collapsed or had been removed. In contrast, in the _J_. _triformis_ complex and other species with distinct patterns the comparable outer layer is very thin and collapses like wet tissue-paper to enshroud the underlying relief.

Table 1 lists the specimens examined and their seed coat patterns. A supplementary list of species studied by Clemants (1979) and Balslev (1982) is provided as Appendix III.

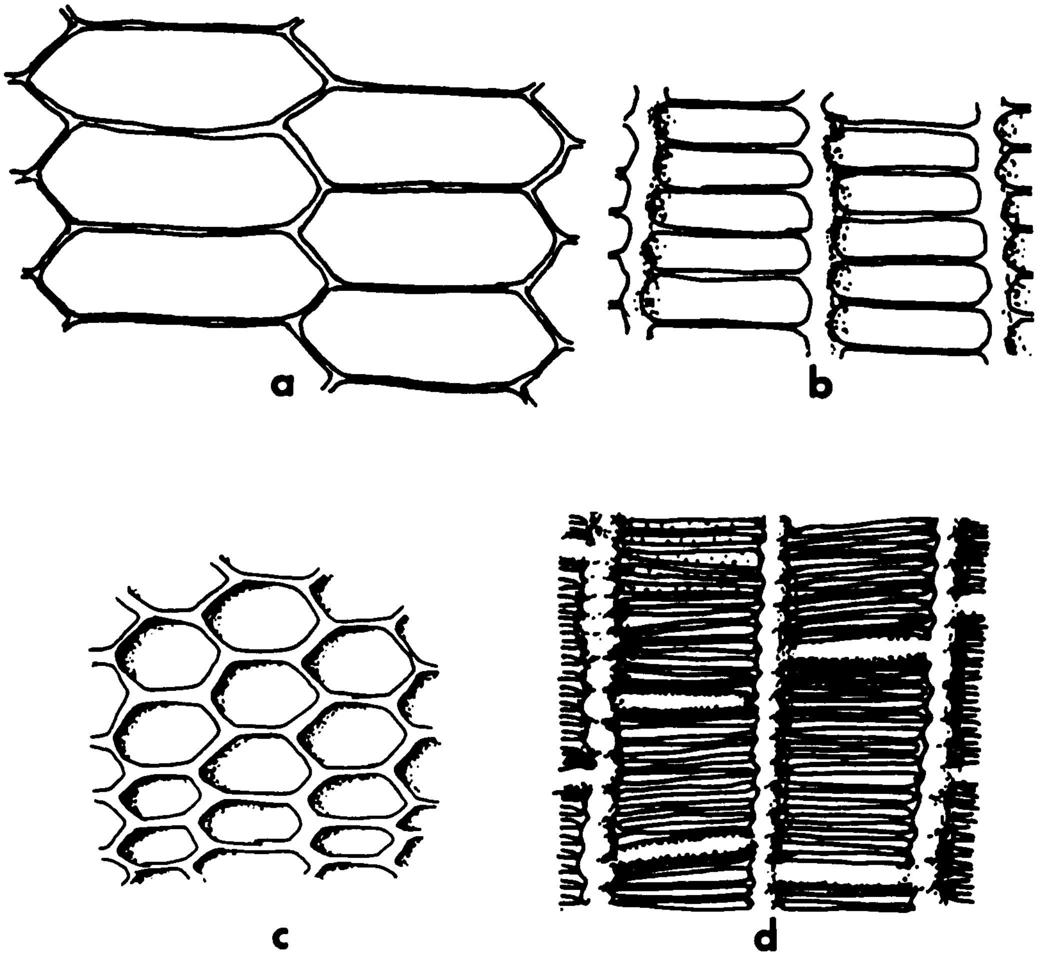


Fig. 5. Seed coat patterns in Juncus subg. Graminifolii.

Fig. 6. Seeds of *Juncus leiospermus*, *J. bryoides*, and Southern Hemisphere perennials.

a - *J. leiospermus* var. *leiospermus* (Ahart 1644, Butte Co., CA)

b - *J. leiospermus* var. *leiospermus*
(Ahart s.n., Red Bluff, Tehama Co., CA)

c - *J. leiospermus* var. *ahartii* (Ertter et al. 3267, Butte Co., CA)

d - *J. bryoides* (Ertter & Strachan 2972, Riverside Co., CA)

e - *J. bryoides*; seeds with nodules
(Ertter & Strachan 3893, Mono Co., CA)

f - *J. bryoides*; enlargement of nodules
(Ertter 220/5, Gooding Co., ID)

g - *J. dregeanus* (Bayliss 8450, South Africa)

h - *J. planifolius* (Belcher 1546, Australia)

i - *J. planifolius* (Eyerdam 10603, Chile)

Bar = 0.1 mm except in 6f, where bar = 0.01 mm

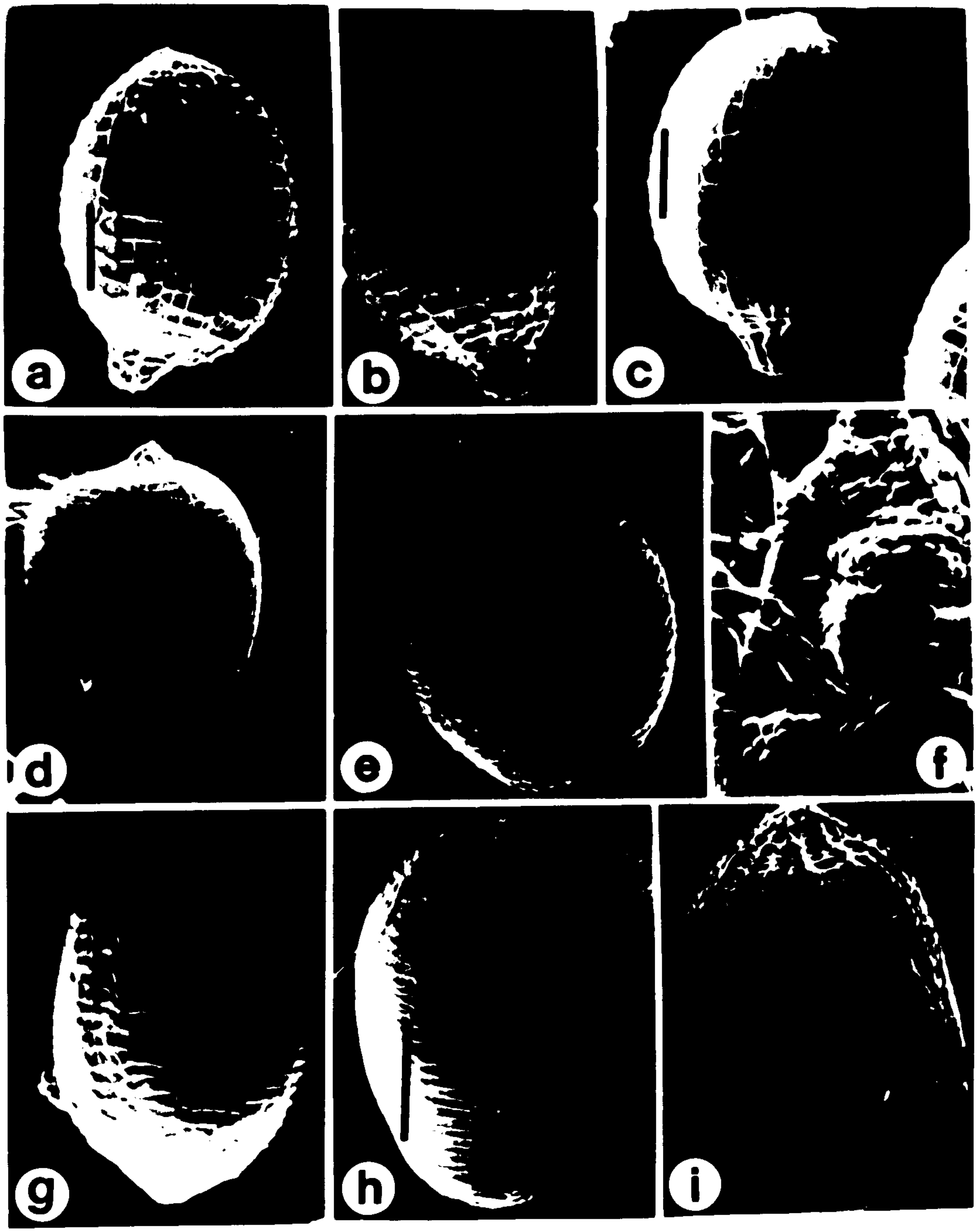


Fig. 6. Seeds of J. leiospermus, J. bryoides, and Southern Hemisphere perennials.

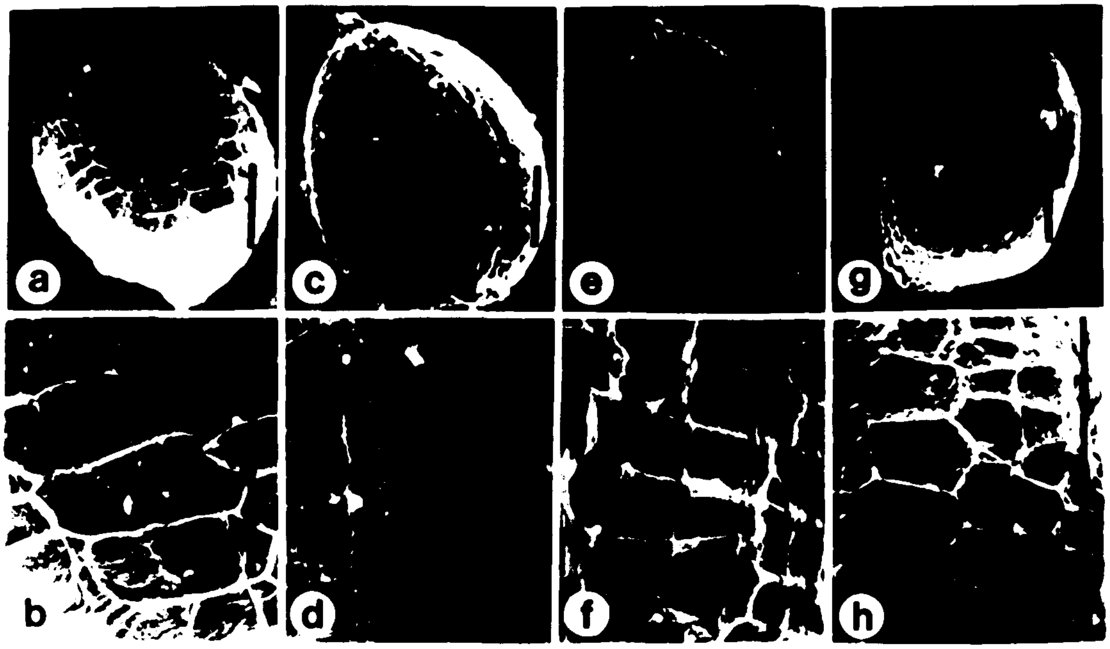


Fig. 7. Seeds of the "uncialis" group and J. antarcticus.

a - J. uncialis (TYPE: Greene s.n., Solano Co., CA)

b - enlargement of a.

c - J. hemiendytus var. hemiendytus (Ertter & Strachan 3933, Tuolumne Co., CA)

d - enlargement of c.

e - J. hemiendytus var. abjectus (Ertter & Strachan 3782, Elko Co., NV)

f - enlargement of e.

g - J. antarcticus (Kirk s.n., New Zealand)

h - enlargement of g.

Bar = 0.1 mm

Fig. 8. Seeds of _Juncus_ _triformis_ and _J_. _capillaris_.

a - _J_. _triformis_; detail of seed (Smiley 739, Tuolumne Co., CA)

b - _J_. _triformis_; detail of seed (Ertter & Strachan 3070, Fresno Co., CA)

c - _J_. _capillaris_; detail of seed with unusually pronounced secondary network of finer lines (Howell 20487, Tuolumne Co., CA)

d - _J_. _triformis_; type of _J_. _megaspermus_ (Hall & Chandler 558, Fresno Co., CA)

e - _J_. _triformis_; unusually smooth (Eastwood s.n., Fresno Co., CA)

f - _J_. _triformis_; unusually large and smooth (Ertter & Strachan 3060, Fresno Co., CA)

g - _J_. _capillaris_ (Raven 3235, Madera Co., CA)

h - _J_. _capillaris_ (Howell 15564, Mariposa Co., CA)

i - _J_. _capillaris_; unusually smooth (Keck & Clausen 528b, Tuolumne Co., CA)

Bar = 0.1 mm

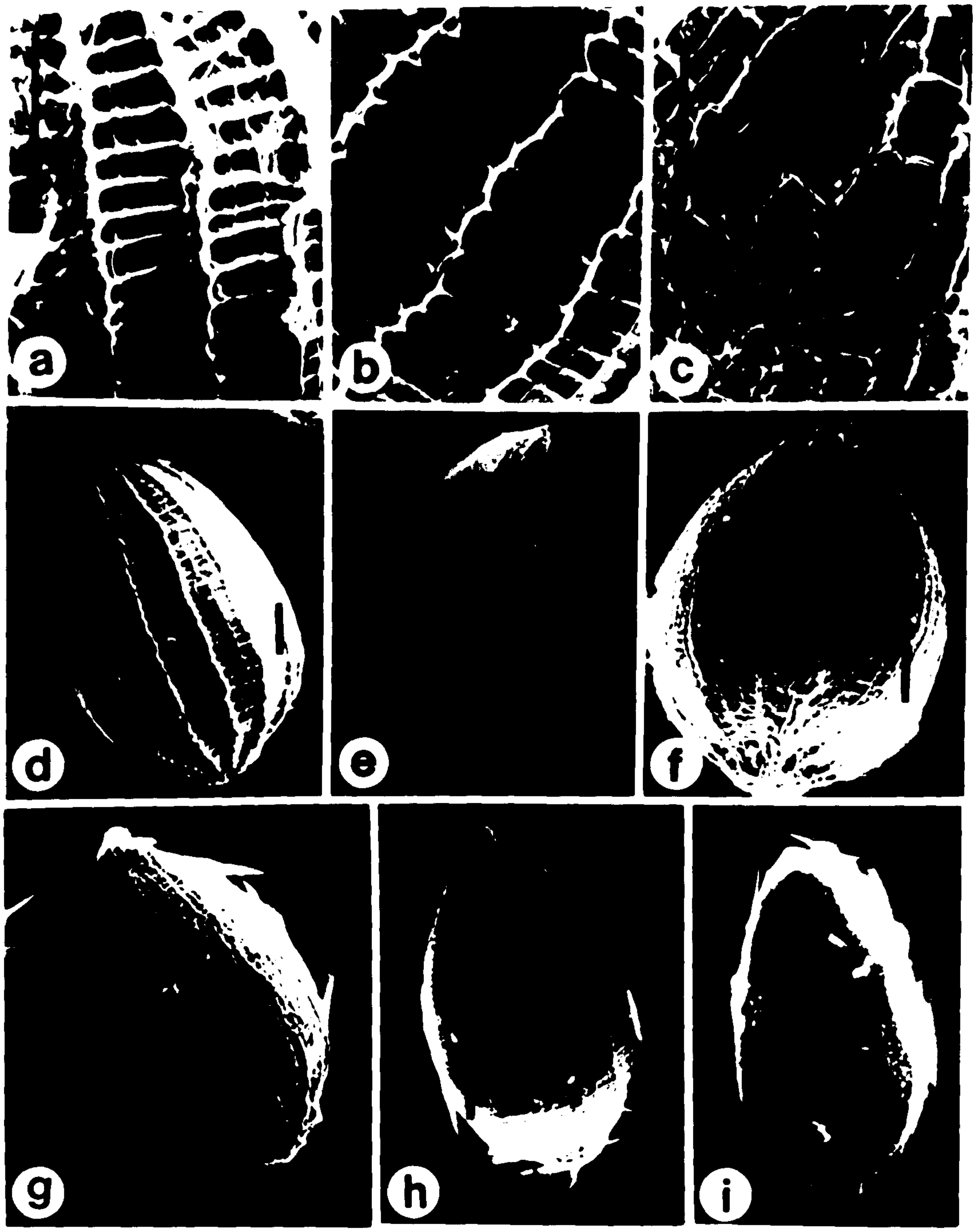


Fig. 8. Seeds of *Juncus triformis* and *J. capillaris*.

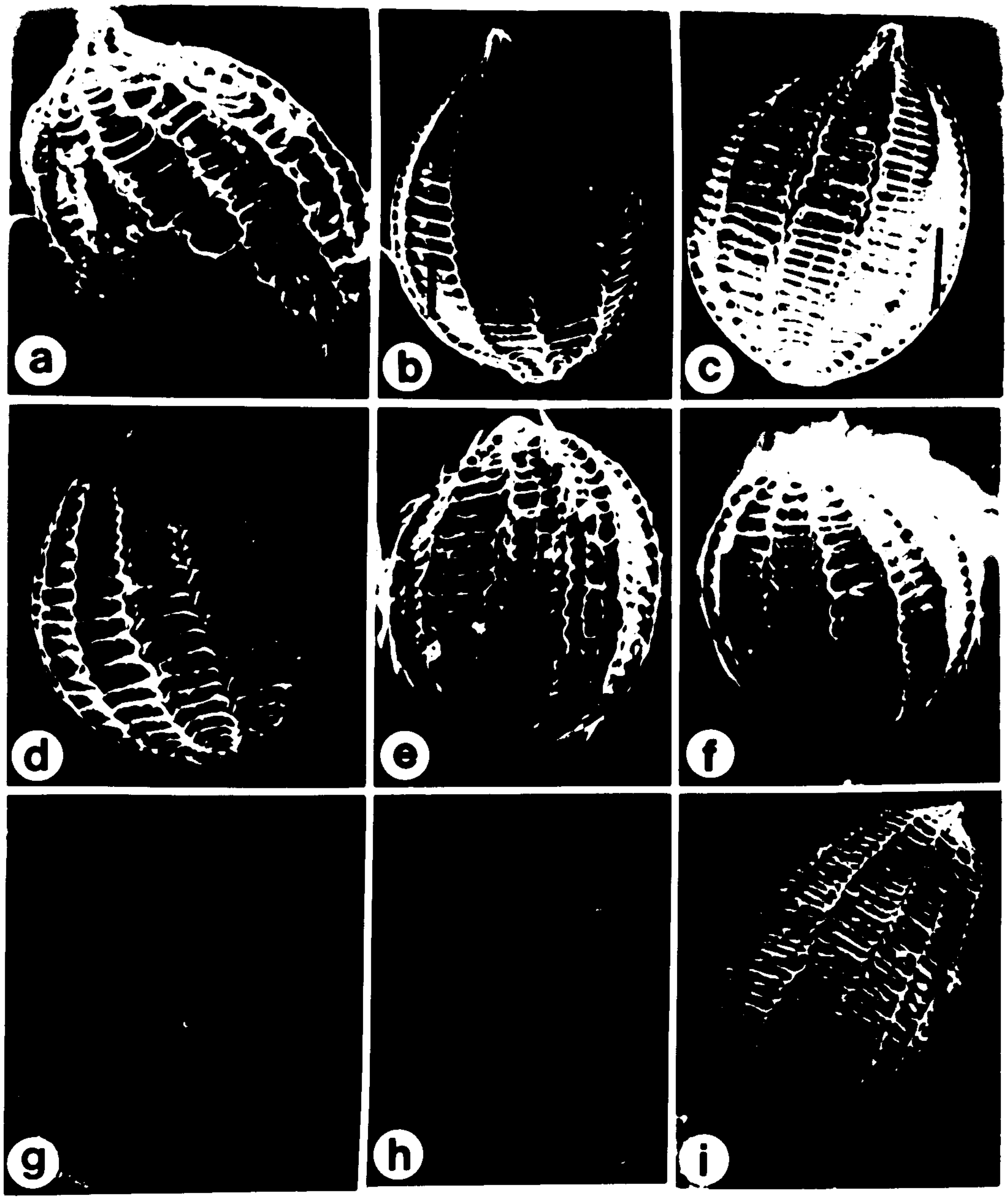


Fig. 9. Seeds of the "kelloggii" group.

a-d: J. kelloggii. a: TYPE (Kellogg s.n., San Francisco, CA). b: (Ertter & Strachan 3369, Monterey Co., CA). c: (Suksdorf 2571, Klickitat Co., WN). d: (Tracy 16592, Monterey Co., CA). e-f: J. luciensis. e: (Ertter & Strachan 3886, Plumas Co., CA). f: TYPE (Ertter & Strachan 3360, Monterey Co., CA). g-i: J. tiehmii. g: (Howell 20441, Tuolumne Co., CA). h: (Ertter & Strachan 3397, San Luis Obispo Co., CA). i: (Ertter 4289, Elko Co., NV). Bar = 0.1 mm.

Fig. 10. Seeds of Southern Hemisphere Juncus subg. Graminifolii and J. capitatus.

a - J. dregeanus (Werdermann & Oberdieck 2131, South Africa)

b - J. capensis (Kuntze s.n., South Africa)

c - J. lomatophyllus (Meebold 12251, South Africa)

d - J. cephalotes (Harvey 353, South Africa)

e - J. cephalotes (Dümmer 106, South Africa)

f - J. caespiticus (Melville & Wakefield 2762, Australia)

g - J. rupestris (Meebold 12249, South Africa)

h - J. capitatus (Prout 145, California)

i - enlargement of h.

Perennials: a-c; f

Annuals: d-e; g-i

Bar = 0.1 mm except 10i, where bar = 0.05 mm

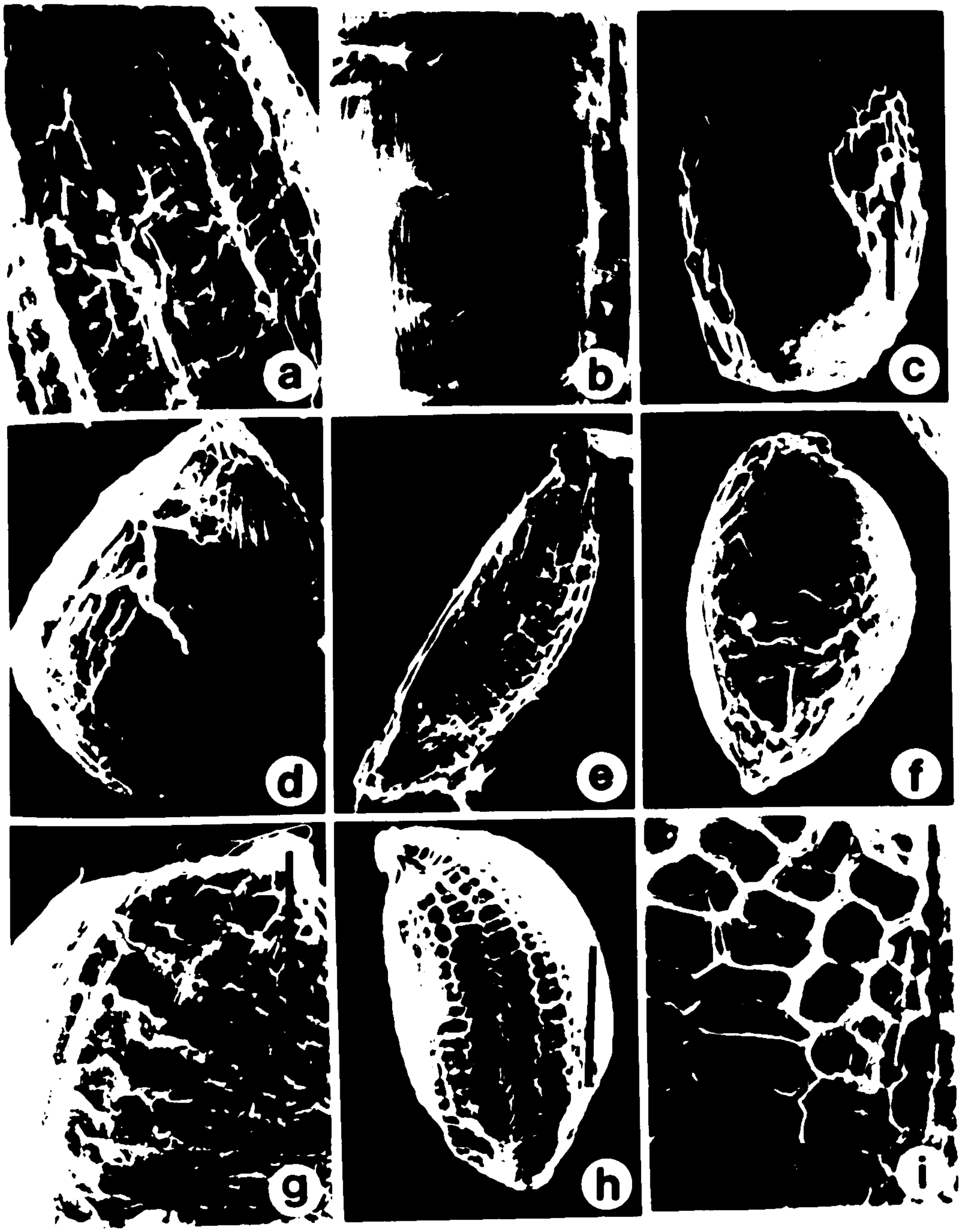


Fig. 10. Seeds of Southern Hemisphere *Juncus* subg. *Graminifolii* and *J. capitatus*.

Fig. 11. Seeds of *Juncus* subg. *Graminifolii*, subg. *Septati*, and *J. bufonius*.

subg. Graminifolii

a - *J. covillei* (Ertter 4300, Idaho)

b - *J. macrophyllus* (Fosberg & Ewan 55527, California)

c - *J. falcatus*; outer coat removed (Wilkes 1515, California)

d - *J. cyperoides* (Castellanos 114288, Argentina)

e - *J. longistylus* (Bolander, Hb. N. 43, California)

f - *J. marginatus* (Tharp 948, Texas)

subg. Septati

g - *J. duranii* (Duran 3527, California)

h - *J. pygmaeus* (Steetz s.n., Europe)

subg.. Poiophylli
i - *J. bufonius* (Ertter et al. 2705, Baja California)

Bar = 0.1 mm

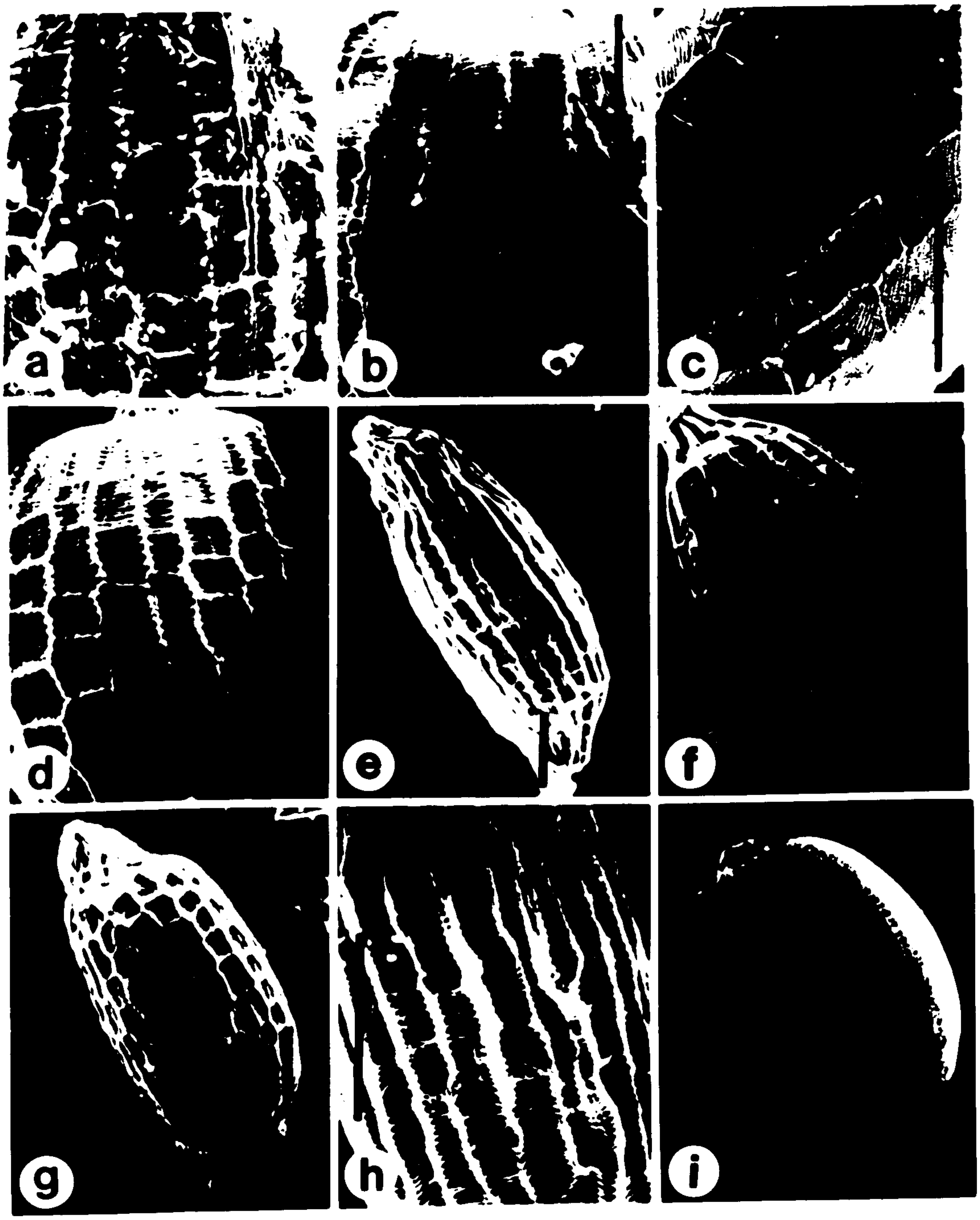


Fig. 11. Seeds of Juncus subg. Graminifolii, subg. Septati, and J. bufonius.

Table 1. SEM Patterns and Sources of _Juncus_ seeds.

KEY:
coat -- + = thick outer coat present, obscuring underlying pattern
± = outer coat sometimes present but not obscuring underlying pattern
- = outer coat thin, not obscuring pattern

pattern -- letters correspond to patterns in Fig. 5
dv = variations of 5d

duration -- a = annual
p = perennial

Unless otherwise indicated, vouchers are at NY

EPROPHYLLATE

				source
subg. _Graminifolii_				
J. triformis	-	b	a	Butte Co., CA: Ahart 2474
				" Jokerst 0830 (CHSC)
				El Dorado Co., CA: Smiley 363a (GH)
				Fresno Co., CA: Eastwood s.n. (CAS)
				" Ertter & Strachan 3060
				" " 3064
				" " 3070
				" Hall & Chandler 558 (UC)
				Madera Co., CA: Brock 233 (RSA)
				" Eastwood & Howell 5454 (US)
				Mariposa Co., CA: Bolander 4864 (UC)
				" " s.n. (MO)
				" Congdon s.n. (MO)
				" Jepson 4414 (JEPS)
				San Diego Co: CA:
				Ertter & Strachan 3521
				" " 3538
				" Gander 3392 (SD)
				" " 3706 (US)
				" " 4064 (SD)
				" " 7215 (SD)
				Tulare Co., CA: Hardham 12090 (CAS)
				" Purpus 5683 (UC)
				Tuolumne Co., CA:
				Ertter & Strachan 3935
				" Mason 11939 (UC)
				" " 11981b (UC)
				" Munz 7364 (POM)
				" Smiley 739 (GH)

J. leiospermus var. *leiospermus*	- a	a	Butte Co., CA: Ahart 1645 (Ahart) " " 1895 (Ahart) " Jokerst 0699 (CHSC) Shasta Co., CA: Baker & Nutting s.n. (UC) " Holland 289 (Holland) " Hoover 2270 (UC) Tehama Co., CA: Ahart s.n. (CAS) " Heller 12326
J. leiospermus var. *ahartii*	- a	a	Butte Co., CA: Ahart 1692 (Ahart) " Ertter et al. 3267
J. kelloggii	- b	a	Butte Co., CA: Ahart 2263 (CAS) Humboldt Co., CA: Tracy 4431 (WTU) Marin Co., CA: Howell 21980 " " 42549 Monterey Co., CA: Ertter & Strachan 3369 " Tracy 16592 San Francisco, CA: Kellogg s.n. (MO) Santa Cruz Co., CA: Ertter & Strachan 3333 Sonoma Co., CA: Eastwood & Howell 7866 (MICH) Josephine Co.,OR: Henderson 13033 (ORE) Marion Co., OR: Hall 543 Klickitat Co., WN: Suksdorf 2571 (MICH)
J. luciensis	- b	a	Monterey Co., CA: Ertter & Strachan 3366 Plumas Co., CA: Ertter & Strachan 3886 San Diego Co., CA: Ertter & Strachan 3529
J. tiehmii	- b	a	Fresno Co., CA: Raven 4299a (CAS) " " 7142a (CAS) Los Angeles Co., CA: Ertter & Strachan 3439 Riverside Co., CA: Ertter & Strachan 2971 " " 3481 San Diego Co., CA: Ertter & Strachan 3517 " " 3518 " " 3530 " " 3541 San Luis Obispo Co., CA: Ertter & Strachan 3397 " Hoover 9907 (OBI)

Tulare Co., CA: Hardham 12090 (CAS)
" Howell & True 43131 (CAS)
Tuolumne Co., CA:
Ertter & Strachan 3927
" Howell 20441 (GH)
Boise Co., ID:
Ertter & Strachan 3796
Owyhee Co., ID: Ertter et al. 4484
Humboldt Co., NV: Ertter 4322
Elko Co., NV: Ertter et al. 4289
Harney Co., OR: Leiberg 2525 (US)
Baja California, MEX: Moran 27464
" " 27740 (SD)

J. *capillaris* - b a Alpine Co., CA: Hardham 21821b (CAS)
Fresno Co., CA: Howell 33948 (CAS)
Madera Co., CA: Raven 3235 (CAS)
Mariposa Co., CA: Bolander 6034 (MO)
" Ertter & Strachan 3075
" " 3076
" Howell 15564
" Sharsmith 2171
Mono Co., CA: Ertter & Strachan 3896
Tulare Co., CA: Howell 15904 (CAS)
" " 17336 (CAS)
" " 25682
" " 27956
Tuolumne Co., CA: Howell 20487 (CAS)
" Keck & Clausen 5289 (DS)
Harney Co., OR: Leiberg 2525 (US)

J. *bryoides* - a a Mono Co., CA: Ertter & Strachan 3693
Riverside Co., CA:
Ertter & Strachan 2972
Moffatt Co., CO:
Weber & MacLeod 12561
Gooding Co., ID: Ertter 220/5
Franklin Co., ID: Magire 21628
Elko Co., NV: Ertter & Strachan 3784

J. *uncialis* - a a Butte Co., CA: Ahart 1695 (Ahart)
" " 3401
San Luis Obispo Co., CA:
Eastwood & Howell 4197
Solano Co., CA: Greene s.n. (NDG)
Harney Co., OR: Ertter 4430

J. hemiendytus var. *hemiendytus*	- a	a	Lake Co., CA: Ertter & Strachan 3086 " Mason 14037 San Bernardino Co., CA: Ertter & Strachan 3004 Sierra Co., CA: Ertter et al. 2765 Trinity Co., CA: Howell 13213 Elmore Co., ID: Ertter 4179 Jackson Co., OR: Chambers 2453 Klickitat Co., WN: Suksdorf s.n.
J. hemiendytus var. *abjectus*	- a	a	Mono Co., CA: Munz 20041 Sierra Co., CA: Ertter & Strachan 3695 Elko Co., NV: Ertter & Strachan 3782 Harney Co., OR: Ertter & Strachan 3113
J. capitatus	- c	a	California: Ahart s.n. " Prout 145
J. planifolius	± a	p	Oregon: Correll & Correll 37804(LL) Chile: Eyerdan 10603 Australia: Belcher 1546 " Boorman 19897
J. antarcticus	± a	p	New Zealand: Kirk s.n. " no collector
J. dregeanus	± a	p	South Africa: Bayliss 98 " " 8450 " Fries 163 " Werdermann & Oberdieck 2131 (A)
J. caespiticus	+ a	p	Australia: Melville & Wakefield 2762 (A) New Zealand: Healey s.n.
J. capensis	+ a	p	South Africa: Burchell 438b (GH) " Kuntze s.n.
J. lomatophyllus	+ ?	p	South Africa: MacOwan s.n. " Meebold 12251
J. cephalotes	+ c/a	a	South Africa: Dregé 2472b " Dümmer 106 (GH) " Harvey 353 " Meebold 12253
J. rupestris	+ ?	a	South Africa: Meebold 12249
J. marginatus	+ d?	p	Texas: Tharp 948
J. macrophyllus	- dv	p	California: Fosberg S5527

J. longistylus	dv	p	California: Bolander, Hb.N. 43
J. falcatus	+ dv	p	California: Wilkes 1515
J. orthophyllus	- d	p	Oregon: T. Howell s.n.
J. covillei	- dv	p	Idaho: Ertter 4300
J. regellii	+ d	p	Idaho: Ertter 3973
J. repens	- c/d	p	South Carolina: Ravenal, Hb.N. 29
J. cyperoides	- d	p	Argentina: Castellanos 114288
J. ochraceus	+ c	p	Himalaya: Kuntze 6742

subg. *Septati*

J. acuminatus	- d	p	Oregon: Ertter 3846
J. chlorocephalus	- d	p	California: Morley 157
J. duranii	- d	p	California: Duran 3527
J. mertensiansus	+ d	p	California: Sharsmith 4086
J. nevadensis	- d	p	California: Howell 14300
J. nodosus	- d	p	Montana: Kirkwood 2495
J. oxycarpus	- d	p	Abyssinia: no coll.
J. pelocarpus	- d	p	Massachusetts: MacKeever 1060
J. prismatocarpus	- d	p	Ceylon: Jayasuriya 184
J. punctorius	- d/a	p	South Africa: Kuntze s.n.
J. pygmaeus	- d	a	Europe: Steetz s.n.
J. torreyi	- d	p	Idaho: Ertter 143/3

subg. *Ensifolius*

J. ensifolius	- d	p	Idaho: Ertter 4532

subg. *Thalassii*

J. acutus ssp. *leopoldii*	+ c?	p	California: Dudley 612

PROPHYLLATE

subg. *Poiophylli*

J. bufonius	±	c	a	Nevada: Tiehm 4398 Baja California: Ertter
J. dichotomus	+	c	p	North Carolina: Godfrey s.n.
J. gerardii	+	a/c	p	Connecticut: Hill 9322
J. homalocaulis	-	b	p	Australia: Melville 2775
J. imbricatus	+	a/c	p	Australia: McKee 6812
J. salsuginosus	+	a	p	Altai: Krylov s.n.
J. setaceus	-	c	p	New Jersey: Mackenzie 6752
J. vaseyi	-	d	p	Michigan: Bigelow s.n.

subg. *Genuini*

J. balticus	+	c	p	New Mexico: Crutchfield 2381
J. pallidus	-	c	p	Australia: Melville 3202

subg. *Subulati*

J. subulatus	+	c?	p	Egypt: no coll.

Discussion:

I did not investigate internal seed anatomy in my study, but this aspect was included in Clemants' (1979) work on the Minnesota rushes. He examined sections of rehydrated seeds using light microscopy and compared them to the patterns revealed by SEM of their conterparts, from which the outer layer had been removed by sonication. Comparing our results, I found that if the outer layer is thin enough, as is the case in the J. triformis complex, removal of this layer does not significantly alter or improve recognition of the basic pattern. This conclusion is shared by Balslev (1982).

According to Buchenau (1906) and Clemants (1979), the basic pattern is imprinted on the outer surface of the lignified tegumen, which is derived from the inner integument, while the outer layer that is removed by sonication is the testa, consisting of one or two layers of mucilaginous cells. Clemants did not attempt to correlate seed sculpture with cell arrangement, but it appears that the inner cells of the testa nestle in the depressions of the pattern. If so, the pattern correlates with the arrangement of cells in the testa and not the tegumen. The secondary network that overlays the basic pattern is removed by sonication and corresponds to the longitudinally oriented cells of the outer layer of the testa.

In relation to Engelmann's categories, the patterns illustrated in Fig. 5a & c would collectively correspond to his "Semina transverse lineolata". Fig. 5d fits the description of his "Semina reticulata", but he placed many species with seeds of this pattern in his "Semina costata" along with those more comparable to Fig. 5b.

In some cases there is a discrepancy between my observations and the descriptions of Engelmann and Buchenau. Of special interest in this respect are J. planifolius and J. marginatus. In Buchenau (1906) the former is drawn to show a pattern like Fig. 5d, while Engelmann compared the pattern of J. marginatus with J. kelloggii. These two species and their seed coat patterns play a significant role in the Infrageneric Relationships section.

Although both Engelmann (1866, 1868) and Buchenau (1890, 1906) included seed coat patterns in their species descriptions, neither correlated patterns with natural groups or phylogenetic trends. This is not surprising, considering the confusing assemblage of species grouped by the seed patterns defined in their treatments. I believe that this resulted from the limitations of the patterns observed using light microscopy, as I find that Juncus seed coat patterns, at least of the eprophyllate subgenera, can be arranged in a credible evolutionary sequence. For a starting point, I agree with Balslev (1982) that the pattern in Fig. 5c is probably primitive in the genus. Not only is it common in both the prophyllate and eprophyllate species of Juncus, but it is also the pattern that occurs on the seeds of Luzula denticulata Liebm., the only species of this related genus that Balslev examined after removal of the thick outer layer that covers most Luzula seeds. This basic pattern was then modified by longitudinal compression of rows, lateral elongation of cells, and differential thickening of walls, all of which are probably easily accomplished by relatively straight-forward changes in the timing and sequence of developmental controls.

If this interpretation is correct, it holds considerable significance for understanding the evolution of the J. triformis complex. I believe that within the complex the transversely elongate version of Fig. 5a is the ancestral type, retained in *J. leiospermus* and *J. bryoides*. From this pattern were derived the more regular honeycomb that characterizes the "uncialis" group and the ridged pattern (Fig. 5b) of *J. triformis* and the "kelloggii" group. The ancestral pattern of the *J. triformis* complex can in turn be easily derived from the generalized ancestral pattern postulated for the genus (Fig. 5c).

At the same time, an examination of possible transitional stages suggests that the pattern of Fig. 5d is derived from 5c by an entirely different route, with only the main cross-bars in the former corresponding to the transverse lines of the latter. If this interpretation is correct, the ancestral pattern has been retained in perennial eprophyllate rushes only in the Southern Hemisphere, while the main thrust of seed pattern evolution in the Northern Hemisphere perennials species has been toward the pattern of Fig. 5d and elaborations thereupon. The implications of this will be further discussed in the Infrageneric Relationships section.

Cytogenetics

Although the Juncus triformis complex itself has not previously been studied cytogenetically, chromosome counts have been made for many other species in the genus (see Appendix IV). Within Juncus a diploid number of $2n = 40$ is most common, especially in the eprophyllate subgenera. Polyploidy and aneuploidy are important, and several species have chromosomal races. Diffuse centromeres, which have been much studied in Luzula (e.g., Malheiros & de Castro, 1947; Brown, 1954), are thus far unreported in Juncus. This phenomenon, known also from some Cyperaceae and certain arthropods, is characterized by chromosomes that lack distinct centromeres. Instead the spindle fibers are attached at a number of points along the chromatids, so that at anaphase the chromosomes appear as "u's" with their ends toward the poles instead of as inverted "v's". Diffuse centromeres play a significant role in both aneuploidy and polyploidy, as both halves of a broken chromosome retain centromeric capabilities.

Snogerup (1963) made somatic counts on root-tips of both annual and perennial species of Juncus. He observed that the genomes were separable into two categories: those with very small, uniform, spherical or shortly rod-shaped chromosomes; and those with slightly larger, more variable chromosomes, some of which were noticeably two-armed even at somatic metaphase. For the most part the two groups corresponded with the prophyllate and eprophyllate subgenera respectively.

Harriman and Redmond (1976) also relied on root-tips in their survey of North American perennials. Unlike Snogerup they pretreated with colchicine and were therefore unable to determine centromere position, satellites, or other chromosomal details. The chromosomes thus treated were 1--1.5 µm in size.

In their study of chromosomal races of Juncus bufonius s.l., van Loenhoud and Sterk (1976) used the primary leaf meristem of seedlings. They discovered that "It is usually not at all easy to obtain good chromosome counts of Juncus bufonius s.l. The chromosomes are not only minute (0.4-1.0 µm) and numerous, but often present in a globular arrangement or in dense clusters. For this reason observational errors are bound to occur".

Members of the J. triformis complex do not provide a good selection of root-tips, but fortunately they produce new flower buds for as long as conditions are favorable. Meiotic material could therefore be collected from specimens that had mature capsules for positive identification. I had good results with Snow's stain (Snow, 1963), also used successfully on Juncus pollen mother cells by Riebe (1978) and Reinking (1981).

Methods:

Individual young elongating culms or whole plants, either from the field or cultivated, were fixed in Farmer's solution (absolute ethanol:glacial acetic acid, 3:1) or Newcomer's solution (isopropyl alcohol:proprionic acid:petroleum ether:acetone:dioxane, 6:3:1:1:1). Langlet's modification of Navashin's solution was also tried but with unsatisfactory results. Fixed material was stored refrigerated either in the fixative or in 70% ethanol.

Staining was accomplished by placing the fixed material in vials partly filled with Snow's stain and incubating at 60° C until good staining was achieved, usually three to seven hours. Stained material was stored in 70% ethanol. Hoyer's solution was used as the mounting medium. Snow (1963) recommended overstaining and then destaining in 45% acetic acid, but I did not find this approach satisfactory.

Results:

Only a few counts were obtained from the I and II meitoic divisions, but fortunately both mitotic divisions in the formation of the mature pollen grain were clearly visible. In addition, somatic counts were often available from the meristem of the elongating culm.

Like van Loenhoud and Sterk, although I am confident in the correctness of most of my counts, I must confess to a relative amount of uncertainty in others due to the difficulty of working with such small chromosomes. Table 2 lists the number I encountered most frequently with the greatest assurance for each species, along with a range of variation that may or may not be due to observational error. Known numbers of other species in subg. Graminifolii are included for comparison. Selected micrographs and accompanying interpretations are presented as Fig. 12, and drawings of less photogenic figures are in Figs. 13-15. Most of the latter are freehand drawings, as the small size of the chromosomes reduced the efficacy of the camera lucida.

I noticed some size variation but could otherwise discern little or no chromosomal details, including whether or not the centromere was diffuse. Small stained bodies were sometimes present, but as they occurred randomly I believe that they were fragments broken off by too

Table 2. Chromosome numbers of subg. *Graminifolii*

Annuals:

	n	2n
J. triformis	18	
J. leiospermus var. *leiospermus*	16	
J. kelloggii	17 (±1)	
J. luciensis	16	
J. tiehmii	17 (±1)	
J. capillaris	18 (±2)	
J. bryoides		ca 38
J. uncialis	16	
J. hemiendytus var. *hemiendytus*	16	
J. capitatus		18[1]
Perennials:		
J. covillei		38[1]
J. dregeanus		ca 35, ca 40[3]
J. falcatus		38[3]
J. filipendulus		40
J. marginatus		38[1], 40[2]

Sources:

[1] - Snogerup, 1963
[2] - Harriman & Redmond, 1976
[3] - Index to Plant Chromosome Numbers

Fig. 12. Micrographs and interpretations of chromosomes in the *J. triformis* complex.

a. *J. triformis* (Ertter & Strachan 3521, San Diego Co., CA)
prometaphase I $n = 18$

b. *J. triformis* (cult. from Ertter & Strachan 3942, Fresno Co., CA)
1st pollen metaphase $n = 18$

c. *J. capillaris* (Ertter & Strachan 3076, Mariposa Co., CA)
2nd pollen metaphase $n = 18$

d. *J. luciensis* (Ertter & Strachan 3529, San Diego Co., CA)
1st pollen metaphase $n = 16$

e. *J. bryoides* (Ertter & Strachan 3482, Riverside Co., CA)
mitosis in culm $2n = 38$

f. *J. leiospermus* var. *leiospermus* (Ertter et al. 3309, Butte Co., CA)
anaphase I $n = 16$

g. *J. leiospermus* var. *leiospermus* (Ertter et al. 3309, Butte Co., CA)
metaphase II $n = 16$

h. *J. uncialis* (Ertter 4430, Harney Co., OR)
1st pollen metaphase $n = 16$

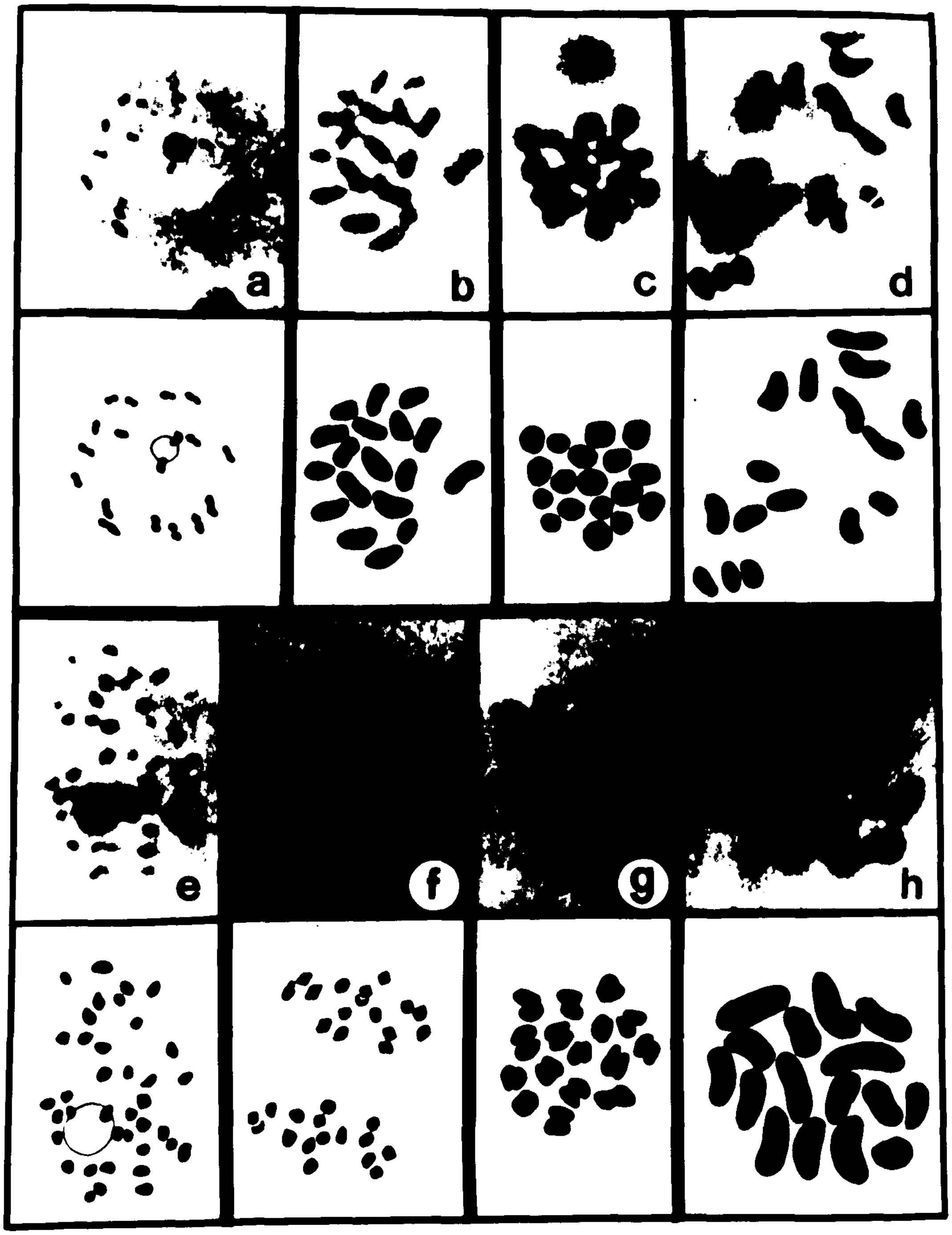


Fig. 12. Micrographs and interpretations of chromosomes in the J. triformis complex. a-b, J. triformis. c, J. capillaris. d, J. luciensis. e, J. bryoides. f-g, J. leiospermus var. leiospermus. h, J. uncialis.

Figs. 13-15. Chromosome drawings of the *J. triformis* complex.

J. kelloggii	
Ertter & Strachan 3333	Monterey Co., Calif.
" 3395	Monterey Co., Calif.
J. luciensis	
Ertter & Strachan 3366	Monterey Co., Calif.
" 3886	Plumas Co., Calif.
J. tiehmii	
Ertter et al. 2766	Sierra Co., Calif.
Ertter & Strachan 3439	Los Angeles Co., Calif.
" 3927a	Tuolumne Co., Calif.
J. capillaris	
Ertter & Strachan 3076	Mariposa Co., Calif.
" 3897	Mono Co., Calif.
J. leiospermus var. *leiospermus*	
Ertter et al. 3309	Butte Co., Calif.
J. uncialis	
Ertter 4430	Harney Co., Oregon
J. hemiendytus var. *hemiendytus*	
Ertter & Strachan 3004	San Bernardino Co., Calif.
" 3770	Elko Co., Nevada

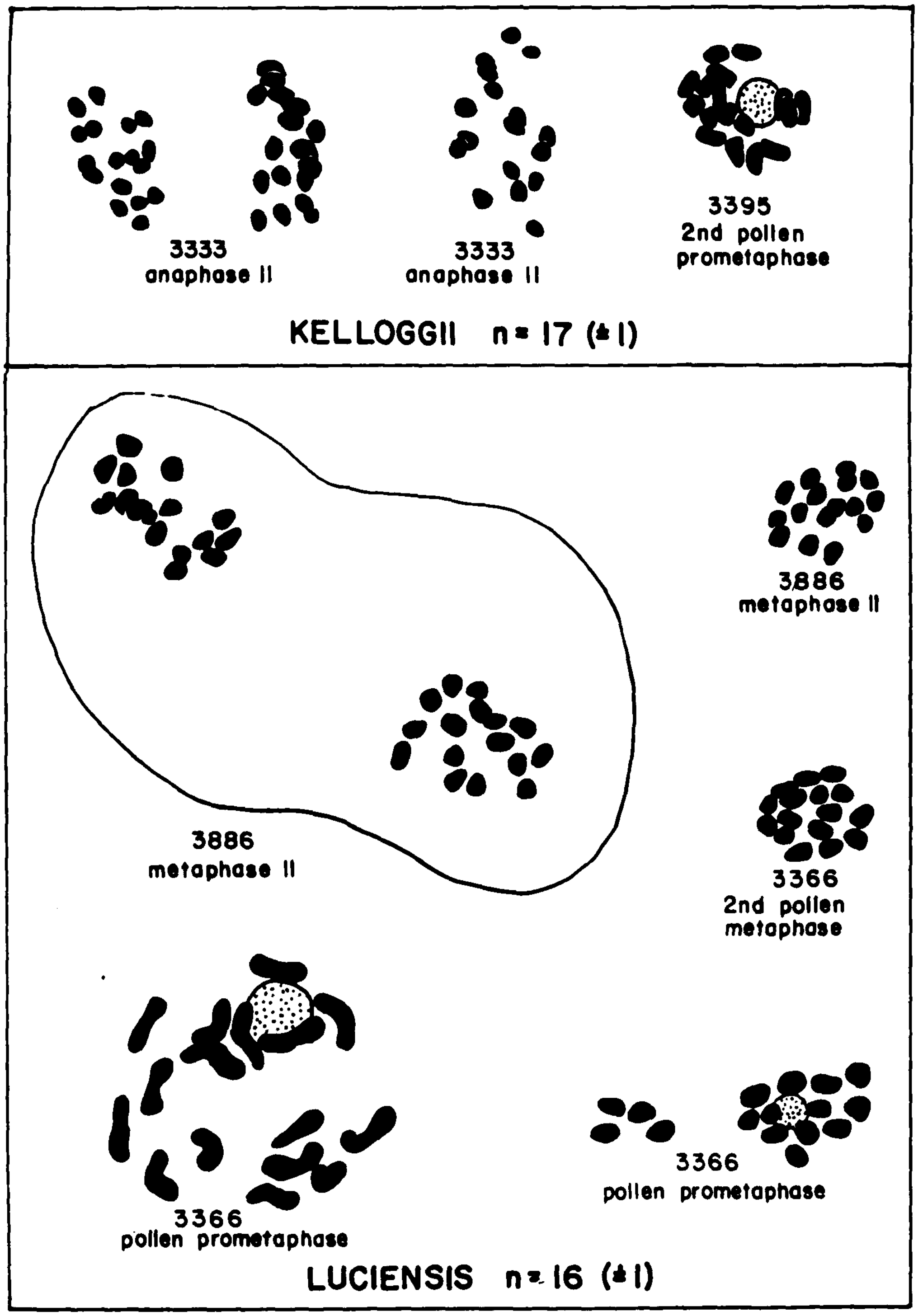


Fig. 13. Chromosome drawings of J. kelloggii and J. luciensis.

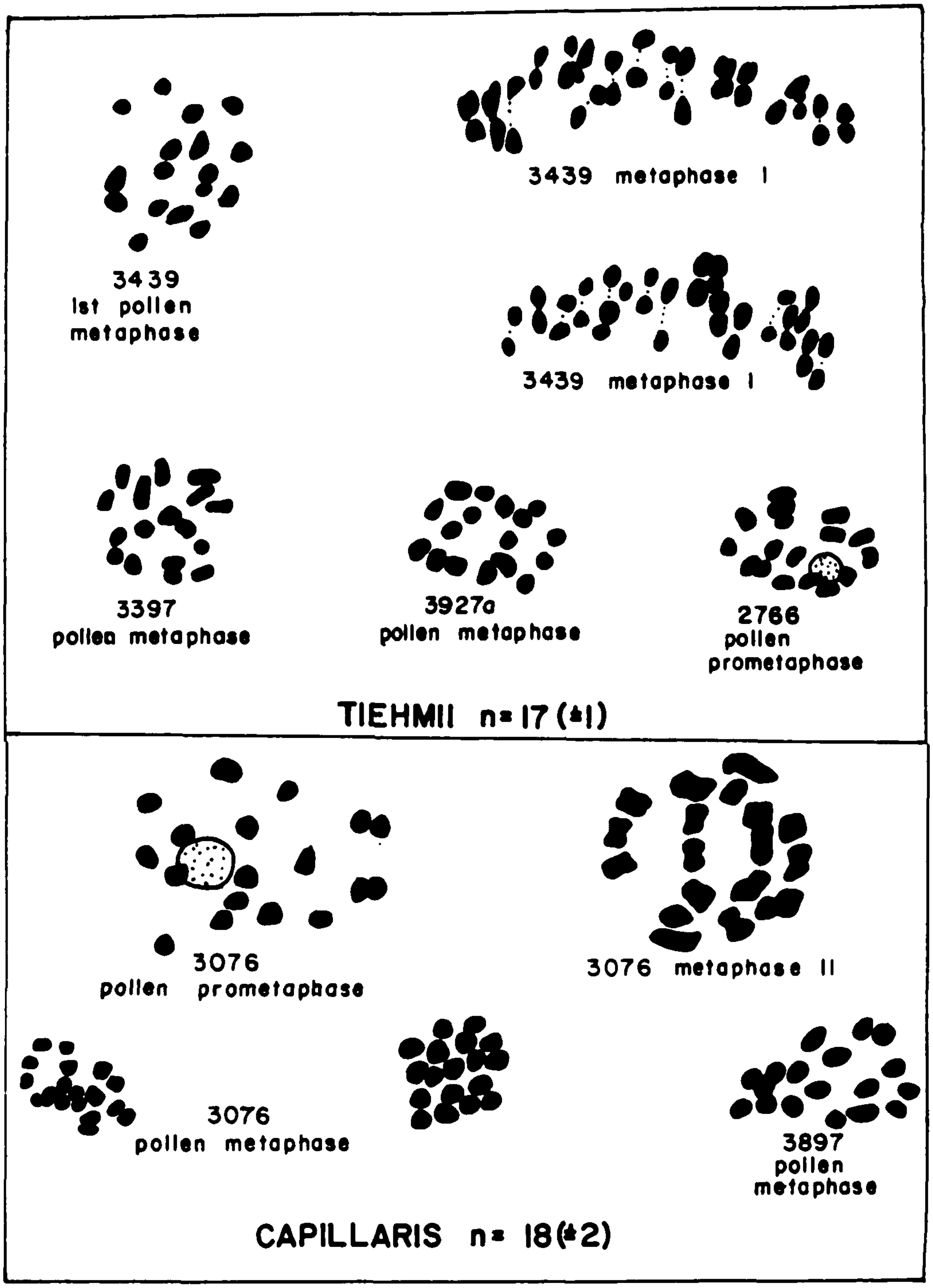


Fig. 14. Chromosome drawings of J. tiehmii and J. capillaris.

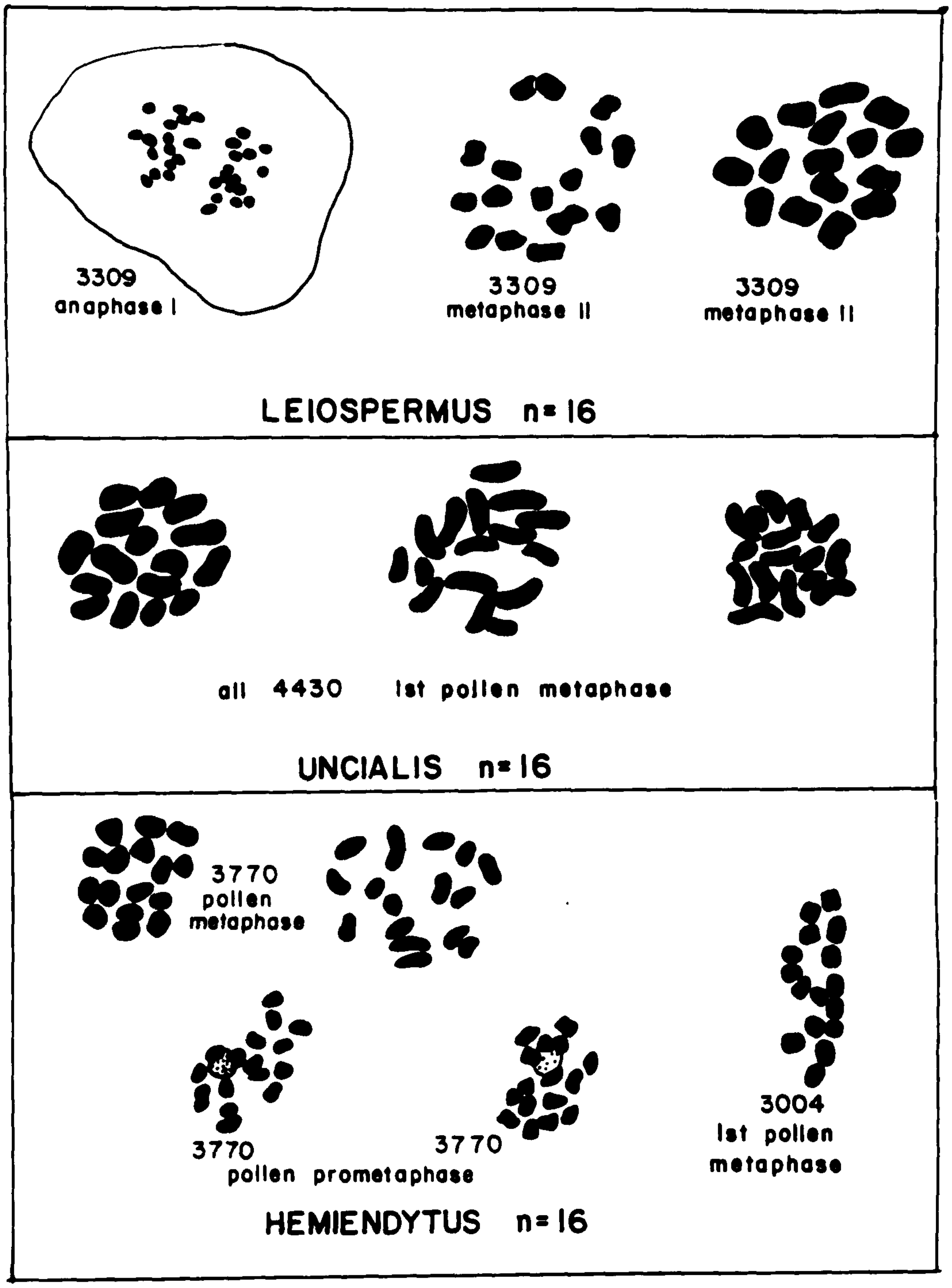


Fig. 15. Chromosome drawings of *J. leiospermus* var. *leiospermus*, *J. uncialis*, and *J. hemiendytus* var. *hemiendytus*.

much pressure during preparation of the slides, rather than B-chromosomes, which have not been reported from *Juncus*.

Discussion:

As diagrammed in Fig. 16, the most immediately noteworthy feature is the aneuploid reduction series paralleling the progressive morphological specialization found in the complex. This is especially well-illustrated by the ridge-seeded species (*J. triformis* and the "kelloggii" group). Starting with *n* = 18, which is near the *n* = 19-20 that characterizes the perennial species of subg. *Graminifolii*, the chromosome number decreases to *n* = 17 for *J. kelloggii* and *J. tiehmii*, and then to *n* = 16 for the solitary-flowered *J. luciensis*. In general, low nuclear DNA content in angiosperms has been correlated with short generation time (Bennett, 1972) and increased morphological specialization (Bachmann et al., 1979). This would seem to be the case in the *J. triformis* complex.

The only annual member of subg. *Graminifolii* that has previously been counted is *J. capitatus* by Snogerup (1963). He found that "the diversity in size and the general appearance of the chromosomes are reminiscent of sect. *Graminifolii*", but he nevertheless believed that the low number of 2*n* = 18, less than half that known for any eprophyllate perennial species, supported the separation of subg. *Juncinella* from subg. *Graminifolii*. My counts in the *J. triformis* complex do not support such a separation. An in-depth investigation of the chromosomes of the Southern Hemisphere species would obviously be pertinent.

n = 19	BRYOIDES
n = 18	TRIFORMIS CAPILLARIS
n = 17	KELLOGGII TIEHMII
n = 16	LUCIENSIS LEIOSPERMUS UNCIALIS HEMIENDYTUS

Fig. 16. Aneuploid reduction in chromosome numbers.

Cultivation Experiments

The _Juncus_ _triformis_ complex is potentially well-suited for biosystematic studies, as the plants have short generation times, possess distinct morphological markers, and take up little space. Buchenau (1892) cultivated many species of _Juncus_, including _J_. _capitatus_ and _J_. _lomatophyllus_ Spreng. in subg. _Graminifolii_, in order to study their flowering behavior. He did not, however, grow any members of the _J_. _triformis_ complex. Edgar (pers. comm.) has similarly cultivated some New Zealand species.

I wanted to cultivate specimens of the _J_. _triformis_ complex for a number of reasons:

1) to determine if the defining morphological characters were maintained in cultivation.
2) to observe germination, growth, and flowering behavior.
3) to obtain cytogenetic material from species or important populations of which I had seeds but no buds.
4) to attempt experimental crosses.

The first two goals were generally achieved, the third goal was met in a single case, and the last goal was not attained. Results have been intercalated where pertinent throughout this paper.

Cultivation experiments were not a major aspect of my study, and as it happened, in the experiments where I kept careful records the seeds either did not germinate or else the seedlings promptly died. Vigorous plants resulted only under conditions of benign neglect. I therefore have no rigorous quantitative or qualitative data to present. I nevertheless believe that the following results are worth noting, both in reference to the present study and to aid anyone else who may wish to grow members of the group.

Methods and Results:

Cold treatment appeared to be a prerequisite for germination, and as could be expected the high altitude montane taxa required a longer and harsher cold treatment than the low altitude valley taxa did. A long daylight period was necessary to trigger flower production. Although I had some success placing the seeds on moist soil in the refrigerator or freezer for several weeks and then using artificial light to prolong the winter sunlight, best results were achieved by placing pots outside during a New York winter and then bringing them in onto a sunny windowsill in the spring.

Soil should not be allowed to dry out, but excessive saturation led to the demise of most plants, possibly because of increased nematode activity. A compromise could be reached by keeping the pots in standing water, provided that the soil level was at least two inches above the water line. Sandy loam and fine sand were used as substrates because of their availability; both gave similar results. I suspect that difficulties with growing members of the "uncialis" group were due at least partly to inadequate clay content in the soil, especially since the only seedlings of this group successfully grown to flowering grew in soil that had been collected with the seed source.

Under proper conditions, seeds began germinating only two days after being removed from cold treatment, and most seeds that were going to germinate had done so after two weeks. In general, only a certain percentage of seeds germinated after a given cold treatment, leaving a reserve of seeds in the soil. If the first batch of seedlings all died, I would simply subject the same pot to a second or even third cold treatment to obtain a new batch of seedlings. This is in contrast to my one test with *J. capitatus*, wherein almost every seed germinated at the same time.

Germination and development followed the pattern described in detail by Buchenau (1906), except that the first flower-bearing culm often appeared immediately after the first leaf. The record was set by seeds of *J. leiospermus* var. *leiospermus*, which first bloomed about two weeks after being removed from cold treatment. This was exceptional; most other seedlings experienced a distinct lag period between the production of cotyledons and the appearance of leaves and culms. I do not know if this lag occurs in nature or is a consequence of suboptimal growing conditions. Application of fertilizer a few days after germination appeared to encourage development of leaves and culms, which is not surprising considering the minute size of the seeds.

I was able to germinate seed of all taxa in the complex except *J. hemiendytus* var. *abjectus*, and of these all except *J. uncialis* matured to the point of flowering. In general, the groups can be arranged in the following sequence from easiest to hardest to cultivate: "triformis", "kelloggii", "bryoides", and "uncialis". Once a plant in the *J. triformis* complex is established it will continue producing new leaves, culms, and flowers for as long as the plant lives and conditions are suitable.

A few albino seedlings of *J. triformis* (seeds from Ertter & Strachan 3942) and *J. bryoides* (seeds from Ertter 2438) were noted. These soon died, as expected, but so did all other seedlings in that experiment.

Discussion:

The difficulties involved in successfully growing members of the *J. triformis* complex undoubtedly contribute to the restriction of the complex to western North America. A comparison can be made with the cosmopolitan *J. bufonius*, stray plants of which thrived under conditions that killed all seedlings of the *J. triformis* complex. I presume that both the seed reserve and exacting demands for particular germination requirements are compensation for the restricted ecological amplitude and adaptibility of the complex, much more limited than those of *J. bufonius*. It is probably not coincidental that the species that are the most difficult to germinate (*J. bryoides* and *J. hemiendytus*) are also the ones that have the best representation in the climatically unreliable areas outside of California. As an example of the finely tuned synchronization of germination with suitable growing conditions, notes on *Moran 23340* from Baja California record the local occurrence of *J. bryoides* at a site in 1976, its absence in the drier year 1977, and its abundance in the wet year 1978. I noticed a similar pattern at the site of *Ertter 2438* and *Ertter 4180* in Idaho.

Other Approaches

Although SEM and cytogenetics were selected as the primary supplements to classical morphology for this study, several other approaches have been applied to *Juncus* in the past. These other approaches could be of great utility in resolving unsatisfactorily answered questions in the *J. triformis* complex and subg. *Graminifolii*. A few are discussed here.

Anatomy has long been important at both subgeneric and specific levels in the genus, to the extent that Stace (1970), in his anatomical study of subg. *Genuini*, stated that "it is important that all monographers should in the future incorporate anatomical data into their formal taxonomic descriptions". Other examples of anatomical studies applied to Juncaceae systematics are those of Buchenau (1906), Peisl (1957), Cutler (1969), and Balslev (1982). Features of the stems, leaves, and rhizomes that have been used taxonomically in *Juncus* include epidermal and cross-sectional characteristics, such as stomata and arrangement of vascular and mechanical tissues. Members of subg. *Graminifolii* that have previously been examined are *J. covillei* (Buchenau, 1906), *J. capensis*, *J. falcatus*, *J. planifolius*, and *J. capitatus* (Cutler, 1969). Of relevance here is the fact that Cutler emphasized the anatomical differences between *J. capitatus* on the one hand and *J. falcatus* and *J. planifolius* on the other as support for the segregation of subg. *Juncinella*.

There also exists a solid base of Juncaceae chemotaxonomy on which to build. The primary publication is Williams and Harborne's 1975 survey of the flavonoids in the family, used to relate Juncaceae to other families. In an unpublished thesis, Joughin (1976) studied the flavonoids of Australian rushes. Although she concentrated on subg. *Genuini*, she also examined other Australian species for comparison, including *J. antarcticus*, *J. planifolius*, *J. caespiticus*, and *J. capensis* in subg. *Graminifolii*. Stasiak (1978a, b) used chemical characters to study variation within and between populations of two species of *Juncus* in Poland. Flavonoid comparison and enzyme electrophoresis were used in support of Reinking's (1981) description of a new hybrid rush.

Ontogeny, floral histogenesis, and embryology of Juncaceae have also been studied (e.g., Brenner, 1922; Barnard, 1958; Shah, 1963), but as far as I know no systematic significance below the generic level has been suggested.

Finally, numerical analysis, both phenetic and cladistic, of data from all these sources could prove extremely effective, particularly in resolving interrelationships in the entire subgenus *Graminifolii*.

Ecology

As does the genus as a whole, members of the Juncus triformis complex grow in at least seasonally wet soils. The primary modification of the group is for habitats that are saturated or even flooded early in the season and bone-dry later on, as discussed in the Evolution section. Examples would be vernal pools, sandbars in streams, and seepage areas on outcrops. A moderately wet period is necessary for germination, while yearly flooding and desiccation reduce competition. For the most part members of the J. triformis group do not handle competition well and characteristically occur on bare ground.

Granite and basalt are common parent rocks of substrates while limestone is not. I know of no populations from calcareous areas. Although vernal pools are often alkaline, according to Holland and Jain (1977) the vernal pools on the terraces of the Central Valley of California in which members of the complex typically grow are neutral to slightly acidic; the San Diego vernal pools also tend to be acidic (Purer, 1939). Members of the J. triformis complex are therefore associated with acidic rather than alkaline substrates.

A general correlation can be made between soil preference and seed coat pattern. The ridge-seeded species (J. triformis and the "kelloggii" group) prefer fine sandy or silty soils, often derived from granite. Examples would be sandbars and seepage on granite or sandstone outcrops. In constrast the smooth-seeded species (J. leiospermus and the "uncialis" group) are associated with more clayey soils, often of basaltic origin, such as those found in vernal pools and mudbanks. The anomalous *J. bryoides*, although smooth-seeded, is most commonly found on the fine sandy-silty substrates, which furthermore are often somewhat drier than those associated with the other species.

Individual edaphic preferences also exist, though with considerable overlap. For example, *J. uncialis* often grows in heavier clays than does *J. hemiendytus*, and likewise *J. kelloggii* tolerates or prefers more clayey soils than do the other members of the "kelloggii" group. *Juncus capillaris* does not require bare ground and instead thrives in short turf and mossy areas. These differences are manifested in mixed populations, where there is a distinct tendency for each component to be concentrated in a certain microhabitat. For example, *J. tiehmii*, *J. bryoides*, and *J. hemiendytus* often grow together, and while many plants occur side by side one can nevertheless expect to find more *J. bryoides* on the higher and drier spots and *J. hemiendytus* on the more clayey spots.

Members of the *J. triformis* complex are found at elevations from sea level (*J. kelloggii*) to over 3500 m (*J. bryoides*). As with substrate, each species has an altitudinal range that may be of taxonomic importance. This is best seen in the elevational stratification that has developed within each group, as summarized in Fig. 17.

The edaphic and elevational correlations support the recognition of the components of the *J. triformis* complex as valid species and varieties.

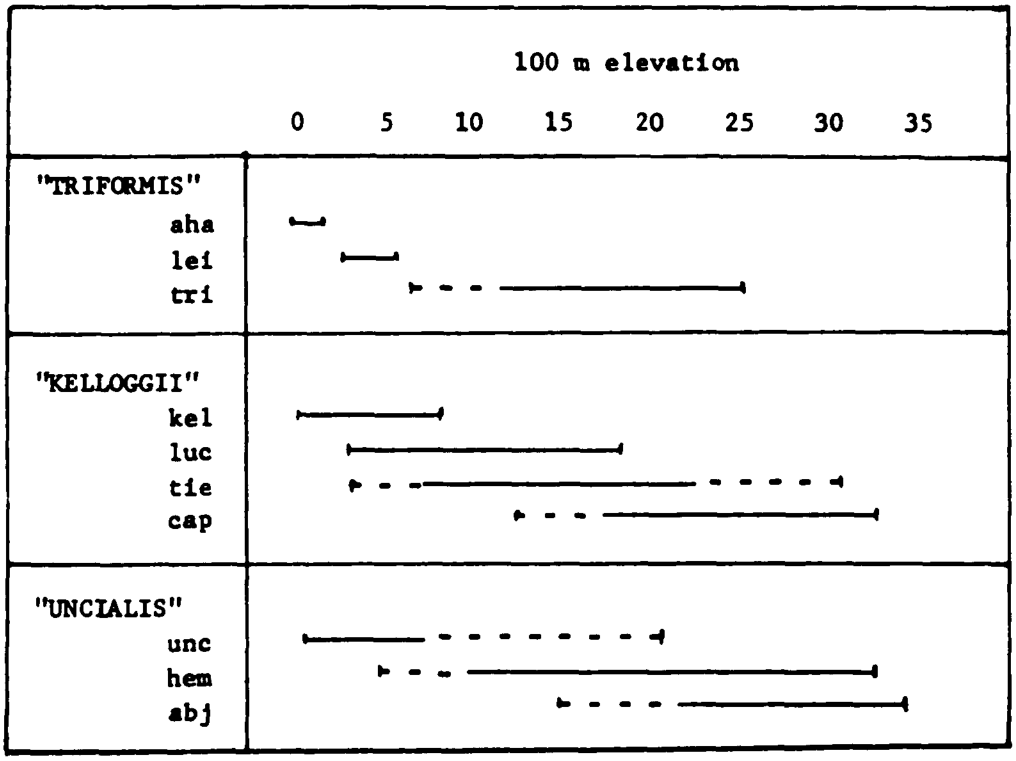


Fig. 17. Elevational stratification within groups.

Distribution

The *Juncus triformis* complex is endemic to western North America, from the south tip of Vancouver Island in Canada to the mountains of extreme western Colorado and northern Baja California del Norte, Mexico. Within this general area the most important determinants of distribution are climate (winter wet, summer dry), geology (non-calcareous), and evolutionary history.

The complex occurs in greatest abundance and diversity in California, and the long-styled species representing the archaic "triformis" group are confined to California, primarily to the west side of the Sierra Nevada and the northern Sacramento Valley. On the basis of this distribution, cismontane California would most likely be where the complex originated. The more advanced short-styled species have spread throughout the rest of California except for the Mojave and Colorado deserts, the offshore islands, and all but the edges of the San Joaquin Valley.

According to Hermann (1948),

> The center of distribution of this group of species seems to be from Humboldt and Shasta counties south to Monterey and Tulare counties, California, and only three of the nine species are found with any degree of frequency beyond the borders of the State. . . . How far this extra-limital paucity of collections represents the actual distribution of the plants at present and how far it is merely an index of Mr. Howell's greater activity within California than in the neighboring States, it is difficult to judge.

Hermann's misgivings were justified. Additional collections since 1948 have shown that, although the complex is indeed centered in California, a significant part of its range lies outside the boundaries of the state.

To the south the complex extends into Baja California along the Peninsular Ranges to the Sierra San Pedro Mártir. To the north different species are scattered throughout Oregon and southern Idaho, in the Willamette Valley, along the lower Columbia River, through the Cascades, in the Wallowa Mountains, and on the Idaho Batholith. Old collections also exist from southern Washington and the south tip of Vancouver Island, British Columbia. In addition the complex has been shown to be a component of the wetland flora of the northern Great Basin in southeastern Oregon, southwestern Idaho, and northern Nevada, primarily in the mountains. Farther east only a handful of widely scattered populations are known from the Wasatch and Uinta ranges and Colorado Plateau in Utah and in extreme western Colorado. Careful search in these areas may reveal that the spotty distribution is in part an artifact of inadequate collecting.

Even if the shortage of collecting is taken into consideration, the *J. triformis* complex in the northern part of its range unmistakably exists as small localized widely separated populations. Many of these populations probably have been established by bird dispersal; the tiny seeds would be transported easily in mud adhering to the feet and feathers of waterfowl flying from one wet spot to another. I suspect that during the pluvial periods of the Pleistocene suitable habitats were more abundant throughout the northern Great Basin, and the present populations are to a certain extent relictual in nature. One is otherwise hard-pressed to explain, for example, the occurrence of *Ertter 4321* (*J. bryoides*), *4322* (*J. tiehmii*), & *4323* (*J. hemiendytus* var. *hemiendytus*) all growing around a single tiny spring in the Santa

Rosa Range, Nevada, miles from any other known populations.

As a generalization, the "kelloggii" group has most of its distribution to the south and west, while the "uncialis" group lies more to the north and east. Geographic factors have probably played a significant role in speciation within these two groups.

Because of the modern concern for endangered and threatened species, it is appropriate to summarize the status of the members of the complex. The most precarious taxon is *J. leiospermus* var. *ahartii*, known for certain only from a few vernal pools on a single ranch. The var. *leiospermus* is more abundant than once thought, but nevertheless it is essentially restricted to the heavily agricultural Sacaramento Valley and is therefore threatened by further development. *Juncus uncialis* and *J. kelloggii* have wider distributions, but because much of their ranges are marked only by older collections from areas that are now heavily developed, such as the Willamette and Central valleys, they too could bear watching. *Juncus triformis*, *J. luciensis*, *J. capillaris*, and *J. hemiendytus* var. *abjectus* are not abundant, but enough of their ranges lies in non-threatened areas that their continued existence in the forseeable future is probably assured. The remaining three taxa (*J. tiehmii*, *J. bryoides*, and *J. hemiendytus* var. *hemiendytus*) are relatively common and widespread.

On a state by state basis, the only records of the complex for Washington are turn-of-the-century collections by Suksdorf from Klickitat County. One of the species he collected, *J. hemiendytus*, is widespread elsewhere, but the other, *J. kelloggii*, has a rapidly diminishing range. It is possible that both have already been extirpated from the state.

In Oregon, the numerous collections of J. kelloggii from the Willamette Valley all antedate 1930; the species' present status in the state is probably precarious at best. Three other species (J. capillaris, J. tiehmii, and J. bryoides) are known in Oregon only from single collections from Steens Mountain. These are peripheral populations of species that are otherwise in no danger, but their isolated presence on Steens Mountain (where J. uncialis and both varieties of J. hemiendytus can also be found) supports the recognition of Steens Mountain as a botanically unique area deserving general protection. Juncus uncialis probably belongs on the state's watch list; it has lost much of its range in California but can apparently persist at the edges of some stockponds that are not too heavily trampled. Juncus uncialis has been recently collected from one site in Nevada and therefore should be considered for this state's watchlist as well. It is possible that J. triformis, J. capillaris, or J. luciensis may be found in the Sierran part of Nevada, in which case these would be the only records for the state.

Several other species in the complex are scattered in northern Nevada and Idaho, but none seems to be immediately threatened. Distributions in Utah and Colorado are not well enough known to evaluate properly, and only the most common taxa are involved. It is possible that peripheral populations of these easily overlooked plants may one day be discovered in western Wyoming, southwestern Montana, or northern Arizona.

Evolution

The evolution of the Juncus triformis complex is linked to the evolution of the California climate and flora. The drying trend that began in the Miocene has left much of California with a mediterranean climate, complete with cool wet winters and hot dry summers. Elsewhere the climate of much of the western United States is also characterized by winter precipitation and summer aridity, though not with the temperature regime necessary to qualify as truly mediterranean. The components of the earlier mesic forests either disappeared, became restricted to localized mesic sites, or gave rise to descendents adapted to the summer xeric conditions.

The perennial ancestor of the J. triformis complex combined the last two options, and the evolution of the complex illustrates a progressive adaptation to the seasonally moist habitats that developed with the mediterranean climate. These habitats display a diversity ranging from clay-bottomed vernal pools to sandy seepage areas. Although quite different geologically, all provide similarly restrictive growing conditions, as the soil is usually shallow and submerged or at least saturated early in the season but completely desiccated by late summer. In contrast, most perennial rushes grow in more or less permanently mesic habitats, such as wet meadows or edges of streams. If these habitats do not remain wet year-round, the soil is usually deep enough to protect the rhizomes. The challenge facing the ancestors of the J. triformis complex was therefore that of adapting large rhizomatous perennials to ephemerally wet habitats that are parched during part of the year.

The first critical step was undoubtedly the attainment of an annual life-cycle, usually accompanied by a reduction in size of plant, thus allowing the species to survive unfavorable seasons as drought-resistant seeds. Once the annual condition was reached, anything that would further speed up the life cycle would be an additional adaptation. In effect, the less time it took to get through a generation, from seed to mature plant to more seeds, the better. Reduction in size and number of parts was one of the simplest ways this acceleration could be accomplished. One gets the impression of a general "stripping down" so as to speak, an elimination of excess baggage in the rush to set seed.

In the case of the _J_. _triformis_ complex, these additional adaptations have taken the form of a further reduction in size, a reduction in the number of heads per inflorescence, a reduction in the number of flowers per head, a loss of the inner whorl of stamens, and a transition from trimery to dimery. This general morphological reduction has tended to coincide with an aneuploid decrease in chromosome number. An additional transition has been a shift from outcrossing to selfing as the dominant mode of pollination. Like the morphological reduction, this might be seen as a means of shortening the time necessary to produce seeds for the next generation. Its usefulness to species colonizing marginal, unreliable, and isolated habitats is obvious.

At the extreme are healthy mature plants only one or two centimeters tall, each culm bearing a single dimerous self-pollinating flower. Under particularly adverse conditions further concessions can be made, so that depauperate specimens can be found only a few millimeters tall, with a single leaf and a single culm, bearing a single flower within which a single seed matures in each locule. This brings up an important point: many of the adaptations are genetically fixed as specific characters, but they may also be options available to a species with opportunistic potentials. In the latter case a young or depauperate plant may exhibit the reduced form under unfavorable conditions so as to set at least some seed, but if favorable conditions develop and persist the same plant can reach its full potential morphological development and begin mass-producing seeds. This flexibility is standard in the more archaic members of the J. triformis complex but is lost to a greater or lesser extent as the reduction become fixed in the more derived species (see, for example, the discussion on dimery in the Morphology section). This combination of opportunistic tendencies and genetically fixed characters has been responsible for much of the taxonomic uncertainty in the complex.

Although a good transitional series exists between large, multi-headed, six-anthered perennials and small, single-headed, three-anthered annuals in the South African Graminifolii, comparable intermediate stages in the evolution of the J. triformis complex apparently do not exist. The two most archaic species in the complex, J. triformis and J. leiospermus (as indicated by their relatively large size, predominately out-crossing mode of pollination, and distribution primarily limited to the mediterranean parts of California), are already dwarf annuals possessing the derived features of solitary terminal heads and three anthers. It is conceptually useful to consider these two species as the extant representatives of the ancestral annual stock, the "triformis" group. In my understanding the remaining members of the complex have evolved from this basal group as three independent parallel lineages: the "kelloggii", "uncialis", and "bryoides" groups. Each group is defined by style length, flower number, seed coat pattern, and other morphological characters. The groups are further natural in that they correspond to a variety of non-morphological features. For example, in general the microsporocytes of the "uncialis" group squash flatter and have a clearer cytoplasm when stained than do those of the other groups, while the seeds are difficult to germinate and die before flowering under conditions that have allowed members of the other groups to flourish.

The "kelloggii" group is closely related to and may even be directly derived from J. triformis in the basal group, as both have characteristic ridged seeds and grow in sandy soils. In a similar manner the "uncialis" group probably originated from the ancestral stock somewhere near J. leiospermus, with which it shares such characteristics as chromosome number, seed coat pattern, and a preference for clay soils. In contrast, although J. bryoides is clearly a member of the J. triformis complex, it does not appear to be more closely related to any one species than to the others. I believe it is the sole surviving representative of the oldest of the three derivative lineages, the "bryoides" group. Figure 18 summarizes my understanding of the relationship and parallel adaptations of the three lineages.

The "kelloggii", "uncialis", and "bryoides" groups have spread into the northern Intermountain Region, the Sierra Nevada, and other mountain ranges in the western cordillera. Although summer aridity may not be as harsh in many of these places as in central California, the added stresses of extreme winter cold, short summers, and erratic weather patterns, especially in conjunction with the extremes of the Pleistocene and Holocene, have provided a tremendous challenge to the survival and adapatability of the *J. triformis* complex.

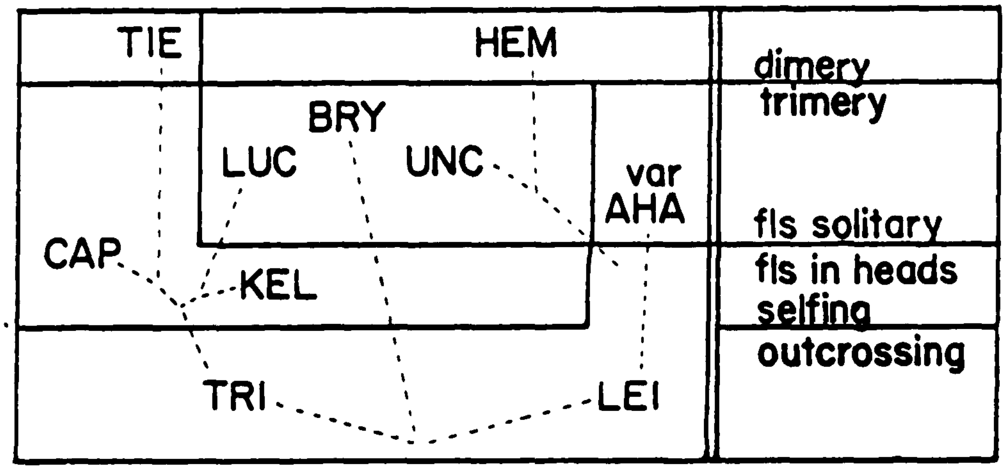


Fig. 18. Parallel adaptations in the *J. triformis* complex.

Infrageneric Relationships

Historical Placements:

When Engelmann (1866) first introduced *Juncus saginoides*, he intended to place it in its own subgenus *Juncellus*,[1] but instead he left both subgenus and species undescribed. Although he did not use any other formal infrageneric ranks, in 1868 he did compare *J. triformis*, the nomenclatural equivalent of *J. saginoides*, with the perennial three-anthered *J. marginatus* and the Mediterranean annual *J. capitatus* in his "section" *Juncus graminifolii*: *Graminei*. Engelmann treated only the North American species of *Juncus* and therefore made few comparisons with species growing elsewhere in the world.

Buchenau (1880, 1890) placed *J. triformis* and *J. kelloggii* with the other annual species of subg. *Graminifolii*, which he subdivided so that *J. triformis* was grouped with some of the South African species while *J. kelloggii* was placed by itself. In his 1906 key to the species of subg. *Graminifolii*, he referred to the annuals as "Series II. Junci graminifolii annui", but did not otherwise propose a formal taxonomic category.

Rydberg (1917) treated all members of the *J. triformis* complex growing in the Rocky Mountains as *J. uncialis*, for which he created the infrageneric category *Unciales*. Although descriptions were provided for Rydberg's numerous infrageneric categories in the form of

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[1] *Juncellus* (Griseb.) C. B. Clarke has been used for a section or segregate genus of *Cyperus* in the Cyperaceae.

keys, no formal ranks were designated. The name Unciales is therefore validly published but has no bearing on priority except as a homonym (ICBN Art. 35). It is worth noting that Snogerup (1963) adopted Rydberg's Ensifolii as a section of Juncus, elevating this to a subgenus in 1978.

The annual species of subg. Graminifolii were given formal recognition as a distinct subgenus ("podrod") Juncinella by Krechetovich and Goncharov (1935) in their treatment of Juncaceae for the flora of the USSR. They accredited the name to Fourreau (1869), who had used it as the name of a segregate genus composed of J. capitatus and J. pygmaeus Thuill. (an annual member of subg. Septati). Fourreau, however, provided no descriptions, and the genus was therefore not validly published. The descriptions in Krechetovich and Goncharov are in Russian, not Latin, but in my understanding the inclusion of Buchenau's (1906) "Junci graminifolii . . . pro pl. annuis" in synonymy qualifies as a reference to a previously published Latin diagnosis (Art. 32.1), thereby completing the requirements of valid publication of the subgenus. Only J. capitatus was treated in their work, but the reference to Buchenau (1906) indicates that the South African annuals and the J. triformis complex also belong in subg. Juncinella.

In his treatment of the African Juncaceae, Weimarck (1946) also separated the annuals but as section (not subgenus) Juncinella, thereby inadvertently creating a new status for the name even though he ascribed it to Krechetovich and Goncharov. According to Weimarck, "15 species belong to the section, 13 of them are endemic in S. Africa, 1, J. capitatus, has a wide distribution area in the northern hemisphere and has scattered localities in the southern, and, finally, 1 species, *J. triformis*, is endemic in pacific N. America."

The South African perennial and annual species of subg. *Graminifolii* have been revised several times since their initial discovery and treatment by Thunberg (1794). Buchenau (1875) recognized seven perennial and 10 annual species, Adamson (1935) 13 perennial and 12 annual species, and Weimarck (1946) eight perennial and 13 annual species. These numbers do not include the numerous infraspecific categories or *J. capitatus*, which is established in but probably not native to South Africa.

Because many of these taxa were based on single collections, it is not surprising that a recent manuscript treatment of Juncaceae for the Flora of South Africa recognizes only three perennials and five annuals (Mauve, pers. comm. 1981). The perennial species extend into other parts of Africa, and *J. capensis* has also become established in Australia. In contrast the annuals are all narrow endemics in the mediterranean regions of southwestern South Africa, and none is particularly common.

Implicit in the recognition of subg. *Juncinella* as circumscribed is the concept that *J. capitatus*, the *J. triformis* complex, and the South African annuals form a natural monophyletic group. Both Hermann and Howell (1950) accepted *J. capitatus* as a close relative of the *J. triformis* complex. On the other hand, the South African/North American disjunction and the relative ease of developing an annual habit leads one to suspect that subg. *Juncinella* is artificial, especially since a diversity of potentially ancestral perennial members of subg.

Graminifolii exists in both South Africa and North America. This alternative was voiced by Raven and Axelrod (1978), who used Juncus as an example of a genus whose "annual species seem to have been independently derived from perennial species in the Old World and in the New". Most modern treatments of Juncaceae in these two regions that include infrageneric categories do not recognize subg. Juncinella (e.g., Munz, 1959; Hermann, 1975; Mauve, mss.). It is probably significant that subg. Juncinella is apparently in favor only in Europe (Nilsson & Snogerup, 1971; Snogerup, 1980), where J. capitatus is the only representative.

Infrageneric Comparisons:

Before accepting the association of the J. triformis complex with subg. Graminifolii, I considered as alternatives the ubiquitous annual _. bufonius in subg. Poiophylli and certain members of subg. Septati. Foremost among the latter were the reduced monocephalous perennial J. duranii, which is endemic to the Transverse Ranges of California, and the European annual J. pygmaeus, which was included by Fourreau in the original Juncinella with J. capitatus. If only the single-flowered species of the J. triformis complex were known, they could conceivably be linked to J. bufonius, but the distinct capitulum of the less-derived species places the complex unequivocally in the eprophyllate half of the the genus. At the same time, although one can easily accept the loss of septations in reduced leaves, the seed coat pattern of subg. Septati is consistently that of Fig. 5d (see Fig. 11g,h).

With these alternatives eliminated, the J. triformis complex remains firmly associated with subg. Graminifolii. Although Buchenau placed this subgenus at the end of his treatments, it probably represents the ancestral group for at least the eprophyllate species. As a result the subgenus has in effect been used as a catch-all for a diversity of species that have little in common other than flat or canaliculate leaves and a lack of the derived features that characterize the other subgenera.

The species in subg. Graminifolii that should be considered as possible relatives of the J. triformis complex can be arranged into the groups listed below, based on information drawn from both published and unpublished sources, combined with my own observations of material at NY, TEX-LL, and GH-A. Circumscription of species in South Africa is based on Mauve's manuscript revision of the South African Juncus.

1) J. capitatus.
2) The South African annuals.
3) The temperate Southern Hemisphere perennials.
4) The western North American perennials.
5) The J. marginatus group.

In Table 3 statistics on various relevant features of each of these groups are compiled. A discussion of each follows.

1) Juncus capitatus verges on being a weed in Europe and northern Africa and has become established in Australia, South Africa, temperate South America, and parts of the North America. In North America it was apparently first collected in 1934 in California and reported by Wadmond (1938), who discounted Buchenau's (1906) earlier citation of a specimen from Newfoundland as probably erroneous. Collections in 1944

Table 3. Comparison of groups in subg. Graminifolii

Explanation of abbreviations used

DUR (duration)
a = annual
p = perennial
* = sometimes blooms first year

BASE of plant
t = tufted
m = matted
r = rhizomatous
s = stoloniferous

SIZE of plant

POS (leaf position)
b = basal
c = cauline (often on lower stem)

SH (shape of leaf)
cn = canaliculate
fl = flat
in = involute

AUR (auricles)
+ = present
- = absent

BRT (bracts)
i = inconspicuous
f = foliose

#HD (# of heads per infl.)
∞ = numerous

#FLS (# of flowers per head)

STA (# of stamens)

STY (style length)
s = short
m = medium
l = long

PR (proportion inner/outer tepals)
i = inner longer
o = outer longer
= = subequal

TEX (texture of tepals)
th = thin
f = firm
n = nerved
p = papillate

TP (relation capsule/tepals)
> = capsule longer
< = capsule shorter
= = subequal

PLAC (placentation)
3-loc = 3-locular
3-sep = 3-septate
free = pseudo-free-central

TEX (texture of capsule walls)
th = thin
m = medium
in = indurate

CO (thick outer seed coat)
+ = present, obscuring
- = absent
± = sometimes present but not obscuring
t = tailed

PAT (seed coat pattern)
see Fig. 5
dv = modified 5d

N (haploid chromosome number)

Table 3.

				leaves			inflorescence					tepals		capsules			seeds			
	dur	base	size	pos	sh	aur	brt	#hd	#fls	sta	sty	pr	tex	tp	plac	tex	co	pat	n	natural range
triformis complex	a	t	1–15	b	cn	-	i	1	1–8	2–3	l s	=	th	> = <	3–loc	th	-	a b	16–19	western North America
J. capitatus	a	t	1–20	b	cn	-	f	1–4	(1)5–10	(2)3	s l	o	th n	<	3–loc	m	-	c	9	Mediterranean
South African annuals	a	t	2–15(30)	b	cn fl	-	i f	1–7	1–12(20)	(3)6	s m l	= i	th	=	3–loc	th m	+	c/a		South Africa
southern hemisphere perennials	p*	m t	2–80	b	in cn fl	-	i	1-∞	2–20	3,6	s m l	=	m f n	≤ =	3–loc	in m	+ ± -	a	c 18 c 20	South Africa, Australia/New Zealand Chile
western North American perennials	p	r	5–60	c	fl	+ -	i	1-∞	3–15	6	m l	=	m p	= < >	3-sep	in m	+ ± t	dv	19	western United States Japan Australia
eastern North American perennials	p	r t	15-100	c b	fl	+	i	1-∞	2–15	3,6	s l	= i	th f n	= <	3-sep	m	+	dv ?	19 20	eastern United States California Central America South America
J. repens	p*	s	5–30	c	fl	+	i	1–10	3–12	6	s	=	f n	= >	free	m	-	c/d		southeast US Caribbean
J. cyperoides	p	r	5–40	c	fl	-	i	5–40	3–10	6	s	=		=	3–sep		=	d		South America

from Texas are annotated by Tharp and Barkley as cotypes of a name that was apparently never published but which would have been a later homonym of J. minimus Buchenau. The species has also been reported from Louisiana (Kral, 1966) and is included in the floras of California (Munz, 1959), Texas (Correll & Johnston, 1970), and the southeastern United States (Godfrey & Wooten, 1979).

Wadmond (1938) believed that J. capitatus was introduced into North America, a belief no one has been inclined to challenge, especially given the numerous examples of other Mediterranean annuals that have become established in California. It is now a common component of the Central Valley vernal pool flora, sometimes growing with J. leiospermus and J. uncialis.

Juncus capitatus resembles the J. triformis complex in its annual habit, flowers that are grouped in terminal heads (usually solitary), and uniseriate stamens. Buchenau (1906) noted and illustrated both long-styled chasmogamous and short-styled cleistogamous forms of J. capitatus but did not assign taxonomic significance to these extremes. The seeds have a thin outer layer clearly showing the underlying pattern to be that of the putatively primitive type shown in Fig. 5c (see Fig. 10h-i).

In spite of these similarities, J. capitatus sheds no light on the origin of the J. triformis complex. For one thing, the species has some very prominent differences, specifically the long foliose lower bracts, the firm acuminate outer tepals that are much longer than the delicate obtuse inner ones, and the capsules which are decidedly shorter than the tepals and much more indurate than those of the J. triformis complex. It is difficult to visualize that either one is derived from the other. The Mediterranean-Californian disjunction, although not insurmountable, is nevertheless an additional drawback.

Even if J. capitatus were associated with the J. triformis complex, the question of origin would still not be resolved, as the relationships of J. capitatus are if anything even more obscure than those of the J. triformis complex. Europe and northern Africa have no native perennial species of subg. Graminifolii, although J. sparganifolius Boiss. & Kotschy occurs in Asia Minor and J. planifolius has become established in Ireland. Perhaps one should look at the three-anthered leafy bracted South African annual J. obliquus Adams., or even the New World perennial J. marginatus, for insight on the origin of J. capitatus.

2) Among the South African annuals, I was able to examine specimens referable to J. cephalotes Thunb. and J. rupestris Kunth. These were much more comparable than J. capitatus to the J. triformis complex in spite of the fact that most of them have six anthers, more numerous heads, and thickly coated seeds (Fig. 10d-g). As in the J. triformis complex, the bracts are mostly membranous and inconspicuous, the tepals are either subequal or the inner are longer, and the capsules are delicately thin-walled. In contrast to the situation in J. capitatus, a direct morphological transition from the South African annuals to the J. triformis complex can easily be visualized, and the South African annuals in turn blend almost imperceptibly into the perennials.

There are still some problems, however, in particular the thickly coated seeds. More important, such a connection is suspect for biogeographic reasons, as valid examples of disjunctions between South Africa and western North America are extremely rare. Bird migration patterns are not applicable, and one certainly cannot suggest that California and South Africa were directly connected, especially within the evolutionary history of the *J. triformis* complex. It is possible that both groups are remnants of a formerly widespread annual complex, but considering how exacting members of the *J. triformis* complex are in terms of growth requirements, it is hard to believe that they could have survived where a widespread, presumably more versatile relative perished.

3) This group consists of perennial species in the temperate parts of the Southern Hemisphere, specifically in South Africa, Australia-New Zealand, and Chile. The distances between these continents are impressively large, but within the group *J. planifolius* is apparently native in Australia, New Zealand, and South America, while the African *J. capensis* has become established in Australia. Disjunctions between Australia-New Zealand and temperate South America, and to lesser extent South Africa, are not uncommon and are represented elsewhere in the Juncaceae by *J. scheuchzerioides* Gaud. and *Rostkovia magellanica* (Lam.) Hook. f.

Further support for the unity of this group is the similarity of the seed coat patterns of *J. planifolius* and the African *J. dregeanus* (Fig. 6g-i). It was in fact the seed coat patterns that first drew the Southern Hemisphere perennials to my attention, when I was trying to find a match for the patterns in the *J. triformis* complex. Figures 6 and 7 are deliberately arranged to emphasize the similarities between the patterns of these two groups. The cogency of this point is increased by contrast with the diversity of seed coat patterns displayed by the other species that were considered as possible relatives (Figs. 10 & 11).

It is, of course, completely possible that the similarities in seed coat pattern are the result of convergence or even retention of an ancestral type. It is therefore worth noting that the three species whose seeds have this pattern also have three anthers (three to six in J. dregeanus), strictly basal leaves, no auricles, and completely plurilocular capsules, all of which are distinctive features of the J. triformis complex.

As for biogeographic difficulties, the relative unity of the Southern Hemisphere perennials in spite of the distances between South Africa, Australia-New Zealand, and South America has already been noted. An even better documented pattern of disjunction is that between temperate South America and western North America, particularly involving annuals of wet habitats in the mediterranean regions of California and Chile (e.g., Raven, 1963). The importance of the Gondwanaland break-up has been put forth as a factor in the formation of some southern taxa, such as Nothofagus, but it is unlikely to have any bearing on the distribution of modern species. Instead I find the most convincing explanation for both the antarctic and amphitropical disjunctions to be long-distance dispersal, either by birds, wind, or water (cf. Darlington, 1965; Constance, 1963; Carlquist, 1981). In any event the important point here is not how such disjunctions occurred but the fact that they do occur.

Of particular relevance are two Australia-New Zealand species. Juncus antarcticus, which grows both in the uplands and along the coast, is a dwarf, canaliculate-leaved, monocephalous perennial (Moore &

Edgar, 1976). If it grew in California it would undoubtedly have been nominated as a potential ancestor long ago. It is a close relative of J. planifolius, a larger, broader-leaved, many-headed species that also occurs in temperate South America. Outside of the Southern Hemisphere J. planifolius has been collected in Ireland, Hawaii, and Oregon. I agree with Balslev (1980) that it probably has a natural distribution in Australia, New Zealand, and South America but is recently introduced in the Northern Hemisphere. Perring (1974) believes the vector of distribution may have been birds rather than humans. Whatever the cause, the ability of J. planifolius to become widely dispersed and subsequently established is undeniable, and similar abilities would have been required in a Southern Hemisphere perennial ancestor of the J. triformis complex.

It is also worth noting that J. planifolius, along with J. caespiticus, is capable of flowering the first year. Furthermore, depauperate specimens from Valdivia, Chile, are known that are less than a decimeter tall and have narrow leaves and only 1-3 heads. Such plants were described by Steudel (1855) as J. demissus, later reduced by Buchenau (1890) to a variety of J. planifolius.

Because of the number of differences that do exist, however, such as the hard texture of the tepals and capsules, it is unlikely that J. planifolius is a plausible ancestor of the J. triformis complex. Instead it may be that both are remnants of what could have been a widely distributed ancestral group. If so, a logical explanation for the present distribution of the descendents in the New World is that the same increasingly xeric climatic conditions that favored the development of the J. triformis complex simultaneously eliminated the perennial analogues in North America and restricted their distribution in South America.

4) The western North American species *J. falcatus* E. Meyer, *J. covillei* Piper, *J. orthophyllus* Cov., *J. howellii* F. J. Hermann, and *J. regellii* Buch. form a closely knit natural group. One of the most distinctive features tying the group together is the prominent papillae that are usually present on the tepals, and often on the culms and leaves as well. The color pattern of the tepals is also a unifying feature, consisting of a green herbaceous central band edged by light brown borders and broad membranes. The heads tend to be few-flowered, and the flowers and capsules are unusually large. The group shares much of the range of the *J. triformis* complex in California and the Pacific Northwest; the coastal species *J. falcatus* also grows in Japan and Australia.

Aside from this sympatry, however, this group has little to suggest a close connection to the *J. triformis* complex. The same features that tie the group together give it a different aspect from anything in the *J. triformis* complex. In addition all the species in the group have six anthers, well-developed rhizomes and cauline leaves, and partially three-septate rather than fully trilocular capsules. Some have auricles and cataphylls as well. The seed coat patterns are also very different (Fig. 11a,c). In all, any common ancestor with the *J. triformis* complex must be very distant.

5) The *J. marginatus* group consists of *J. marginatus* s.l., *J. filipendulus*, *J. longistylus*, and *J. macrophyllus*. The group is

somewhat arbitrarily circumscribed, as both *J. longistylus* and *J. macrophyllus* are more or less transitional to the preceding group. The four species are associated here because of their firm, pale, prominently nerved tepals, which are unlike those of the western perennials. The group generally has a more eastern distribution as well. *Juncus marginatus* ranges from South Dakota and Nova Scotia south to montane Central America, and also occurs in much of temperate South America, while *J. filipendulus* is endemic to Texas and adjacent Oklahoma. *Juncus longistylus* is widespread from the eastern United States to California, and *J. macrophyllus* grows only in southern California. *Juncus marginatus* and *J. filipendulus* are three-anthered, while *J. macrophyllus* and *J. longistylus* are six-anthered. It is the first two species that I wish to concentrate on.

Besides having only three anthers, both *J. marginatus* and *J. filipendulus* resemble the *J. triformis* complex (and differ from the western North American perennials) in their more basally positioned leaves and compact small-flowered heads. Rhizomes are not as well developed, so that the plants are generally tufted. *Juncus filipendulus* is particularly interesting in its reduced size and few heads; at first glance it looks very much like a possible *J. triformis* ancestor. Furthermore, under the light microscope the seeds appear ridged like those of *J. triformis*. It is therefore not at all surprising that Engelmann (1868) associated *J. triformis* with *J. marginatus*.

On the other hand, two major differences between these two species and the *J. triformis* complex are the well-developed auricles and the incompletely three-septate capsules of the former, such that the valves curl inward after anthesis in a distinctive manner. The firm prominently nerved outer tepals are also very different. The seeds of *J. marginatus* that I examined with SEM (Fig. 11f) were obscured by a thick outer layer, but those studied by Balslev (1982) show an underlying pattern that comes closest to that of Fig. 5d. If my interpretation of the evolution of seed coat patterns is correct, the resemblance of the ridged seeds of *J. marginatus* to those of the *J. triformis* complex is the result of convergence. Finally, the short stigmas and small anthers are incompatible with my concept of an ancestor for the *J. triformis* complex, considering that the putatively archaic species are decidedly long-styled and large-anthered.

Interestingly enough, some of these drawbacks are shared with the Southern Hemisphere perennials. In fact, *J. marginatus* and *J. planifolius* have enough resemblance to suggest that they may be derived from a common ancestral complex (Southern Hemisphere?), which could also have given rise to the *J. triformis* complex. In such a case, however, the connection of *J. marginatus* to the six-anthered *J. longistylus* would need to be considered.

Two other members of subg. *Graminifolii* occur in the New World, but there is no reason to consider either one a close relative of the *J. triformis* complex. *Juncus repens*, a species of the southeastern United States and the Caribbean, is the North American perennial that comes closest to being an annual, but it is otherwise so unusual that it was once segregated as the genus *Cephaloxys* Spreng., largely because of its pseudo-free-central placentation.

The South American perennial *J. cyperoides* is if anything an even less likely relative than _J_. _repens_. Its seeds are identical to those in subg. _Septati_ (Fig. 11d).

In addition to these New World species, Buchenau (1906) included four other perennial species in the subgenus. All were eliminated from consideration, largely because of a lack of anything to recommend them, often combined with some unusual derived feature. These are _J_. _sparganifolius_ (Asia Minor: linear unilocular capsule), _J_. _ochraceus_ Buch. (Himalayan: peculiar feathery inflorescence), and the two east African six-anthered species _J_. _bachtii_ Hochst. and _J_. _engleri_ Buch.

In conclusion, in deciding which of the groups just discussed contains the closest extant relatives of the _J_. _triformis_ complex, the eastern North American perennials must remain contenders, and the South African annuals cannot be completely eliminated either. However, my own preference is for the temperate Southern Hemisphere perennials, largely on the basis of seed coat pattern, capsule structure, and lack of auricles and cauline leaves. In any event, I reject the inclusion of the _J_. _triformis_ complex in subg. _Juncinella_ and recommend that formal attempts to divide subg. _Graminifolii_ be avoided pending a more complete understanding of the entire subgenus.

Taxonomy

The Juncus triformis complex may be distinguished from all other dwarf annual rushes by a unique combination of narrow, canaliculate, strictly basal leaves lacking auricles; membranous inflorescence bracts that are shorter than the flowers; strictly solitary terminal heads or flowers (these often dimerous); four to six subequal ± acute tepals; uniseriate stamens; delicately thin-walled, rounded to retuse, completely plurilocular capsules; and thin-coated, ridged or faintly reticulate, ecaudate seeds. The complex is also geographically and phylogenetically well-defined; as such it could justifiably be dignified with a formal taxonomic rank and name. However, I refrain from doing so, primarily because the infrageneric classification of Juncus at comparable levels is itself in need of resolution.

Likewise, I am reluctant to recognize formally the subsets of the complex that I call the "triformis", "kelloggii", "bryoides", and "uncialis" groups. Nevertheless they are natural groups, and a brief description has been placed as an introduction to each group, along with a discussion where pertinent.

In order to determine how many taxa are to be delimited within the J. triformis complex, several questions must be addressed. First, how many entities are there that possess a correlated set of morphological and other characters? Second, is there a lack of intermediates that fill in and obliterate the differences (implying a lack of reproductive barriers) between these entities? Third, are the entities ecogeographically coherent? Finally, do the entities maintain their distinctiveness in mixed populations and in cultivation?

When these questions are applied to Hermann's nine species the answers for all but *J. megaspermus* are in general "yes". In addition three other taxa are distinguishable, for a total of 11 taxa in the *J. triformis* complex. These may be identified by the following key, which also includes the other two annual rushes occurring in California that may be confused with members of the complex.

KEY TO THE ANNUAL JUNCUS OF WESTERN NORTH AMERICA

1 Flowers solitary at the nodes (sometimes compact but not truly capitate), forming drepania, prophyllate; stems commonly branched; stamens commonly 6 . . . . *J. bufonius* s. l.

1 Flowers terminal, either solitary or in heads, eprophyllate; stems unbranched (except sometimes in *J. capitatus*, which is clearly capitate); stamens commonly 2--3

  2 Lower bracts foliose, clearly surpassing inflorescence; outer tepals much larger and more acuminate than inner . . . . . *J. capitatus*

  2 All bracts commonly inconspicuous, membranous; inner and outer tepals similar in size and shape

    3 Flowers clearly chasmogamous, style and anthers more than (0.5) 1 mm long; plants to 13 (17) cm tall ("triformis" group)

      4 Seeds with longitudinal ridges decidedly more distinct than horizontal cross-bars (usually obvious at 10x); culms capillary, 0.1--0.4 mm thick; capsules usually distinctly shorter than tepals; mountains and lowlands in the Sierra Nevada and San Diego County, California . . 1. *J. triformis*

4 Seeds with longitudinal and horizontal lines equally faint, even at 30x; culms stouter, (0.1) 0.2--0.8 mm thick; capsules usually subequalling the tepals; vernal pools in the Sacramento Valley, California . . . . . . 2. J. leiospermus

5 Flowers in heads . . . . 2a. var. leiospermus

5 Flowers commonly solitary . . . . . . 2b. var. ahartii

3 Flowers largely autogamous, style and anthers less than 0.5 (0.7) mm long; plants rarely to 6.5 cm tall

6 Seeds with prominent longitudinal ridges more distinct than horizontal cross-bars (at least at 30x); flowers often several per culm; bracts acute to acuminate; seeds to 0.8 mm long ("kelloggii" group)

7 Capsules usually subequalling or exceeding and similar in shade to the acute to acuminate tepals; seeds obviously ridged at least at at 30x, less than 0.55 mm long, often more than 3 per row and 9 per capsule

8 Flowers commonly trimerous; capsules usually subequalling tepals

9 Flowers (1) several per culm; capsules and tepals commonly turning dark reddish; seeds 0.4--0.55 mm long; Vancouver Island, British Columbia, to the Santa Lucia Range, California . . . 3. J. kelloggii

9 Flowers usually solitary; capsules and tepals commonly remaining pale yellow-green until seeds ripen; seeds 0.3--0.4 mm long; Santa Lucia Range to San Diego Co., and in Plumas & Lassen cos., California . . . . 4. J. luciensis

8 Flowers usually dimerous; capsules often longer than tepals; flowers often several per culm; capsules and tepals pale green or pink; seeds 0.35--0.55 mm long; widespread from central Idaho to the Sierra San Pedro Martir in Baja California del Norte . . . 5. *J. tiehmii*

7 Capsules usually distinctly shorter than and contrasting strongly with the darkly pigmented acuminate tepals, commonly pale green until the seeds ripen; seeds often only faintly ridged even at 30x, 0.5--0.8 mm long, not more than 3 per row or 9 per capsule; middle to high elevations in the Sierra Nevada of California and on Steens Mt., Oregon . . . . 6. *J. capillaris*

6 Seeds with longitudinal and horizontal lines equally faint even at 30x; flowers uniformly solitary; bracts acute to truncate or lacking; seeds less than 0.6 mm long (see also depauperate specimens of *J. capillaris*)

10 Tepals curving inward to enwrap the shorter capsule at maturity, mostly less than 2.3 mm long, lustrous; flowers mostly trimerous; culms capillary, 0.1--0.2 mm thick; widespread from Colorado and Oregon to the Sierra San Pedro Martir, Baja California del Norte ("bryoides" group) . . . . 7. *J. bryoides*

10 Tepals erect to recurved at maturity, subequalling or shorter than the capsule, often more than 2.3 mm long, not lustrous; flowers trimerous or dimerous; culms stouter, often more than 0.2 mm thick ("uncialis" group)

11 Flowers commonly trimerous; bract solitary, truncate,

completely sheathing culm; vernal pools at relatively low elevations from southern Oregon to San Diego Co., California . . . . 8. _J_. _uncialis_

11 Flowers commonly dimerous; bracts 0--2, rounded to ovate, not sheathing culm; widespread mostly at moderate to high elevations from Idaho and Oregon to the San Bernardino Mts., but missing from the Central Valley of California . . . . 9. _J_. _hemiendytus_

12 Bracts 1 or 2; culms 0.1--0.3 mm thick, not dilated directly below the flower; capsule often exceeding tepals; from the Willamette Valley of Oregon and North Coast Ranges of California inland to Idaho and Utah . . . . 9a. var. _hemiendytus_

12 Bracts absent; culms 0.2--0.5 mm. thick, dilated directly below the flower; capsule usually not exceeding tepals; Sierran-Cascade axis east to Idaho and Nevada . . . . 9b var. _abjectus_

I. THE "TRIFORMIS" GROUP

Plants 2--12 (17) cm tall; leaves 1/5--3/4 the height of the plant, the blade ca 0.2 mm wide; culms slender or stout, mostly 0.1--0.7 mm thick; bracts 2 or more, subequal, rounded to broadly lanceolate, usually ± acute; flowers frequently several (except J. leiospermus var. ahartii), commonly trimerous; tepals linear to ovate or oblong, obtuse to attenuate, usually erect to recurved; anthers (0.6) 0.9--3.2 mm long, 1--4 times the length of the filaments; style (0.5) 0.9--4 mm long; capsule globose to ellipsoid or oblong, 1/2 the length of to longer than the tepals; seeds in 2--4 rows per valve, variable; n = 16 or 18. Clayey or sandy soils. 2 spp.

The "triformis" group is the putatively ancestral annual stock containing as extant representatives J. triformis and J. leiospermus. These two species have in common relatively large size and predominantly outcrossing mode of pollination, as indicated by their long styles and large anthers, all of which I take to be primitive characters within the complex. In my understanding the common ancestor of J. triformis and J. leiospermus probably had seeds similar to those of the latter species, the "uncialis" group, and some Southern Hemisphere perennials. That J. leiospermus has itself diverged from the ancestral stock is indicated by its relatively low chromosome number of only n = 16, among the lowest in the complex.

Juncus leiospermus differs from J. triformis not only in seed sculpture and chromosome number, but also in habitat preference, geographic and altitudinal range, and a combination of subtle morphological characters such as coarser appearance and more castaneous coloration. The main range of *J. triformis* lies well to the south of *J. leiospermus*, the main exception being the outlying populations of *J. triformis* in Butte County. Although on a map these localities appear adjacent to the range of *J. leiospermus*, they are nevertheless separated both by altitude and substrate.

Some populations of *J. triformis* from higher altitudes have unusually smooth seeds (e.g., *Ertter & Strachan 3060*, Fig. 8f), but these are considerably larger than any found in *J. leiospermus* and under SEM clearly show a "triformis" rather than "leiospermus" pattern. These populations may also be distinguished from *J. leiospermus* by their slender culms, delicate flowers, and geographic range.

1. JUNCUS TRIFORMIS Engelm. (Fig. 19)

Juncus triformis (triformis L., three-formed, referring to the three varieties) Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1868. Lectotypified by S. Wats. in Appendix to King, Rep. Geol. Explor. 40th Parallel 5: 493, 1871, on J. triformis var. α stylosus (referring to the long styles) Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1869. (Orthographic variant stilosus, Buchenau in Engler, Pflanzenreich IV, 36: 258. 1906). -- LECTOTYPE: (designated by Hermann, Leafl. W. Bot. 5: 114. 1948): UNITED STATES. CALIFORNIA: Mariposa Co.: DeLong's Ranch, on Yosemite Valley Trail, in fine loose sand of bed of rivulet, dry in summer, under Quercus sonoma, elev. 4000', 10 Jun 1866, Bolander 4864 (distributed as Engelmann's Herb. Norm. 30) (Lectotype: MO!; Isolectotypes: CAS!, F!, GH!, ISC!, JEPS!, MICH!, MO!, NA!, NY!, POM!, RM!, RSA!, UC!, US!).

Juncus megaspermus (megas Gr., great, sperma Gr., seed) F. J. Hermann, Leafl. W. Bot. 5: 114. 1948. -- TYPE: UNITED STATES. CALIFORNIA: Fresno Co.: North Fork of King's River, Sierra Nevada, elev. 6200', Jul 1900, Hall & Chandler 558 (Holotype: US!; Isotypes: DS!, MICH!, MO!, NY!, UC!, US!).

Plants (2) 5--12 (17) cm tall, often turning reddish, usually drying reddish or occasionally stramineous; leaves to 5 cm long, 1/5--1/3 the height of the plant; culms to ca 60 (120), 1.8--11.5 (16.5) cm long, 0.1--0.4 mm thick; bracts 2--10, ovate to broadly lanceolate, acute,

Fig. 19. Illustrations of members of the "triformis" group. a–b, *J. triformis*. a, habit. b, flowers in head. c–d, *J. leiospermus* var. *leiospermus*. c, habit. d, flowers in head (stigmas shriveled, covered with pollen). e, *J. leiospermus* var. *ahartii*, flower.

unpigmented or castaneous, 0.7--2.4 mm long; pedicels 0.6--1.6 mm long; flowers (1) 2--8, usually trimerous, occasionally dimerous; tepals (4) 6, linear to lanceolate, (1.3) 1.9--4.5 mm long, 0.5--1.1 mm wide, the inner usually 0.2--0.8 mm longer (rarely subequal or shorter) than the outer, (acute) acuminate to attenuate, erect to recurved (rarely incurved), the central band remaining green or turning pale to dark reddish, 0.15--0.3 mm wide, the membranes unpigmented or castaneous, 0.15--0.4 mm wide; stamens (2) 3, 1.5--3.1 mm long, ca 1/2--3/4 the length of the tepals; filaments 0.4--1.1 mm long; anthers often somewhat sagittate-based, (0.6) 1--2.2 mm long, ca 1 1/4--3 times the length of the filaments; style (0.5) 0.9--3.2 mm long; stigmas (2) 3, 0.5--2.5 mm long, often reddish, exserted beyond the tepals at anthesis; capsule (globose) ovoid to ellipsoid or oblong, (2) 3-valved, somewhat tapered to slightly retuse with the base of the style usually persisting, often only 1/2 the length of (= to 2.4 mm shorter than), sometimes subequal to, rarely longer than the tepals, (1.1) 1.6--2.5 (2.9) mm long, 1.1--1.8 mm wide, usually pale to dark reddish, similar in color to the tepals; seeds to 6 (8) per row and ca 35 (50) per capsule, variable in size and shape even in the same capsule, subglobose to ellipsoid, 0.3 (in San Diego Co.) to 0.7 (in the Sierra Nevada) mm long, usually apiculate and umbonulate, from strongly ridged at 10x to lightly ridged at 30x (but then seeds at least 0.5 mm long) (Figs. 8a-b,d-f, 21); n = 18.

Most common on shallow soil of seepage at the edge of granite outcrops, less often in sandy stream beds or vernal pools, in the Sierra Nevada from Butte and El Dorado cos. to Kern Co. from 600 to 2500 m elevation, and in San Diego Co., California, from 50 to 1100 m elevation. Flowering from April to August. (Fig. 20)

Rarely growing with J. tiehmii, and possibly J. uncialis.

Engelmann defined J. triformis so as to consist of three varieties, hence the derivation of the specific epithet. The species was effectively lectotypified on the long-styled α var. stylosus by Watson (1871) in his adaptation of Engelmann's revision. Watson dropped the epithet "stylosus" and referred simply to "the typical form", contrasting it with var. brachystylus and var. uniflorus. Buchenau (1890) dismissed Watson's nomenclature with the comment "varietas α stylosus errore omissa est". Most subsequent authors except Jepson (1922, 1923) did not retain var. stylosus, using instead simply J. triformis while raising the β and γ varieties to specific rank. Jepson curiously retained the spelling "stylosus" for the long-styled variety even while accepting Buchenau's orthography "brachystilus" for a short-styled one.

Engelmann gives as the type of var. stylosus "Yosemite Valley, alt. 4,000 feet, Bolander, Hb. n. 30, fl. July". Of the several sheets at MO, one has only a packet labelled "Yosemite Valley, Calif. H. Bolander. July 8 1866" in Engelmann's hand. Another sheet bears two small pieces of paper, one white with the number "4864", the other brown with "sandy ditches, about 4000 feet, Sierras, June" in pencil and "4864","triformis var. stylosus" in ink. The handwriting in ink is Engelmann's, while that in pencil is probably Bolander's, as it matches that on the Geological Survey of California label on a sheet at UC: "Bolander 4864, Juncus triformis α stylosus, DeLong's (4000 alt.) gravelly beds, June 1866". The corners of both pieces of paper on the

Fig. 20. Distribution of species in the "triformis" group.

second MO sheet are overlain with one of Engelmann's Herb. Norm. labels, no. 30, which is absent from the "Yosemite" sheet. This printed label, which is found on a large set of duplicates normally accepted as the type collection, gives the location as DeLong's Ranch on the Yosemite Valley trail, alt. 4000', the collector as H. Bolander, and the date as 10 June 1866, comparable to the information on the Geological Survey label. According to Whitney's (1870) Yosemite Guide Book, DeLong was on DeLong Creek near White & Hatch, a common rest area at the edge of the forest at about 3000' on the old trail from Mariposa to the south entrance of Yosemite. From Whitney's map it would appear that the modern coordinates of DeLong's are T5S R20E near the corners of sections 28, 29, 32, and 33. If Bolander's altitude is correct, he either collected on the hillsides around DeLong or farther up the trail.

We have here three disparate sets of data: the Yosemite Valley label, the DeLong label, and the protologue which gives the location and date of the former but the elevation and Herb. Norm. number of the latter. The plants on the Yosemite Valley sheet have slightly paler inflorescences, wider tepals, and more mature capsules, just enough differences to support the idea that it is indeed a separate collection. Alternatively it may have been confused with a different Bolander collection from Yosemite Valley (6034) of J. capillaris. I know of no other collections of J. triformis from the intensively studied Yosemite Valley, whereas J. capillaris is well known. Furthermore the single sheet at MO is the only one with a Yosemite Valley label, while those with DeLong are numerous. Recourse to Bolander's fieldbook at GH does not help, as specific epithets are not generally included and

Juncus was collected many times.

In any event, it is apparent that at least at the time of publication Engelmann believed that all the specimens of J. triformis sent to him by Bolander represented a single collection, or at least were not worth differentiating. If, however, two separate collections are indeed involved, lectotypification is necessary. This has in effect been done by Hermann, who cited the Yosemite Valley sheet separately from the DeLong set, which he considered the type collection. Previously both Jepson (1922) and Abrams and Coville (1923) had quoted Yosemite Valley as the type locality, but this was undoubtedly a mere repetition of Engelmann's publications and was not based on a critical examination of the specimens at MO (see ICBN, Guide for the Determination of Types, 4f). I agree with Hermann that the DeLong material, which was widely distributed by Engelmann to represent the variety, is the better choice. The MO sheet with the number "4864" and the brown paper label is therefore designated the lectotype.

Juncus triformis is not a frequently collected species; I have seen fewer than 50 collections. It is nevertheless flourishing at lower elevations in the southern Sierra Nevada, at least in Fresno County where several vigorous populations occur around Shaver Lake. Other populations have been found scattered at various elevations throughout the Sierra Nevada from Butte County and Lake Tahoe south to the Greenhorn Mountains of Kern County. The species skips the Transverse Ranges and reappears in San Diego County. In all parts of its range it is most frequently found in the shallow sandy soil at the edge of seepage areas on granite outcrops. It has also been collected around vernal pools on the eastern edge of the San Joaquin Valley and around San Diego. In 1937 it was even collected inside the city limits of San Diego (Gander 7215), but the species has since then suffered the fate of most other San Diego vernal pool plants and is possibly extirpated from the area by urban development.

Juncus triformis displays a degree of morphological variation unusual for a relatively uncommon species. Coloration, shape, and relative proportions of inner tepals, outer tepals, capsules, and seeds are all variable. This diversity led Hermann to segregate *J. megaspermus*, which in Hermann's view had few slender culms, few-flowered pale heads, acute to acuminate erect bracts, and large umbonulate seeds. In contrast he limited *J. triformis* to more densely caespitose plants with stout culms, many-flowered dark heads, widely spreading blunt bracts, and small apiculate seeds. The contrasts in seed size and sculpture between the extremes of high altitude Sierran plants and those in the foothills and San Diego County are indeed impressive, but the complete intergradation is equally so. The scanning electron micrographs shown in Fig. 21a-g were selected to demonstrate both the extremes and the intermediates; all are the same magnification. Variation of seed size within populations is illustrated in Fig. 21h-j.

It is possible that the extremes were once or someday will be better separated, but unlike Hermann I do not find a sharp break presently existing between them, nor do I discern any pattern or correlation in the variability of the other characters. Many of these features, particularly those relating to size and number of parts, are strongly influenced by microhabitat and resulting vigor of the plant. There may be some genetic variation as well, as is only to be expected in a

Fig. 21. Seeds of *Juncus triformis*.

a - Ertter & Strachan 3935	Tuolumne Co., Calif.
b - Hardham 12090	Tulare Co., Calif.
c - Mason 11981b	Tuolumne Co., Calif.
d - Munz 7364	Tuolumne Co., Calif.
e - Bolander 4864; TYPE	Mariposa Co., Calif.
f - Ertter & Strachan 3521	San Diego Co., Calif.
g - Gander 7215	San Diego Co., Calif.
h - Ertter & Strachan 3935	Tuolumne Co., Calif.
i - Ertter & Strachan 3070	Fresno Co., Calif.
j - Ertter & Strachan 3538	San Diego Co., Calif.

Bar = 0.1 mm, a-g all at same magnification

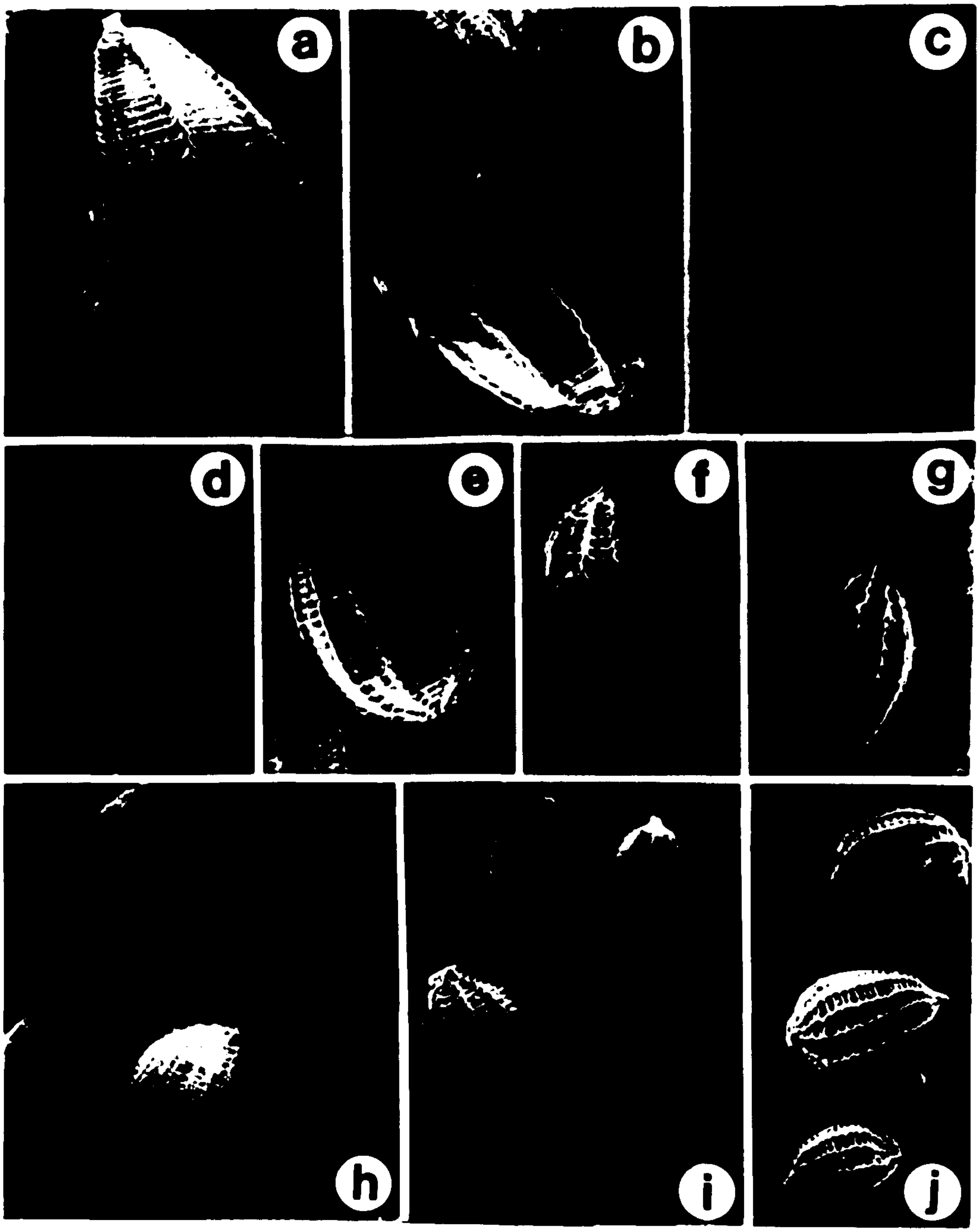

Fig. 21. Seeds of Juncus triformis. a-g, interpopulational variation. h-j, intrapopulational variation.

predominantly out-crossing species whose range has alternately contracted and expanded in response to Pleistocene and Holocene climatic fluctuations. Some of the variation may conceivably have resulted from introgression from *J. capillaris*, a short-styled species with the same chromosome number as *J. triformis* along with several of the morphological characteristics that Hermann used to distinguish *J. megaspermus*. It is worth noting that no mixed populations of *J. capillaris* and *J. triformis* are known, even though their ranges are broadly overlapping. The seeds can also be very similar as shown in Figures 8d-e and 8g-h. In any event I do not recognize *J. megaspermus*, though I realize that a statistical analysis may reveal correlations of which I am presently unaware.

Juncus triformis has been well illustrated in Buchenau (1906), Jepson (1922, 1923), and Abrams and Coville (1923). Vernacular names used in reference to this species have been Dwarf Rush (Jepson, 1923), Yosemite Dwarf Rush (Abrams & Coville, 1923), and Pacific Rush (Gorman, 1916). Long-styled Dwarf Rush is a more appropriate and definitive name.

Specimens examined: UNITED STATES. CALIFORNIA: **Butte Co.**: Little Bald Rock 15 mi NE of Oroville, *Ahart 2474* (CAS, CHSC, NY); Big Bald Rock N of Lake Oroville, *Jokerst 0830* (CHSC). **El Dorado Co.**: near Camp Agassiz above Fallen Leaf Lake, *Smiley 363a* (GH). **Fresno Co.**: Huntington Lake, 30 Jul 1938, *Campbell s.n.* (CAS); East Lake, S Fork King's River, 1-13 Jul 1899, *Eastwood s.n.* (CAS, NA); Warm Creek 0.8 mi W of Lake Edison, *Ertter & Strachan 3060* (CAS, DAV, FSC, GH, MICH, MO, NY, PH, RM, RSA, TEX, UC, UTC, WTU);

Stevenson Creek NW of Shaver Lake, *Ertter & Strachan 3064* (ASU, BKL, CAS, CHR, CPH, ISC, LE, MARY, MONTU, NA, NSMC, NSW, NY, PRE); Big Sandy Bluff between Prather & Pine Ridge, *Ertter & Strachan 3070* (CAS, NY, OS, OSC, RENO, RSA); N of Shaver Lake 1.8 mi E of Big Creek Road, *Ertter & Strachan 3942* (BRY, CAS, CHSC, DAV, F, FSC, GH, HSC, K, LA, MICH, MO, NY, OBI, PH, RM, RSA, SACT, SBBG, SD, SFSU, TEX, UC, UCSB, US, UTC, WS, WTU); 1 mi W of Alder Springs, *Howell & Barneby 29354* (CAS); between Mountain Lakes and Auberry, *Howell & Barneby 29369* (CAS); 3/4 mi S of Hume Lake, *Iverson 5* (FSC); Jose Basin SSE of Italian Bar, *Quibell & Brock 2* (FSC); S of Shaver Lake-Dinkey Creek road, *Quick 48-61* (CAS); Dora Belle campground, Shaver Lake, *Quick 52-232* (CAS); Blue Canyon near Shaver Lake-Dinkey Creek road, *Quick 52-239* (CAS). **Kern Co.**: Wagy Fire Road, Greenhorn Mts, *Hardham 3680A* (CAS). **Madera Co.**: Wahlberg Ranch 1 1/2 mi SE of South Fork, *Brock 233* (FSC, RSA); midway between Coarse Gold & Raymond, *Eastwood & Howell 5454* (CAS, GH, NA, NY, US); 1.5 mi N of Oakhurst, *Howell 41192* (CAS); Ahwahnee, *Jepson 12835a* (JEPS). **Mariposa Co.**: Yosemite Valley, 8 Jul 1866, *Bolander s.n.* (MO); Lower Mariposa Creek, 13 Apr 1902, *Congdon s.n.* (BKL); Mariposa, 15 Jun 1902, *Congdon s.n.* (US); below Mormon Bar, 19 Apr 1903, *Congdon s.n.* (MO); between Mariposa and Humbug creeks, *Hoover 3444a* (UC); Lake Merced, Yosemite Valley, *Jepson 4414a* (JEPS, US). **San Diego Co.**: Ramona, *T.S.Brandegee 3375* p.p. (GH, LL, MICH, MO, ND-G, NY, POM); 0.3 mi SW of Four Corners W of Moreno Reservoir, *Ertter & Strachan 3521* (CAS, GH, MO, NY, RSA, SD, UTC); Highland Valley Road SE of Escondido, *Ertter & Strachan 3538* (ASU, CAS, FSC, GH,

LA, MEXU, NY, OBI, RSA, SBBG, SD, TEX, US, UTC, WTU); Kearney Mesa, Gander 1189 (SD); near Ramona, Gander 3392 (SD); near county line on US 395, Gander 3706 (SD, US); S Fork Featherstone Creek, Barona Valley, Gander 4064 (SD); 6th St near Rt. 395, San Diego, Gander 7215 (SD). **Tulare Co.**: Big Meadow to Manter Meadow, Hardham 12090 p.p. (CAS); Middle Tule River, Purpus 5683 (UC). **Tuolumne Co.**: N side Sand Pit Lake, Dunn 282A (LA); 2.8 mi NE of Mather on Hetch Hetchy road, Ertter & Strachan 3935 (NY); Mather, Keck 1225 (CAS); Miguel Meadow W of Hetch Hetchy, Mason 11939 (UC); Vernon Lake trail N of Hetch Hetchy, Mason 11981b (UC); Mather, Munz 7364 (POM); N of transplant site at Mather, Ornduff 6144 (UC); Tuolumne Meadows, Smiley 739 (GH).

2. JUNCUS LEIOSPERMUS F. J. Hermann (Fig. 19)

Plants 2--12.5 cm tall, often turning reddish-brown, drying pale or dark reddish-brown; leaves to 4 cm long, 1/3--3/4 the height of the plant; culms to about 100, 1.9--11.6 cm long, (0.1) 0.2--0.7 (0.8) mm thick; bracts 2--8, round to acutely ovate, unpigmented or chestnut-brown at center, 0.7--2.4 mm long; pedicels 0.4--2.2 (2.5) mm long; flowers 1--7, commonly trimerous; tepals 6 (10), narrowly lanceolate to ovate or oblong, (1.5) 2.2--4.6 mm long, 0.5--1.4 mm wide, subequal or the inner longer, (rounded) obtuse to acuminate, ± erect and straight, the central band remaining green or turning reddish, 0.15--0.4 mm wide, often poorly differentiated from the 0.15--0.6 mm wide membranes; stamens 3 (5), 1.7--3.7 mm long, ca 3/4 the length of the tepals; filaments 0.5--1.4 mm long; anthers 0.9--3.2 mm long, 1--4 times the length of the filaments; style (0.9) 1.4--4 mm long; stigmas 3 (4), 1.3--4 mm long, white, exserted beyond the tepals at anthesis; capsule globose to ellipsoid or oblong, 3 (5)-valved, terete, acute to ± retuse with ca 0.5--1 mm of persistant style, to 0.5 mm longer or shorter than the tepals, (1.5) 2--4.5 mm long, 1--3 mm wide, light to dark reddish or maroon, not contrasting strongly with the tepals; seeds to 12 per row and ca 150 per capsule, ovoid, 0.35--0.45 mm long, usually umbonulate, sometimes apiculate as well, smooth or faintly reticulate at 30x (Fig. 6a-c).

Edges of vernal pools in the Sacramento Valley of California, from 50 to 500 m elevation. Flowering in April and May. (Fig. 20)

Often growing with *J. uncialis* and *J. capitatus*.

Hermann (1948) based *Juncus leiospermus* solely on a 1916 collection by Heller that had been widely distributed as *J. uncialis*. He separated it from *J. triformis* primarily on the basis of its relatively smooth unridged seeds, combined with the stouter culms, subequal inner and outer tepals, and longer capsules with firmer walls. Although Hermann limited the application of the name to the type collection, two older collections that Hermann annotated and cited as *J. triformis* (*Baker & Nutting s.n.* and *Hoover 2270*) also have the characteristic smooth seeds.

Apparently no other plants referable to *J. leiospermus* were collected until the passage in 1973 of the Endangered Species Act (Public Law 93-205). The species was listed as threatened in the U.S. Fish and Wildlife Service's (1975) review of threatened and endangered plants, while the California rare plant inventory (Powell, 1974) treated it as possibly extinct, "last reported in 1916". Ayensu & DeFilipps (1978) also listed *J. leiospermus* as possibly extinct, the only other species of rush similarly listed being *J. pervetus* Fern. from Massachusetts.

By 1980 the second edition of the California rare plant inventory (Smith et al., 1980) had reclassified the species as rare and endangered because of recently located populations. Many of these new populations were discovered by Lowell Ahart, who was studying the flora of the Peter Ahart Ranch in the Sierran foothills of Butte County. In 1973 and 1974 he found a few plants of the *J. triformis* complex which had solitary flowers, long styles, and smooth seeds. John Thomas Howell of the California Academy of Sciences annotated the three collections as "*J. leiospermus*", "cf. *J. leiospermus*", and "Not J. leiospermus--perhaps a n. sp.!"

In 1978, a particularly excellent year for vernal pool plants because of abundant spring rains, Ahart and Howell joined a California Botanical Club field trip to Table Mountain north of Oroville. According to Ahart (pers. comm.), the group was searching for Downingia when Howell asked Ahart to look for Pilularia americana. Instead Ahart found more plants referable to J. leiospermus, this time with several flowers per head. After examining this new collection, Howell wrote to Ahart (30 Apr 1978):

> Your plant from the ranch collected 4/15/73 is not the same [as that from Table Mountain] since it is uniformly 1-flowered to each peduncle, but it is related . . . I still think it may be a new species!

Howell requested additional material with more mature seeds from both places. After this request was fulfilled Howell again wrote to Ahart (7 May 1978):

> Today I studied them and now I am more puzzled than ever since the Table Mountain plant which I had hoped (!) would be leiospermus has seeds with both longitudinal and transverse lines that tend to mark off rectangular areas. The plant from Peter Ahart Ranch has seeds with much finer, more numerous transverse lines, longitudinal lines not evident. Of course we are dealing with 2 different species (which is obvious from habit and inflorescence) but now I'm at a loss to put a name on either of them! I wouldn't mind having 1 new species but 2 looks suspicious!

Scanning electron microscopy of the seeds from these and other populations, most newly discovered, has revealed that a certain amount of variation in seed coat patterns exists among and within the populations, but it is far outweighed by the overall similarity of the basic honey-comb pattern (Fig. 6a-c). The more numerous transverse lines that Howell noted are indeed present on seeds from the Ahart ranch, but they also characterize seeds from some several-flowered populations (such as Hoover 2270) and can even occur on parts of seeds which otherwise have a looser network. Consequently I am treating all the long-styled, smooth-seeded plants as *J. leiospermus*.

I do agree with Howell that the plants from the Ahart ranch deserve taxonomic recognition at some level. Ahart's notes on the plants in the field over several years, and my own observations on the few plants successfully grown from seed, indicate that the one-flowered condition is stable and in all probability largely genetically determined. However, the condition is not absolute in that additional flowers can develop on particularly vigorous plants, as occurred in the exceptionally wet spring of 1978. Consequently, I am treating them as varieties of one species: *J. leiospermus* var. *leiospermus* and *J. leiospermus* var. *ahartii*. I believe this arrangement best emphasizes both their similarities and their differences.

Juncus leiospermus faces the same threats as do most other Sacramento Valley vernal pool endemics, as this area has been largely converted to agricultural land. Fortunately agricultural activities do not immediately destroy well-established populations of either variety. The type of *J. leiospermus* was collected in a grain field, and according to Ahart the vernal pools where var. *ahartii* grows were once plowed but later allowed to revert because of the shallow, stony soil.

Neither variety has previously been illustrated. The California Rare Plant Project has given the vernacular name Red Bluff Rush to var. *leiospermus*. I would suggest that this be amended to Red Bluff Dwarf Rush. The logical vernacular name for var. *ahartii* is, of course, Ahart's Dwarf Rush.

2a. JUNCUS LEIOSPERMUS F. J. Hermann var. LEIOSPERMUS

Juncus leiospermus (leios Gr., smooth, + sperma Gr., seed) F. J. Hermann, Leafl. W. Bot. 5: 113. 1948. -- TYPE: United States. California: Tehama Co.: low places in grain field, treeless plain, red clay soil, 2 miles S of Red Bluff, 20 Apr 1916, Heller 12326 (Holotype: US!; Isotypes: CAS!, DS!, F!, GH!, MICH!, MO!, NY!, WTU!)

Plants 2--12.5 cm tall; leaves to 4 cm long; culms to ca 20, 2--11.8 cm long, (0.15) 0.2--0.7 (0.8) mm thick; bracts 2--8, round to acutely ovate, usually chestnut-brown at center, 1--2.4 mm long; pedicels 0.5--2.2 (2.5) mm long; flowers (1) 2--7; tepals narrowly to broadly lanceolate, (1.5) 2.2--4.6 mm long, 0.5--1.1 mm wide, the inner usually longer than the outer by up to 0.7 mm, (obtuse) acute to acuminate, the central band usually turning reddish with darker red, brown, or black at the sides and apex, 0.15--0.4 mm wide, often poorly differentiated from the concolorous adjacent portions of the 0.15--0.4 mm wide membranes; capsule ovoid to ellipsoid or oblong, ± retuse, to 0.5 mm shorter (less often to 0.3 mm longer) than the tepals, (1.6) 2--3.8 mm long, 1--2.5 mm wide; n = 16.

Uncommon at the edges of vernal pools, these often on basalt, in the northern Sacramento Valley of California, from 280 to 500 m elevation.

Specimens examined: UNITED STATES. CALIFORNIA: Butte Co.: Table Mt. N of Oroville, Ahart 1644, 1645 (CHSC, Ahart), Ahart 1702, 1703 (CAS, UC, Ahart herb.), Ahart 1854 (CAS, NY, Ahart herb.), Ertter et al. (DAV, F, GH, MICH, MO, NY, OBI, PH, PRE, RM, RSA, SACT, SD, TEX, UCSB, US, UTC, WTU), Hardham 21566 (CAS), Howell 52836 (CAS), Jokerst 0481 (CHSC), Jokerst 0594 (CHSC); 1/2 mi N of Kunkle Reservoir 2 1/2 mi SE of Paradise, Ahart 1857 (UC, Ahart herb.), Ahart 1895 (CAS, NY, UC, Ahart herb.); Cohasset Ridge 1/4 mi E of Cohasset Hwy, Jokerst 0699 (CHSC). **Shasta Co.**: Goose Valley, 26 May 1894, Baker & Nutting s.n. (UC); Millville Plains, Holland 289 (Holland herb.), Holland 500 (Holland herb.); 4 mi E of Redding, Hoover 2270 (LL, OBI, UC). **Tehama Co.**: 15.5 mi N of Red Bluff, 25 Apr 1979, Ahart s.n. (CAS, UC); 16 mi W of Red Bluff, 25 Apr 1979, Ahart s.n. (NY,, UC).

2b. JUNCUS LEIOSPERMUS F. J. Hermann var. AHARTII Ertter

Plants 2--6 cm tall; leaves to 3 cm long; culms to ca 100, 1.9--5.5 cm long, (0.1) 0.2--0.4 mm thick; bracts 2 (3), rounded to obtusely ovate, usually unpigmented, sometimes brown at base, 0.7--1.3 mm long; pedicels 0.4--0.9 mm long; flowers 1 (2); tepals lanceolate to ovate or oblong, (1.9) 2.4--3.6 mm long, 0.6--1.4 mm wide, subequal, the inner to 0.3 mm longer than the outer, (rounded) obtuse to acuminate, the central band remaining green with a black apex or turning reddish, 0.2--0.4 mm wide, the membranes chestnut brown or maroon at least above though often unpigmented adjacent to the midrib, 0.2--0.6 mm wide; capsule globose to ovoid to ellipsoid, acute to retuse, subequal to (sometimes to 0.5 mm longer than, rarely to 0.5 mm shorter than) the tepals, (1.5) 2.5--4.5 mm long, 1.5--3 mm wide;

TYPE: UNITED STATES. CALIFORNIA: Butte Co.: ca 2 mi N and 1/2 mi E of Honcut, wet bare red soil around edges of large vernal pool in farmed field, elev 50 m, 1 May 1982, Ahart 3402 (Holotype: NY!; Isotypes: CAS!, GH!, HSC!, MO!, RSA!, SD!, US!).

Very rare, restricted to edges of vernal pools on the east side of the Sacramento Valley in Butte Co., possibly also in Calaveras Co., California, from 50 to 100 m elevation.

With the plants from Butte County I am tentatively including in var. ahartii a collection of immature plants from Calaveras County. These plants show no indications of developing more than one flower per culm and are in most other respects comparable to Ahart's plants. Mature plants are needed for verification, however. If the Calaveras population does prove to be var. ahartii, it is to be hoped that additional populations may be found between Calaveras and Butte counties.

I am pleased to name this variety so appropriately after its discoverer and patron, Mr. Lowell Ahart, an amateur botanist with a keen eye for small plants. To quote Howell (pers. comm.), "When we lost Ernest Twisselmann a great void came into our botanical life--but how wonderfully Lowell Ahart has filled it!"

Specimens examined: UNITED STATES. CALIFORNIA: **Butte Co.**: Peter Ahart Ranch 1 1/2 mi N & 2 mi E of Honcut, Ahart 192 (CAS, CHSC), Ahart 423 (CAS, Ahart herb.), 5 Jun 1974 Ahart s.n. (CAS), Ahart 1620 (CAS, Ahart herb.), 13 Apr 1978, Ahart s.n. (CAS), Ahart 1648 (CAS, Ahart herb.), Ahart 1661 (UC, Ahart herb.), Ahart 1692 (CAS, CHSC, UC, Ahart herb.), Ahart 2238 (CAS, F, MICH, NY, PH, SACT, TEX, UTC), 14 May 1982, Ahart 3434 (CAS, NY, to be distributed), 6 May 1980, Ertter et al. (NY). **Calaveras Co.**: 2 mi N of Jenny Lind, Breedlove 4726A p.p. (CAS).

II. THE "KELLOGGII" GROUP

Plants mostly 1--5 cm tall; leaves 1/3--2/3 the height of the plant, the blades usually ca 0.2 mm wide; culms relatively slender, mostly ca 0.1--0.2 mm thick; bracts 2 or more, subequal, ovate to lanceolate, usually acute; flowers frequently several (except J. luciensis), trimerous or dimerous; tepals narrowly lanceolate, acute to acuminate, erect to recurved; anthers 0.3--0.5 mm long, 1/3 to 1/2 the length of the filaments; style to 0.5 mm long; capsule globose to narrowly oblong, 1/2 the length of the to longer than the tepals; seeds usually in ca two rows per valve, to 50 per capsule, the longitudinal ridges more distinct and spaced farther apart than the transverse lines; n = 16--18. Most frequent on sandy soils. 4 spp.

Engelmann (1868) spread three of the four species in the "kelloggii" group that were available to him among J. kelloggii, J. triformis var. brachystylus, and J. triformis var. uniflorus, this last variety also including J. bryoides and the "uncialis" group. Not until Hermann's revision was it generally accepted that the ridged seeds were a critical defining character, leading Hermann to group all distinctly ridged-seeded short-styled species as J. kelloggii and to separate the lightly-ridged J. capillaris as a distinct species.

My own investigations have revealed two additional taxa contained within J. kelloggii that I am naming J. luciensis and J. tiehmii. The first is set off from J. kelloggii by its predominantly solitary flowers (see Fig. 2), the second by its predominantly dimerous flowers (see Fig. 3). Although these and other defining characters (such as coloration, seed shape and pattern, and shape and proportion of tepals and capsules) are of such a nature as to require the terms "predominantly", "most", "usually", etc., they are nevertheless well-correlated and obvious enough so that most plants can be quickly and unambiguously sorted, even when they occur (as they frequently do) in mixed populations. The defining characters are maintained in cultivation and are consistent throughout the range of each species. The ranges themselves are reasonably well-defined, and certain edaphic and ecological correlations also exist.

There are chromosomal differences between the four species as well. However, Juncus may eventually prove to have diffuse centromeres like those of Luzula, and if so chromosome numbers could change without necessarily affecting meiotic pairing. In any event, the chromosome differences probably are no more effective as reproductive barriers than are the distances between populations or the predominance of self-pollination.

The "kelloggii" group lends itself well to evolutionary speculations. One possibility is that the three species J. kelloggii, J. capillaris, and J. tiehmii evolved independently from the polymorphic J. triformis. Juncus kelloggii has retained the most similarities to J. triformis and could have arisen from it on the east side of the Sacramento Valley, where the present ranges of the two species approach one another. Ancestral J. kelloggii would then have spread to the other side of the Central Valley, most likely during the moister periods of the Pleistocene when suitable habitats would have been more abundant. If the hypsithermal interval did indeed occur, fringe populations would have been isolated and reduced to the point where they were susceptible to genetic drift and rapid selection; this could have led to the development of J. luciensis from J. kelloggii in the Santa Lucia Mountains.

Some of the defining characters of J. tiehmii and J. capillaris can be found in some populations of J. triformis: in particular the dimerous flowers of J. tiehmii and the large seeds of J. capillaris. It is interesting that the core of the range of J. tiehmii in southern California is flanked by the two parts of the present-day range of J. triformis, as if a chunk had been removed from a once more continuous range and converted into something else. Additional support for the idea that J. tiehmii evolved directly from J. triformis independently of J. kelloggii is the almost complete absence of dimerous flowers in the latter, while they occasionally occur in J. triformis.

Dimerous flowers are also common in J. capillaris, but here the seeds and range indicate a relation to and possible origin from the expression of J. triformis that Hermann segregated as J. megaspermus, which likewise occurs in the Sierra Nevada and has small capsules and large smooth seeds. It is possible that such plants could have been directly ancestral to J. capillaris, perhaps near Yosemite National Park, the present heart of the range of J. capillaris.

By this first reconstruction, at least three of the species would not have a common ancestor short of J. triformis. A contrasting possibility is that all four species arose from a common short-styled ancestor. Radiation from this ancestor could have been similar to that outlined in the first scenario, except that similarities to different expressions of J. triformis would have resulted from parallel development, possibly in response to the same unknown selection pressures, or from hybridization and introgression.

3. JUNCUS KELLOGGII Engelm. (Fig. 22)

Juncus kelloggii (Albert Kellogg, 1813-1887, premier Californian botanist & co-founder of the California Academy of Sciences) Engelm., Trans. Acad. Sci. St. Louis 2: 494. 1868. TYPE: UNITED STATES. CALIFORNIA: San Francisco, "Turk St., N. Border of Park", sandy soil, 22 Apr 1866, Kellogg s.n. (Holotype: MO!; Isotypes: GH!, US!. Photograph of US isotype at DS!, MICH!).

Juncus triformis Engelm. var. β brachystylus (brachus Gr., short, stylos Gr., style) Engelm., Trans. Acad. Sci. St. Louis 2: 492. 1868. (Orthographic variant brachystilus, Buchenau in Engler, Pflanzenreich IV, 36: 258. 1906). -- J. brachystylus (Engelm.) Piper, Contr. U.S. Natl. Herb. 11: 181. 1906. -- TYPE: UNITED STATES. CALIFORNIA: Mendocino Co.: near Ukiah, dry plains, "hard clayey soil, overflowed in winter", May 1866, Bolander 4646 (= Herb. Norm. 31) (Holotype: MO!; Isotypes: CAS!, DS!, F!, GH!, ISC!, JEPS!, MICH!, MO!, NA!, NY!, RM!, RSA!, UC!, US!).

Plants 1--5.5 (6.5) cm tall (the tall extreme in the North Coast Ranges), usually soon turning reddish, drying reddish; leaves to 2.5 cm long, the blade 0.1--0.4 mm wide; culms to ca 100, (0.1) 0.5--5 (6) cm long, 0.1--0.3 mm thick, turning dark reddish below; bracts 2--5, ovate to lanceolate, obtuse to more frequently acute, reddish-brown at least below, occasionally with a herbaceous midrib, 1--2.5 mm long, rarely tepaloid and to 4 mm long; pedicels 0.3--0.6 mm long; flowers 1--4, usually trimerous; tepals (4) 6, (1.5) 2.0--3.2 mm long, 0.4--1

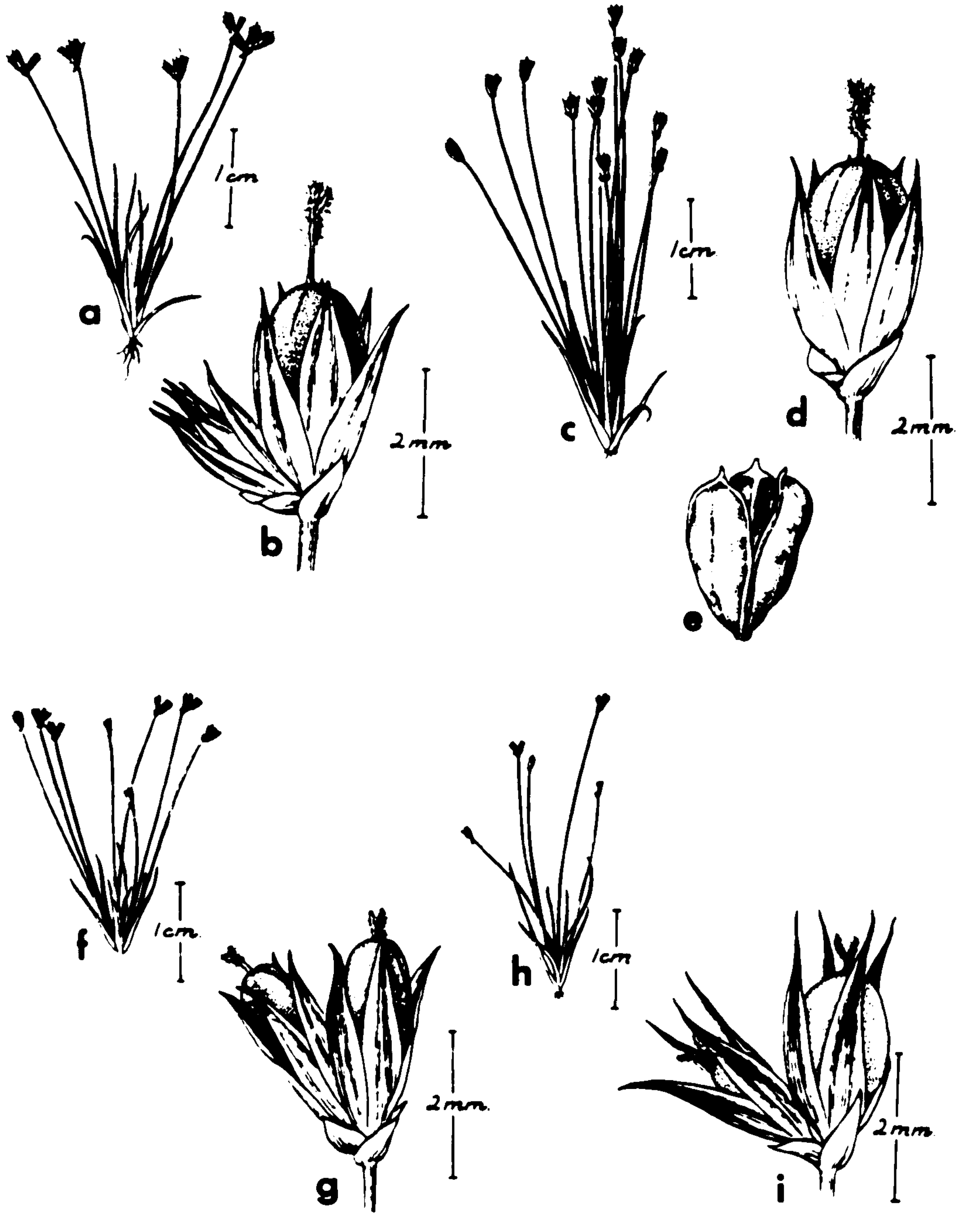

Fig. 22. Illustrations of species in the "kelloggii" group. a-b, *J. kelloggii*. a, habit. b, flowers in head. c-e, *J. luciensis*. c, habit. d, flower. e, opened capsule. f–g, *J. tiehmii*. f, habit. g, flowers in head. h–i, *J. capillaris*. h, habit. i, flowers in head.

mm wide, the inner to 0.2 mm longer or 0.4 mm shorter than the outer, acute to acuminate, the central band soon turning dark reddish-brown to black at least distally, 0.1--0.4 mm wide, the membranes unpigmented, 0.1--0.3 mm wide; stamens (2) 3, 1.2--1.8 mm long, ca 2/3--3/4 the length of the tepals; filaments 0.7--1.3 mm long; anthers 0.3--0.5 mm long, 1/3--1/2 the length of the filaments; style 0.2--0.5 mm long; stigmas (2) 3, 0.4--1.3 mm long, pinkish, the tips just barely exserted beyond the tepals at anthesis; capsule obovoid to elliptic, (2) 3-valved, terete, rounded to retuse, subequalling the tepals, differing by up to 0.3 mm, (1.5) 1.8--2.9 mm long, 1.2--1.6 mm wide, usually soon turning dark reddish, similar in color to the tepals; seeds to 7 per row and ca 50 per capsule, ovoid, 0.4--0.55 mm long, apiculate, the longitudinal ridges distinct at 10x (Fig. 9a-d); n = 17.

Sandy to clayey damp soils in a variety of habitats, such as vernal pools, seepage areas, and low spots in fields and meadows, from Vancouver Island in British Columbia, Canada, and the Columbia River in Washington and Oregon, south through the Willamette Valley, Oregon, to the foothills of the North Coast Ranges and the Sacramento Valley, to Monterey Co., California, from near sea level to 800 m elevation. Flowering from April to July. (Fig. 23)

Often growing with J. hemiendytus, sometimes with J. luciensis, less often with J. uncialis, rarely with J. bryoides, possibly with J. tiehmii and J. leiospermus.

Engelmann based Juncus kelloggii on a single set of diminutive plants collected in San Francisco in 1866. A hand-written label on the holotype at MO specifies "Turk St., N. Border of Park", 22 April 1866.

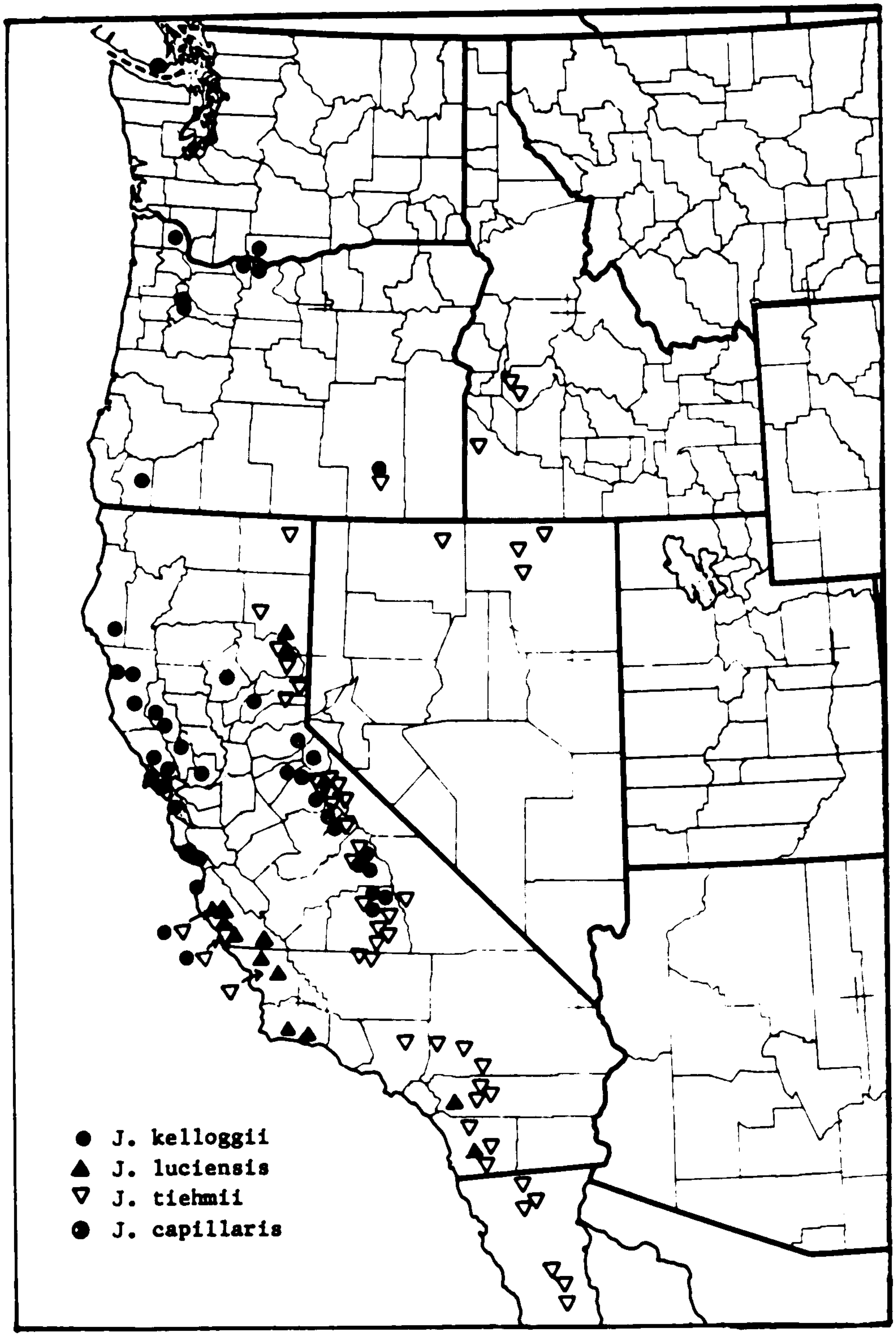

Fig. 23. Distribution of species in the "kelloggii" group.

The label on the US isotype gives the additional information "Found with fragmentary specimens of Bolelia, received with Dr. Brewer's California collections." According to Howell et al. (1958), "The 'Park' probably refers to present-day Jefferson Square, not to Golden Gate Park".

Engelmann described the plants thus:

> Nearly allied to the last [J. triformis] but differing in many striking points, this little species represents a glomerule of a few lines in diameter, pushing out in all directions a number of thread-like leaves; these are 6-10 lines long, and 1/4-1/2 line wide; the short terminal heads are quite loose, the flowers on such distinct peduncles that one would be inclined to consider them as single, if the pair of bracts were not wanting which always surround the base of single flowers in this genus; the lowest axils of a branch often produce longer peduncles, elevated above the glomerate mass, but shorter than the leaves, and bearing small heads, usually of two flowers only. Flowers pale green and whitish, and, especially the capsule, of very delicate structure, . . . seeds . . . similar to the seeds of the last species [J. triformis], but with much more prominent dark ribs, 4 of which are visible on a side.

Engelmann felt that Kellogg's specimens were unusual enough to stand as a distinct species, even though he grouped all other specimens of the J. triformis complex at his disposal (representing six of the species recognized in the present treatment) into one polymorphic species. Many subsequent floristic workers accepted the name, specifically Bolander (1870), Watson (1871, 1880), and Behr (1888). Katharine Brandegee, ever on the lookout for signs of irresponsible splitting, included J. kelloggii in her 1892 San Francisco flora with the comment "Not since collected. Perhaps only a form of J. triformis." Jepson (1901) included J. uncialis in his flora of western middle California, but oddly enough made no mention of Kellogg's collection, J. kelloggii, or even of J. triformis.

Buchenau (1890) had at his disposal two small plants of Kellogg's collection sent to him by Engelmann. He found them difficult to dissect because of their poor preservation, which he thought might have been due to their being in a humid vasculum too long. The seeds of his specimens, though immature, still showed the longitudinal ridges characteristic of J. triformis and the other members of the "kelloggii" complex. Buchenau apparently did not place much importance on this feature, however, as in 1880 he placed J. triformis and J. kelloggii in different subgroups of his subg. Graminifolii, the first associated with some South African annuals and the second standing alone with the suggestion that it might better be transferred to subg. Poiophylli. He further elaborated in 1890:

> J. Kelloggi ist eine merkwürdige Pflanze, deren Naturgeschichte ich nicht genügend aufklären kann. Sie gleicht auf den ersten Blick ganz dem J. bufonius L. var. pumilio Griseb. und bildet wie dieser niedrige hellgrüne Polsterchen; auch die rinnigen Laubblätter ohne Öhrchen an den Blattscheiden, sowie die breit-dünnhäutigen Perigonblätter erinnern an J. bufonius. Indessen glaube ich doch, dass Dr. Engelmann's Auffassung des Blütenstandes als eines Köpfchens mit Ansätzen von einigen sehr armblütigen seitlichen Köpfchen richtig ist, und dass demnach die Pflanze zu der Untergattung: J. graminifolii, nicht zu den poiophyllis [sic] gehört.
>
> [J. kelloggii is a remarkable plant whose natural history I cannot satisfactorily clarify. It appears at first glance very much like J. bufonius L. var. pumilio Griseb. and like this forms low light-green cushions. The channeled leaves lacking auricles on the sheaths, as well as the broadly membraned tepals, are also reminiscent of J. bufonius. Nevertheless I believe that Dr. Engelmann's interpretation of the inflorescence as a head with the attachment of several few-flowered lateral heads is correct, and that therefore the plants belong to the subgenus J. graminifolii and not to the poiophylli.]

In spite of this reasoning, in his 1906 treatment of the family Buchenau reversed his conclusion without explanation and reduced J. kelloggii to a synonym of J. bufonius var. pumilo, where it remained in obscurity until re-established by Hermann 42 years later.

Hermann recognized, as had Brandegee (1892) earlier, the close alliance between Kellogg's plants and J. triformis. He treated the collection as an aberrant population of J. triformis var. brachystylus with the following discussion:

> Engelmann described his Juncus Kelloggii from a single freak specimen, overlooking its identity with his J. triformis var. brachystylus which is the normal form of the species. The type of J. Kelloggii, which is apparently either an extreme ecotype or pathologically abnormal, consists of a sessile glomerule of fruiting heads 11 mm. wide and 7 mm. high, the leaves (1.5 cm. long) therefore surpassing the inflorescence.

In contrast, Hoover (1970), like Buchenau (1906), believed that the type of J. kelloggii had little or nothing to do var. brachystylus and was instead "a very young, and perhaps somewhat abnormal, plant of J. bufonius". However, Hoover apparently had only the original description and a photograph of the US isotype to go on.

I have seen seven plants of this collection; five at MO, one at US, and one at GH.[1] A photograph of two plants from the holotype appears in Fig. 24, while Fig. 25 is a diagram of a small particularly loose plant from the packet on the MO sheet. Engelmann's description of these plants as "glomerules" is very apt. Except for a few protruding culms

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[1] Kellogg undoubtedly had specimens at the California Academy of Sciences, but these must have been destroyed when the herbarium burned during the San Francisco earthquake and fire of 1906. Similarly Buchenau's specimens were likely lost in the destruction of the Berlin herbarium during World War II.

Fig. 24. Photograph of two plants from holotype of J. kelloggii.

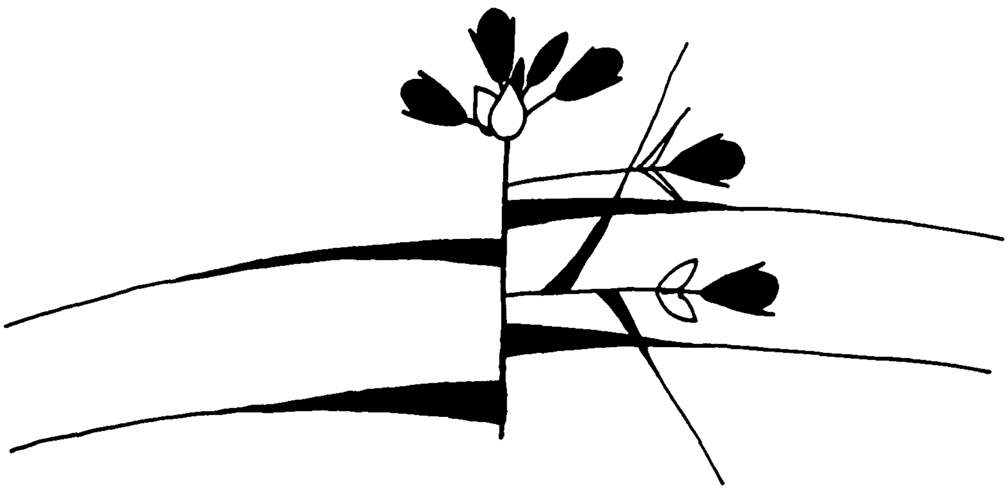

Fig. 25. Representation of unusually loose plant in packet of holotype of J. kelloggii.

on the GH plant, it is impossible to analyze the arrangement of leaves, stems, bracts, and sessile flowers without destroying the specimens. Flowers are trimerous and paired at least on the protruding culms. Tepals are pale green and capsules are also light-colored. Styles are less than 1 mm long, stigmas are less than 1.5 mm long, and anthers are shorter than the filaments. Seeds are distinctly longitudinally ridged (Fig. 9a), clearly indicating that the affinities of the specimens are with the J. triformis complex and not with J. bufonius (Fig. 11i). Within the J. triformis complex, the ridged seeds and short styles connect Kellogg's collection with the "kelloggii" group.

It is significant that it was not a single plant (as Hermann implied) but a whole population that possessed the distinctive morphology (it is safe to say that if "normal" plants had been present Kellogg would have collected them as well). Furthermore no members of the J. triformis complex have ever been collected in San Francisco proper since, even before the area became so heavily urbanized. Brandegee (1892) noted its absence in her San Francisco flora, and Howell et al. (1958) did not find any after collecting over 5200 specimens in the city. Nevertheless, the possibility cannot be ruled out that something so small, so inconspicuous, and so (apparently) insignificant could be repeatedly overlooked or mistaken for J. bufonius.

Kellogg's collection is unique; no other specimens come close to matching it. Similarly sessile specimens of J. bryoides and J. hemiendytus can occasionally be found, but this feature is otherwise essentially lacking from the "kelloggii" group. His specimens may therefore actually represent the sole collection of a fifth species in the "kelloggii" group endemic to San Francisco and now likely extinct.

Several other plants are endemic to San Francisco, such as *Clarkia franciscana* Lewis & Raven, *Arctostaphylos franciscana* Eastwood, and *Grindelia maritima* (Greene) Steyermark.

Unless similar plants are rediscovered in San Francisco, however, I will refrain from recognizing Kellogg's collection as a distinct taxon. There are simply too many other possibilities. The plants may indeed have been, as Hermann suggested, "pathologically abnormal". The population may have been the last remnant of one of the other species in San Francisco, stunted and ultimately extirpated by increasing urbanization. It may have been accidentally introduced and inadequately adapted to the San Francisco environment. Even if the aberration were shown to have a genetic basis I would be reluctant to resurrect a distinct species based solely on a single 1866 collection and what little information is available.

The trimerous pale green flowers of Kellogg's collection are reminiscent of *J. luciensis*, which ranges not far to the south of San Francisco, but the paired flowers link it instead to the taxon containing the type of *J. triformis* var. *brachystylus*. Although this taxon has not otherwise been found in San Francisco proper, it occurs both to the north and the south, including just across the Golden Gate in Marin County. One population from the Monterey Peninsula (Tracy 16592) even has the same pale green coloration of Kellogg's collection and *J. luciensis*. The ovoid distinctly apiculate seeds are also comparable (Fig. 9a-c). I therefore agree with Hermann that the type of *J. kelloggii* is best associated with the taxon containing the type of var. *brachystylus*. At the time of Hermann's revision the name *J. kelloggii* could have been dismissed from consideration of priority because of

Art. 71 of the ICBN. This provision, which allowed the dismissal of names based on monstrosities, was deleted by the Leningrad Congress in 1975. Juncus kelloggii antedates the combination J. brachystylus and must therefore be used as the name of the species containing the types of both, exactly as Hermann used it in 1948.

As with typification of the α and γ varieties of J. triformis, that of the β var. brachystylus is not without problems. Engelmann (1868) gave as locations of var. β, "Ukiah, Mendocino county, the same [Bolander], Hb. n. 31, fl. May, also 'Fort Bragg, near the coast' (1-3-flowered)". Among the seven sheets annotated as this variety by Engelmann in his herbarium at MO are three with the Herb. Norm. 31 label: "On hard clayey soil, overflowed in winter, near Ukiah, Mendocino county, California, with Pinus ponderosa, Quercus Wislizeni, Arctostachylos glauca. H. Bolander leg. Apr., Mai. 1866." On one of these sheets the label is pasted over the corner of two pieces of brown paper with "4646" and "Ukiah, Mendocino Co, sterile soil, May", apparently written by Bolander. This sheet is the logical holotype, analogous to the lectotype of the α var. stylosus. No month is specified on the Geological Survey specimen of Bolander 4646 at UC, nor on a duplicate at JEPS.

The appearance of both April and May as collection dates on the Herb. Norm. 31 label indicates that Bolander may have passed through Ukiah in both months, and either he or Engelmann subsequently combined the two or more collections. If so, it is virtually impossible to tell which plants were collected in April and which in May, and all are probably from the same general area anyway. I am therefore accepting all as isotypes, including a Bolander specimen at GH which gives the location simply as "Mendocino" and bears an Engelmann label with "26‘" written over "31".

Three other sheets at MO have hand-written labels with the collection data "Ukiah, California, April 1866, H. Bolander". One has floral dissections, including one of a flower with seven tepals and a four-valved capsule. As the date of April contradicts the published type date, and none is accompanied by a *Herb. Norm. 31* label, these sheets have not been accepted as isotypes.

A final sheet from Engelmann's herbarium has written on it in his hand "wet sandy places, Long Valley, Mendocino County, California", collected in 6 May 1866 as *Bolander 4691*. In all likelihood this represents a separate collection, from the same place and time as *Bolander 4691b*, the lectotype of the γ var. *uniflorus* (distributed as *Herb. Norm. 32*). One sheet of *Bolander 4691b* at MO contains intermixed a few plants of var. *brachystylus*, presumably from *Bolander 4691*, verifying that the two were indeed found growing together (see discussion of *J. hemiendytus* var. *hemiendytus* for more information on this collection).

I have seen only a GH specimen of the other collection mentioned by Engelmann, "Fort Bragg, near the coast", although Hermann cited another at UC. The specimen is an 1866 Bolander collection with an Engelmann label. Hermann annotated it as *J. capillaris* and cited it as such in his revision. Although when immature these two taxa are similar, and the seeds of the collection are not ripe, the uniformly trimerous flowers and dark capsules of the Fort Bragg plants are more reminiscent of *J. kelloggii*, and Fort Bragg is far outside the geographical and altitudinal ranges that otherwise characterize *J.*

capillaris. In any event, in my understanding Engelmann cited the Fort Bragg collection merely as an additional specimen seen, and lectotypification of the variety is not necessary.

In general, J. kelloggii prefers or tolerates more clayey soils than do the other species in the J. kelloggii group (for example, see the type collection of J. triformis var. brachystylus). For this reason it often enters into mixed populations with J. hemiendytus var. hemiendytus (e.g., Hall 543), which also prefers clayey soils. It is a component of the vernal pool flora, one of California's most endangered ecosystems.

Only older scattered collections exist from the California North Coast, the Willamette Valley in Oregon, and along the lower Columbia River on the Oregon-Washington border. The species has also been collected once on the southern tip of Vancouver Island in British Columbia, the only record of the complex in Canada (Scoggan, 1978). Elihu Hall's widely distributed 1871 collection (543) of mixed J. kelloggii and J. hemiendytus var. hemiendytus from near Salem, Oregon, was "collected in immense abundance" (Gray, 1872). Gorman (1916) listed J. triformis (probably J. kelloggii) as a component of the flora in the vicinity of Portland, Oregon; from the several locations mentioned ("Roadsides East Portland, Albina, etc."), the plant was apparently not rare at that time. In spite of these earlier indications of abundance, I know of no collections from anywhere outside of California since 1930, when Peck found some near Aumsville not far from Portland. I fear that even if J. kelloggii has not been extirpated from Oregon, Washington, and Canada, its numbers have been seriously reduced by agriculture and urbanization, especially in the Willamette Valley.

Hall 543 is the model for Fig. 119: A-L in Buchenau (1906). The illustration of *J. brachystylus* in Abrams and Coville (1923) is probably also meant to be of this species. It is the member of the "kelloggii" group that is illustrated in *Vascular Plants of the Pacific Northwest* (Hitchcock, 1969). [The illustration in the Intermountain Flora (Cronquist, 1977) labelled *J. kelloggii* is actually *J. hemiendytus* var. *hemiendytus*, which was treated as a synonym of *J. kelloggii*.]

Vernacular names applied to the taxon are Short-Styled Dwarf Rush (Abrams & Coville, 1923), Short-Stemmed Dwarf Rush (Peck, 1941), Kellogg's Dwarf Rush (Peck, 1961) and Kellogg's Rush (Hitchcock & Cronquist, 1973). The most appropriate is Kellogg's Dwarf Rush.

Specimens examined: UNITED STATES. CALIFORNIA: no location, *Kellogg & Harford 1039* (MO, NY, US). **Butte Co.**: 3 mi S of Paradise, *Ahart 2240, 2263* (CAS, NY). **Humboldt Co.**: Fort Seward, *Tracy 4431* (JEPS, UC, WTU). **Lake Co.**: 8.9 mi S of Kelseyville, *Baker 10418* p.p (RSA), *Howell 18033* (GH, MO, MICH); Lakeport, May 1884, *Brandegee s.n.* (UC, US); Manning Flat NW of Lower Lake, *Ornduff 6154* (JEPS, UC). **Marin Co.**: Mt. Tamalpais, Kent Trail, *Howell 16354* (NA); Lagunitas Meadows, *Howell 20785* (NA, SFSU); Rocky Ridge Fire Trail, Mt. Tamalpais, *Howell 21980* (NY, UC); Point Reyes Peninsula, *Howell 25337* (DS, MO, RSA, UC); northern Nat'l Seashore beach area, *Howell 42549* (NA, OSC, RSA, TEX). **Mendocino Co.**: Ukiah, Apr 1866, *Bolander s.n.* (MO); Long Valley, *Bolander 4691* (MO); Fort Bragg, *Bolander s.n.* (GH). **Monterey Co.**: Jolon, *Eastwood 4136* p.p.

(CAS); The Indians heliport near Memorial Park campground, Ertter & Strachan 3369 (BRY, FSC, MICH, NY, OBI, OSC, SACT, SBBG, SD, US, WS), 3379 (LA, NY, UC, UCSB), 3381 (CAS, NY); Milpitas Road near The Indians & Road 8, Ertter & Strachan 3395 (CAS, HSC, NY, RSA); Jolon, Hardham 3100 p.p. (RSA, UCSB); The Indians, Santa Lucia Mts., Hardham 5342B p.p. (CAS, RSA), Hardham 5433 p.p. (RSA); mouth of Los Burros Creek, Hardham 5573 p.p. (RSA); Monterey Peninsula near Cypress Point, Tracy 16592 (UC). **Napa Co.**: 3-4 mi E of Angwin's, Tracy 1534a (JEPS, UC, US, UTC), Tracy 1555 (UC, US). **Nevada Co.**: Cherokee Diggings W of North Columbia, True & Howell 6601 (CAS). **Santa Cruz Co.**: NW of Boulder Creek between Jamison Creek Road & Rt. 236, Ertter & Strachan 3333 (CAS, CHR, CHSC, GH, MO, NY, ORE, PRE, RM, SFSU, TEX, UTC, WTU); Jamison Creek Road ca 3 mi N of Boulder Creek, Hesse 599 (DS, NA, UC, WTU); Graham Hills between Felton & Santa Cruz, Hesse 614 (JEPS); Locatelli Ranch near Eagle Rock, Hesse 3342 (DS). **Solano Co.**: near Suisan City, May 1886, Greene s.n. (US); summit of Bennett Valley Road, Eastwood & Howell 7866 (GH, MICH, POM); hills E of Agua Caliente, Howell 17925 (MICH). **OREGON**: **Columbia Co.**: St. Helens, May 1887, Howell s.n. (F, MO, NA, NY, ORE, UC, US); St. Helens, Suksdorf 2524 (US, WS). **Hood River Co.**: Hood River, Henderson 812 (ORE, US?). **Josephine Co.**: Grant's Pass, Henderson 1029 (OSC); New Hope Road, Henderson 13033 (ORE); Grant's Pass, 24 Jun 1884, Howell s.n. p.p. (DS, GH, MICH, NY, ORE, US, WTU). **Marion Co.**: Salem to Silverton, Hall 543 p.p. (F, GH, LA, MICH, MO, NA, NY, PH, RM, UC, US); 3 mi S of Salem, Nelson 4863 (MICH, PH); pool margins 2 mi S of Salem, Peck 13718 (WILLU); damp fields near

Aumsville, Peck 16292 (DS, WILLU). **WASHINGTON: Klickitat Co.:** Columbia River, 19 Jun 1882, Suksdorf 427 (F, MICH, NY, PH, UC, WS), near Bingen, May 1885, Suksdorf s.n. (WS); damp bare ground near Bingen, Suksdorf 2571 (BKL, DS, ISC, MICH, NY, ORE, US, WS). **CANADA. BRITISH COLUMBIA:** Oak Bay, Vancouver Island, 17 Jun 1902, Diehl s.n. (POM); Vancouver Island, 18 Jun 1902, Diehl s.n. (POM).

4. JUNCUS LUCIENSIS Ertter (Fig. 22)

Plants 0.7--5.5 (6.5) cm tall, remaining green or only slowly turning pale reddish, drying stramineous; leaves to 1.5 cm long, the blade 0.1--0.3 (0.4) mm wide; culms to ca 160, 0.4--5.2 (6.2) cm long, 0.1--0.3 mm thick, remaining green; bracts 2, rounded to acutely ovate, usually unpigmented, sometimes brown-flecked or reddish at the base, 0.4--1.6 mm long; pedicels 0.3--0.6 mm long; flowers 1 (2), usually trimerous; tepals (4) 6, 1.6--3 (4.2) mm long, 0.4--0.6 mm wide, subequal or differing by up to 0.2 mm (in the Santa Ynez Mts. the long-acuminate outer tepals are up to 1 mm longer than the inner), acute to acuminate, the central band dark-tipped but otherwise remaining pale yellow-green and only slowly turning reddish, 0.1--0.2 mm wide, the membranes unpigmented, 0.1--0.2 mm wide; stamens 2--3, 0.9--1.4 mm long, ca 1/2 the length of the tepals; filaments 0.6--0.9 mm long; anthers 0.3--0.5 mm long, 1/3--1/2 the length of the filaments; style 0.2--0.4 mm long; stigmas (2) 3, 0.6--1.1 mm long, white, just barely exserted beyond the tepals at anthesis; capsule obovoid to elliptic, (2) 3-valved, terete, rounded to slightly retuse, subequal to the tepals, differing by up to 0.3 mm, 1.3--2.9 mm long, 0.9--1.6 mm wide, remaining pale greenish or turning light reddish above as the seeds ripen, similar in color to the tepals; seeds to 8 per row and ca 40 per capsule, globose-ovoid, 0.3--0.4 mm long, sometimes apiculate, the longitudinal ridges very distinct at 10x (Fig. 9e,f); n = 16.

TYPE: UNITED STATES. CALIFORNIA: Monterey Co.: S side of sandstone knoll near Road 8 between The Indians turnoff and N Fork San Antonio River, shallow wet soil at edge of seepage on exposed sandstone in oak woodland, with moss, Isoetes, annual grasses, and annual forbs, T21S R5E Sec 16/21, 540 m, 12 May 1980, Ertter & Strachan 3366 (Holotype: NY!; Isotypes: CAS!, CPH!, DAV!, F!, GH!, ISC!, K!, LA!, LE!, MICH!, MO!, NY!, OBI!, P!, PH!, RM!, RSA!, SBBG!, SD!, TEX!, UC!, UTC!, WTU!).

Wet sandy soils of seepage areas on sandstone, depressions in meadows, vernal pools, and streamsides, most common in the Santa Lucia Mts. of Monterey and San Luis Obispo cos., south through the Transverse and Peninsular ranges to San Diego Co.; also in the Diamond Mts. of Plumas and Lassen cos., California, from 300 to 1860 m elevation. Flowering from April to July. (Fig. 23)

Often growing with J. kelloggii, less often with J. tiehmii, occasionally with J. uncialis and J. hemiendytus, rarely with J. bryoides.

Juncus luciensis is the member of the "kelloggii" group centered in the Central Coast Ranges, in particular the Santa Lucia Range. Alice Eastwood, the first person to do extensive collecting in the area (Hoover, 1970), found the plants growing near Jolon in 1915. She identified her collection of immature plants as Eleocharis sp.; Hermann annotated and cited it as J. capillaris. Howell (1963) disagreed with Hermann's identification and placed it in J. kelloggii. The seeds are not ripe, but the coloration, bracts, and number of flowers indicate that the collection is a mixture of J. luciensis and J. kelloggii. Since 1915, Clare B. Hardham and others have made additional collections of this species near Jolon and other localities in Monterey, San Luis Obispo, and Santa Barbara counties. In my field work I had no trouble finding several populations in this region, one of which is used as the type.

A second small isolated center for the species is in the Diamond Range of Plumas and Lassen county, over 250 miles northeast of the nearest known population in the Santa Lucia Range. It was here that A. A. Heller and P. B. Kennedy made the first collection of the species, in July 1907, on the road from Beckwourth to Genesee in Red Clover Valley [= Clover Valley]. These specimens were widely distributed as J. uncialis. A 1974 collection by Howell from near Janesville, identified as J. hemiendytus, also proves to belong to J. luciensis. I found the species in several places in Squaw Valley and along Dixie Creek to the north of Clover Valley in 1980.

Single collections of J. luciensis have also been made from isolated stations in Riverside and San Diego counties. Perhaps additional populations are waiting to be discovered that will link these stations in the Peninsular Ranges to those in the Central Coast Ranges, or extend the range south into Baja California.

Although there may be some subtle morphological differences among these populations, none appears to be taxonomically significant. Cytogenetic data do not contradict the concept that they are all the same species; counts from Monterey, Plumas, and San Diego counties are all n = 16.

Hermann noted the one-flowered condition that characterizes J. luciensis on specimens in his herbarium (now at MICH) but made no mention of this feature in his revision. Howell (1963) also noted the predominance of solitary flowers in the Santa Lucia material. An annotation in Hoover's hand on Eastwood & Howell 4198 (CAS) from Estrella notes "Scapes all one-flowered -- wholly unlike some spms. labelled J. Kelloggii. Diverges even more widely from type photograph & original description." In his flora of San Luis Obispo County, Hoover (1970) elaborated:

> Our plants differ from typical J. brachystylus as found elsewhere in having the peduncles nearly always one-flowered. In appearance they closely match J. uncialis, from which they are distinguished by their different seeds.

Juncus luciensis does indeed strongly resemble J. uncialis and has often been misidentified as such, though the seeds and bracts are reliably different. Even the chromosome numbers are the same. Moreover, the two species occasionally occur in mixed populations, such as at Jolon and Estrella. It is not inconceivable that J. luciensis is more closely related to J. uncialis than suggested here; it may be an alternate ancestor of J. uncialis or a hybrid derivative of J. uncialis and one of the other ridge-seeded species. If J. luciensis is of hybrid origin, it is even possible that the isolated populations arose from independent hybrid events.

The epithet "luciensis" refers to the Santa Lucia Range, where the species is most abundant. I also chose the name because of its quasi-anagrammatical similarity to "uncialis".

The species has not been illustrated before. I recommend Santa Lucia Dwarf Rush as a vernacular name.

Specimens examined: UNITED STATES. CALIFORNIA: Lassen Co.:

Elysian Valley (near Janesville), Howell 50538 (CAS). **Monterey Co.:** Jolon, Eastwood 4136 p.p. (CAS); Del Venturi Road 4 mi S of San Antonio River, Ertter & Strachan 3365 (ASU, BRY, CAS, ISC, MICH, NY, PH); The Indians heliport near Memorial Park campground, Ertter & Strachan 3369a (BRY,NY), 3378 (CAS, MARY, NY, OSC), 3380 (MO, NMSC, NY, OS, RSA, WIS); junction Milpitas Road and Road 8 near The Indians, Ertter & Strachan 3394 (CAS, CHR, NSW, NY, ORE, PRE, RSA, TEX, WS); Jolon, Hardham 3100 p.p. (RSA, UCSB); Hanging Valley, Arroyo Seco, Hardham 4519 p.p. (MICH); The Indians, Santa Lucia Mts, Hardham 5242B p.p., 5433 p.p. (CAS, RSA); mouth of Los Burros Creek, Hardham 5573 p.p. (RSA); Los Burros Creek near Nacimiento, Hardham 5896A (RSA, SBBG); Hog Canyon - Parkfield Road, 2.1 mi E of Pass, Hardham 10707 p.p. (RSA). **Plumas Co.:** 5 airmi S of Milford on Beckwourth road, Ertter & Strachan 3881 (NY); W end Dixie Valley E of Beckwourth - Milford Road, Ertter & Strachan 3885 (CAS, CHSC, NY, RENO, TEX); Dixie Creek 3/4 mi E of Beckwourth - Milford Road, Ertter & Strachan 3886 (NY, UC, UTC); Red Clover Valley, Heller & Kennedy 8695 (DAV, DS, F, GH, ISC, MO, NESH, NY, PH, US, WTU). **Riverside Co.:** Mesa de Burro 3 mi W of Murrieta, Lathrop 5451 (RSA). **San Diego Co.:** Hwy S1 1 mi S of road to Cuyamaca, Ertter & Strachan 3529 (ASU, BKL, CAS, FSC, HSC, MEXU, MO, MONTU, NA, NY, RSA, SACT, SD, SFSU, TEX, UTC, WTU). **San Luis Obispo Co.:** near Estrella, Eastwood & Howell 4198 (CAS, F, GH, MICH, NY, US); 3 mi N of La Panza Guard Station, Ertter & Strachan 3396 (CAS, NY); Navajo Creek 2.5 mi S of Hwy 58, La Panza Range, Ertter & Strachan 3398 (NY); Creston Road 6 mi E of Paso Robles, Hardham 3094 (SBBG, UCSB); 18 mi E of Creston on La

Panza Road, Hardham 8472 p.p. (OBI, OSC, RSA). **Santa Barbara Co.:** top of Big Pine Grade, San Rafael Mts., Piehl 63586 p.p. (SBBG); Camino Cielo between Camp Goddard & Brush Peak, Santa Ynez Mts, 16 May 1956, Pollard s.n. (US); ca 3 mi W of San Marcos Pass, Camino Cielo, 22 Jun 1956, Pollard s.n. (RSA, US).

5. JUNCUS TIEHMII Ertter (Fig. 22)

Plants 0.8--5 (6.3) cm tall, becoming pink-tinged, drying pinkish-stramineous; leaves to 2.2 (2.5) cm long, the blade 0.1--0.3 mm wide; culms to ca 150, 0.5--4.8 (6) cm long, 0.1--0.2 mm thick, often turning pinkish; bracts 2--4 (8), ovate, acute, unpigmented, sometimes reddish-brown at base, 0.6--1.5 mm long, rarely tepaloid to 2 mm long; pedicels 0.1--0.5 mm long; flowers 1--4 (7), usually dimerous; tepals 4 (6), (1) 1.9--2.9 mm long, 0.4--0.6 mm wide, subequal, rarely differing by 0.1 mm, acute or acuminate, the central band pale green with pinkish edges and dark tip, sometimes darker reddish throughout, 0.1--0.3 mm wide, the membranes unpigmented, 0.1--0.2 mm wide; stamens 2 (3), 0.8--1.2 mm long, ca 1/2 (3/4 in small flowers) the length of the tepals; filaments 0.5--0.8 mm long; anthers 0.3--0.4 mm long, ca 1/2 the length of the filaments; style to 0.3 mm long; stigmas 2 (3), 0.2--0.7 mm long, white, shorter than the tepals at anthesis; capsule (obovoid) elliptic to narrowly oblong, 2 (3)-valved, usually flattened, rounded to slightly retuse, usually equalling or exceeding the tepals by up to 0.9 mm, rarely to 0.3 mm shorter, (1.5) 1.9--2.9 mm long, 1.1--1.5 mm wide, usually pink-tinged, similar in shade to the tepals; seeds to 7 per row and ca 30 per dimerous capsule, oblong to ovoid, (0.3) 0.35--0.55 mm long, often both apiculate and umbonulate, the longitudinal ridges distinct at 30x, the fainter transverse lines closely spaced (Fig. 9g-i); *n* = 17.

TYPE: UNITED STATES. CALIFORNIA: Riverside Co.: Kenworthy Forest Station on Rt. 74 in Hemet Valley, moist sand of large wash in sagebrush & ponderosa pine zone, San Jacinto Mts., elev. ca 750 m, T6N R3E Sec 25/36, 26 Jun 1979, Ertter & Strachan 2971 (Holotype: NY!; Isotypes: CAS!, F!, GH!, K!, MICH!, MO!, OSC!, PH!, RSA!, SD!, TEX!, UC!, US!, UTC!, WTU).

Most common on bare moist granitic sand along streams and near seepage areas at the edges of outcrops, and in low places in meadows, sometimes almost carpeting the ground, from southeastern Idaho to the mountains of the northern Great Basin in Nevada and Oregon, south through the Sierra Nevada, west in the Transverse and Central Coast ranges to the Santa Lucia Mts. in California, and south in the Peninsular Ranges to the Sierra San Pedro Mártir of Baja California del Norte, Mexico, from 300 to 3090 m elev. Flowering from May to September. (Fig. 23)

Often growing with J. bryoides, J. capillaris, and J. hemiendytus var. hemiendytus, less often with J. luciensis, J. hemiendytus var. abjectus, and J. triformis.

Although J. tiehmii has not previously been recognized as a distinct taxon it is the most abundant species in the "kelloggii" group. It was also one of the first members of the J. triformis complex to be collected, as it was the main component of Bolander's Tuolumne River collection in 1866. This collection was cited by Engelmann as a paratype of J. triformis var. uniflorus. The species was next collected in 1884 in Baja California as Orcutt 1166, although Orcutt (1885) did not list any annual rushes besides J. bufonius in his checklist of southern Californian and Baja Californian plants. Brandegee (1893) also found J. tiehmii in Baja California and noted the dimerous nature of his collection. After it had been gathered many times in southern California the species was again collected in Baja California, this time by Wiggins (1944), who, like Brandegee, noted the dimerous flowers:

> Collections of this species from southern California have been labeled variously as *J. brachystylus*, *J. triformis*, and *J. brachystylus* f. *uniflora* [sic]. The flowers consistently have four perianth-segments and two stamens, these opposite the outer pair of perianth-segments. The general aspect of the plant is similar to that of *J. uncialis* Greene, but that species has six perianth-segments and three stamens.

Hermann did not realize that several discrete entities were included within his own circumscription of *J. kelloggii* and dismissed Wiggins' observation:

> The dimerous condition prevails, it is true, in *Wiggins No. 9884* but even in this some of the flowers are trimerous, and in other collections six sepals and three stamens predominate. In both *J. capillaris* and *J. hemiendytus* the dimerous condition is much more frequent than in *J. Kelloggii*.

In his *Flora of Baja California*, Wiggins (1980) separated *J. kelloggii* from *J. bufonius* by the former's three stamens, four to six tepals, and capsules nearly as long as the perianth. He apparently included the normally trimerous *J. bryoides* in his circumscription of *J. kelloggii*, as it was not mentioned in his flora although it has much the same range as *J. tiehmii* in Baja California.

Juncus tiehmii is one of the most successful species in the *J. triformis* complex, competing for this position with *J. bryoides* and *J. hemiendytus*. It ranges from Idaho to Baja California, primarily at middle elevations. Especially in the southern part of its range it can be so abundant as to carpet the ground. At the higher elevations where it overlaps the range of *J. capillaris* it tends to be rather spindly, few-culmed and single-flowered. This suggests that at such elevations J. tiehmii is at its ecological limits.

North of the Sierra Nevada, J. tiehmii has been collected sporadically along the northern edges of the Intermountain Region and on the Idaho Batholith. How much this sparsity reflects its true distribution is difficult to determine, especially since most collections of the complex in this area have been made only since 1974.

Many of the most valuable finds in Nevada have been made by Arnold (Jerry) Tiehm of Reno, whose special interest in these and other inconspicuous wetland plants has provided many new records from Nevada. He introduced me to J. tiehmii and later made the first collection of the species in Nevada, far from California in Elko County. It is a pleasure to recognize Tiehm's contributions tc the oft-neglected semi-aquatics of the Intermountain Region by naming this species in his honor.

The species has not previously been illustrated. A logical vernacular name would be Tiehm's Dwarf Rush.

Representative specimens: UNITED STATES. CALIFORNIA: Fresno Co.: Bear Creek, Raven 7142a (CAS). Inyo Co.: Cottonwood Creek, Howell 25453 (CAS, NA, US). Kern Co.: 2.4 mi W of Wofford, Greenhorn Range, Howell & True 45586 (CAS). Lassen Co.: 8.3 mi WNW of Harvey Valley Ranger Station, Simontacchi 815a p.p. (UC). Los Angeles Co.: S Fork Big Rock Creek ca 1/2 mi N of South Fork Campground, Ertter & Strachan 3439 (CAS, LA, NSMC, NY, OBI, RSA, SBBG, SD, TEX, UTC). Madera Co.: near Garnet Lake, Howell 16651 p.p. (CAS, GH, US). Modoc Co.: Surprise, Eastwood & Howell 8111

(MICH). **Mono Co.**: 4.5 mi E of Sonora Pass on Hwy 108, Ertter & Strachan 3028 (ASU, CPH, G, HSC, LE, MARY, MEXU, MONTU, NY, P, RM); Honeymoon Flat Campground SW of Bridgeport, Ertter & Strachan 3694 (CAS, NY, RENO, UTC); 4.8 mi E of Sonora Pass Summit, Ertter & Strachan 3896a (CAS, CHR, NSW, NY, OSC, PRE, UTC); 4.4 mi SE of Sonora Pass, Ertter & Strachan 3897a (NY); ca 3 mi SE of Sonora Pass, Ertter & Strachan 3921 (NY); Sonora Bridge Campground, Ertter & Strachan 3924 (CAS, NY); W Fork Warren Creek ca 1 1/4 mi N of Tioga Pass Road, Reveal 536 (US). **Monterey Co.**: Hanging Valley, Arroyo Seco, Santa Lucia Mts., Hardham 4519 p.p. (MICH); Los Burros Creek near Nacimiento, Hardham 5899 p.p. (RSA, SBBG). **Nevada Co.**: S shore Donner Lake, True & Howell 7284 (CAS). **Plumas Co.**: Dixie Creek 3/4 mi E of Milford - Beckwourth Road, Ertter & Strachan 3887 (CAS, NY). **Riverside Co.**: Black Mt. turnoff on Banning - Idyllwild Road, Ertter & Strachan 2987 (ASU, BRY, CAS, CHR, CPH, LE, MARY, MEXU, NSW, NY, OBI, OS, PRE, RM, RSA); Santa Rosa Mt. Road ca 2 mi S of Hwy 74, Ertter & Strachan 3481 (CAS, ISC, LA, NY, RSA, SD, UC); 2 me SE of Ansa, Munz 10862 (POM, SACT). **San Bernardino Co.**: 1 mi N of Holcomb Valley N of Big Bear Lake, Ertter & Strachan 2995 (ASU, BRY, CAS, GH, LA, MICH, NY, PRE, RSA, SACT, SBBG, SD); 2 mi S of Hwy 18 on Forest Road 2N10, Ertter & Strachan 3005 (CAS, FSC, LA, MO, NY, RSA, TEX, UC, UTC); Stockton Flats E of Mt San Antonio, Haid s.n. (RSA). **San Diego Co.**: Rt S1 2.6 mi N of I-8, E of Pine Valley, Ertter & Strachan 3517 (CAS, DAV, F, NY, PH, RSA, SD, WS); Corral Canyon Road 1 1/2 mi SW of Boulder Creek, Ertter & Strachan 3518 (BRY, CAS, NY, SD, TEX, US, WTU); Corral Canyon Road 4.4 mi W of Buckman Spring Road, *Ertter & Strachan 3520* (BRY, CAS, MO, NY, SD, UTC); 1 mi NE of Corral Canyon Forest Station, *Ertter & Strachan 3522* (CAS, NY, RSA, SD); Rt S1 1 mi S of road to Cuyamaca, *Ertter & Strachan 3530* (CAS, NY, RSA, SD, UTC); Hwy S6 0.7 mi S of Palomar Forest Station, *Ertter & Strachan 3541* (CAS, NY, SD); Campo, *Parish 10815* (DS, UC). **San Luis Obispo Co.**: 1.5 mi N of La Panza Guard Station, *Ertter & Strachan 3397* (CAS, DAV, MICH, NY, OBI, RSA, SFSU, UCSB, US); Wilson Canyon Creek ca 1 mi S of Middle Branch Huerhuero Creek, *Hoover 9907* (OBI). **Sierra Co.**: Dog Valley, Mitchell Canyon Road E of Reno, *Ertter et al. 2766* (BRY, CAS, GH, NY, ORE, RENO, RSA, TEX, UTC, WTU). **Tulare Co.**: Cliff Creek between Deer Creek & Pinto Lake, *Howell 17328* p.p. (CAS, MICH); ridge between Cannell Meadow & Pine Flat, Kern Plateau, *Twisselmann 11351* (CAS, RSA, SBBG). **Tuolumne Co.**: upper Tuolumne River [probably near Soda Springs], *Bolander s.n.* p.p. (MO); Dog Lake trail E of Lembert Dome, *Ertter & Strachan 3927* (CAS, MO, NY, SACT, UTC); Glen Aulin Trail, Tuolumne Meadows, *Ertter & Strachan 3928a* (BKL, BRY, CAS, CHSC, DAV, FSC, NY, RSA, SD, TEX, UC). **IDAHO: Boise Co.**: Grayback Gulch SW of Idaho City, *Ertter & Strachan 3786* (CAS, CIC, ID, NY, UTC, WS, WTU); 0.5 mi SW of Centerville, *Ertter & Strachan 3796* (BRY, CAS, CIC, GH, ID, MO, NY, ORE, OSC, RENO, RSA, TEX, UTC, WS, WTU). **Owyhee Co.**: headwaters of Jordan Creek E of Silver City, *Ertter et al. 4484* (CAS, CIC, ID, NY, RENO, UTC). NEVADA: **Elko Co.**: Jack Creek Road 1.9 mi E of Hwy 11/226, *Ertter & Strachan 3776* (CIC, NY, UTC); Chipman Meadow E of Mountain City, *Ertter et al. 4289* (BRY, CAS, CIC, NY, ORE, RENO, RSA, UTC, WTU); 5.5 airmi NNW of Saval Ranch, Independence Mts, *Tiehm 5392*

(NY). **Humboldt Co.**: 1 1/2 airmi SE of Canyon Creek Summit, Santa Rosa Mts., Ertter 4322 (CAS, CIC, NY, UTC). **OREGON: Harney Co.**: Steins Mts opposite Devine Ranch [sic], Leiberg 2525 p.p. (MICH, ORE, US). **MEXICO. BAJA CALIFORNIA DEL NORTE**: San Pedro Mártir, 16 May 1893, Brandegee s.n. (GH); Mesa los Alacranes, Sierra Juárez, Moran 27464 (DAV, NY, SD); Hansen's Ranch, Orcutt 1166 (GH, MO, NA); trail between San Felipe Desert & Los Emes, S part Sierra San Pedro Mártir, Wiggins 9884 (DS, MICH, UC, US).

6. JUNCUS CAPILLARIS F. J. Hermann (Fig. 22)

Juncus capillaris (*capillus* L., hair, alluding to the slender culms) F. J. Hermann, Leafl. W. Bot. 5: 116. 1948. -- TYPE: UNITED STATES. CALIFORNIA: Mariposa Co.: from spray of Yosemite Falls, Jun 1881, *C. C. Parry [343?]* (Holotype: US!; Isotypes: DS!, F!, ISC!, MO!, NY!).

Plants 0.9--5.5 (6) cm tall, often turning dark reddish-brown or black, drying reddish-brown; *leaves* to 2.2 cm long, the blade 0.1--0.3 mm wide; *culms* to 22, 0.7--5.2 (5.7) cm long, 0.1--0.3 mm thick, often turning dark red or black irregularly; *bracts* 2--4, ovate, acute, usually reddish-brown below, (0.4) 0.8--1.5 mm long, rarely tepaloid to 2.5 mm long; *pedicels* 0.3--0.6 mm long; *flowers* 1--2 (3), dimerous or trimerous; *tepals* 4--6, (1.3) 1.8--2.8 mm long, 0.4--0.6 mm wide, the inner to 0.5 mm longer than the outer especially at anthesis, acuminate to attenuate, the central band dark reddish to black at least at the top and sides, sometimes almost throughout, 0.1--0.3 mm wide but often appearing wider because of the concolorous adjacent portion of the otherwise unpigmented 0.1--0.2 mm wide membranes; *stamens* 2--3, 0.9--1.5 mm long, ca 1/2--3/4 the length of the tepals; *filaments* 0.6--1.1 mm long; *anthers* 0.3--0.4 mm long, ca 1/2 the length of the filaments; *style* 0.1--0.3 mm long; *stigmas* 2--3, 0.4--0.6 mm long, the tips exserted at anthesis; *capsule* globose to obovoid (ellipsoid), 2--3-valved, flattened to terete, rounded to slightly retuse, usually 1/2 to 3/4 the length of (= to 0.9 mm shorter than), sometimes equalling, rarely slightly longer than (by 0.2 mm) the tepals,

(1) 1.2--2 (2.2) mm long, 1.1--1.5 mm wide, most often remaining pale greenish with a dark red or black apex, sometimes gradually turning dark red throughout as the seeds ripen; seeds 2--3 per row and 4--9 per capsule, elliptic-ovoid, 0.5--0.8 mm long, often both slightly apiculate and umbonulate, the longitudinal ridges sometimes only barely visible even at 30x but still more distinct than the transverse lines (Fig. 8c,g-i); n = 18.

Moist bare flats, short turf, and mossy areas in meadows, stream banks, and seepage areas on rock outcrops, mostly on granitic substrates, in the Sierra Nevada of California from El Dorado to Tulare cos., disjunct on Steens Mt. in Oregon, from 1200 to 3200 m elevation. Flowering from May to August. (Fig. 23)

Usually growing with J. tiehmii, sometimes also with J. bryoides and both varieties of J. hemiendytus.

The earliest collection of the J. triformis complex, Hillebrand 2333 from the Calaveras Big Trees in 1863, was a specimen of J. capillaris that Engelmann cited as a syntype of J. triformis var. uniflorus (= J. hemiendytus). Engelmann had a second collection of J. capillaris available for study, namely Bolander 6034 from Yosemite Valley, but he did not cite it in his revision and distributed it only as J. triformis without a variety or Herb. Norm. number.

Several herbaria have specimens of J. capillaris collected by Parry in 1881 from Yosemite. Hermann specified the US sheet ("Yosemite, 1881" with 1021 added in pencil) as the holotype and a MO sheet ("Yosemite, Calif., 1881") as an isotype. Another MO sheet ("from spray of Yosemite Falls, June 1881") was cited as a separate collection. A DS sheet ("Yosemite Valley, June 1881", ex herb. Parish), although annotated by Hermann as part of the type collection, was nevertheless cited as yet a third collection, along with a third MO sheet that I have not seen. An F sheet ("Yosemite, 1881, No. 343") was annotated and cited as *J. uncialis*.The specimens on all of these sheets look alike, consisting of mature, slender-stemmed, predominantly uniflorous and dimerous plants nestled in a mat of moss. According to Ewan and Ewan (1981), "Many of [Parry's] labels are exasperatingly inadequate; without coll. nos., or specific place, hence it is difficult to trace authentic material and dupl. of types". Nevertheless I find no reason to treat these sheets as other than duplicates of a single collection, especially since only one ("Yosemite, 1881") was retained in Parry's herbarium at ISC. The most complete information is that on the MO sheet that would have been sent to Engelmann; the other labels are essentially abbreviations. The only conflict is between the numbers on the F and US sheets, and that on the latter is an addition in pencil.

This species has been erroneously ascribed to the Coast Ranges because of confusion with other members of the "kelloggii" group. Hermann cited as *J. capillaris* an immature Bolander collection from Fort Bragg in Mendocino County, a paratype of *J. triformis* var. *brachystylus*. This specimen is morphologically and geographically at home in *J. kelloggii*, (= *J. triformis* var. *brachystylus*). Another collection cited by Hermann as *J. capillaris*, *Eastwood 4136* from Jolon in Monterey County, was re-identified by Howell (1963) as *J. kelloggii*, and is in fact a mixture of *J. kelloggii* and *J. luciensis*. Hoover (1970) attempted to reinstate *J. capillaris* in the Coast Ranges based on his *9907* from San Luis Obispo County, an overmature specimen of *J.*

tiehmii.

Once the preceding specimens are placed in their proper species, *J*. *capillaris* stands as the geographically well-delimited high altitude Sierran member of the "kelloggii" group. Outside of the Sierra Nevada it has been found only once, in 1896 by Leiberg (*2525*) "along streams, alt. 1890 m. Stein's Mts. [Steens Mountain] opp. Devine Ranch", in southeastern Oregon. Although there is no ranch now called Devine Ranch in the area, John Devine was one of the founders of Whitehorse Ranch (McArthur, 1965), which is about 24 miles due east of Alvord Peak at the south end of Steens Mountain. Steens Mountain, an isolated basalt-capped fault block, contains disjunct populations of several other Sierran species, such as *Claytonia* *nevadensis* S. Wats. Some of these species also occur in the Wallowa and Blue mountains and central Idaho; *J*. *capillaris* may eventually be found in one or more of these places.

The Steens Mountain collection, like many from the Sierra Nevada, has *J*. *tiehmii* intermixed (the only collection of *J*. *tiehmii* from Oregon). In such populations separation of the two species can be somewhat arbitrary. This is evident even in the Tuolumne River paratype of *J*. *triformis* var. *uniflorus*, which Hermann apparently did not realize consisted primarily of *J*. *tiehmii* and not *J*. *capillaris*. The relative proportions of and contrast between the tepals and capsules, combined with the size and number of the seeds, are probably the best ways to tell the two species apart. It may be that the reproductive barriers between them might be occasionally breached in spite of different chromosome numbers and selfing as the main form of pollination. The majority of ambiguous plants are not overly vigorous, with few culms, solitary dimerous flowers, and few-seeded capsules. Are they ambiguous because they are not well-developed, or are they instead depauperate because they are ill-adapted, chromosomally maladjusted hybrids?

Previous illustrations of this species apparently to not exist. The only vernacular name used thus far is Hair-Stemmed Rush (Peck, 1961); I suggest Hair-stemmed Dwarf Rush.

Specimens examined: UNITED STATES. CALIFORNIA: **Alpine Co.**: Wolf Creek, Hardham 28181b (CAS). **Calaveras Co.**: Big Trees, Hillebrand 2333 (MO, US). **El Dorado Co.**: Benwood Meadows near Echo Summit, Copeland s.n. p.p. (SACT, UC). **Fresno Co.**: Simpson Meadow, Howell 33948 (CAS); Hutchinson Meadow, Quibell 5821 (FSC); E end Vermillion Valley, Quibell & Quibell 2565 p.p. (FSC); Agnew Meadows to Lake Olane, Raven 3235 (CAS); ridge N of Lake Ediya, Raven 3375 (CAS); Mills Creek, Raven 5676 (CAS); Mono Creek, Raven 5802 (CAS); Pocket Meadow, Raven 6020 p.p. (CAS, UC); near Kip Camp, Bear Creek, Raven 7342 (CAS). **Mariposa Co.**: Yosemite Valley, Bolander 6034 (GH, JEPS, MICH, MO, UC); 6 mi E of Porcupine Creek Campground, Tioga Road, Ertter & Strachan 3073 (CAS, NY, OBI, ORE); 2.5 mi E of Porcupine Creek Campground, Ertter & Strachan 3075 (CHSC, FSC, GH, HSC, LA, MO, NY, RENO, SACT, SBBG); 1 mi W of Olmstead Point, Tioga Road, Ertter & Strachan 3076 (CAS, CHR, NY, TEX, UCSB); Snow Creek Trail, Tenaya Canyon, Howell 15564 (CAS, GH, MICH, NY, POM); above Bridal Veil Fall, Yosemite, Sharsmith 2171 (UC). **Mono Co.**: 4.5 mi E of Sonora Pass on Hwy 108, Ertter & Strachan 3029 (CAS, NSW, NY, OSC); 4.8 mi SE of Sonora Pass summit, *Ertter & Strachan 3896* (DAV, F, K, NY, PH, SFSU, UC, US); 4.4 mi SE of Sonora Pass summit, *Ertter & Strachan 3897* (BRY, CAS, MICH, NY, ORE, RM, TEX, WS, WTU); E side Sonora Pass, *Howell 19892* (CAS, NA, US). Tulare Co.: above Reflection Lake, *Howell 15904* (CAS, MICH); Cliff Creek between Deer Creek & Pinto Lake, *Howell 17328* p.p. (CAS, MICH); between Pinto Lake & Black Rock Pass, *Howell 17336* (CAS, MICH, SFSU); Rock Creek, *Howell 25682* (CAS, NA, NY, RSA, UC, US, UTC, WS, WTU); Monarch Lakes Trail, *Howell 27956* (CAS, NY, RSA); Dorst Creek, Sequoia Park, *Quick & London 52-252A* (CAS); E of Point 11153 at head of Kern River, *Raven 8339* (CAS). Tuolumne Co.: Glen Aulin trail, Tuolumne Meadows, *Ertter & Strachan 3928* (CAS, NY, RSA, SD, UTC); Glen Aulin trailhead, *Ertter & Strachan 3934* (NY); Kennedy Meadows, *Hesse 2326a* (CAS); Eureka Valley Camp, Sonora Pass Road, *Hesse 2353* (CAS); between Dog Lake & Tuolumne Meadows, *Howell 20441* p.p. (CAS, GH, LL); Tuolumne Canyon above Glen Aulin, *Howell 20487* (CAS, LL); 1.5 mi N of O'Shaughnessy Dam, Hetch Hetchy Valley, *Keck & Clausen 5289* (DS). OREGON: Harney Co.: Steins Mts. opposite Devine Ranch [sic], *Leiberg 2525* p.p. (MICH, ORE, US).

III. THE "BRYOIDES" GROUP

Plants mostly 0.3--2 cm tall; leaves 1/4--1 times the height of the plant, the blade usually ca 0.2 mm wide; culms slender, 0.1--0.2 mm thick; bracts usually 2, subequal, usually acutely ovate; flowers strictly solitary, mainly trimerous; tepals lanceolate to oblong, acute to acuminate, incurved over the capsule; anthers 0.15--0.25 mm long, 1/3--1/2 the length of the filaments; style at most 0.1 mm long; capsule ovoid to ellipsoid, shorter than and ± concealed by the tepals; seeds usually in ca 4 rows per valve, to 40 per capsule, the longitudinal and transverse lines equally faint, forming a transversely elongate reticulum. *n* = ca 19. Most frequent on sandy soils. 1 sp.

7. JUNCUS BRYOIDES F. J. Hermann (Fig. 26)

Juncus bryoides (resembling a moss, *Bryum*) F. J. Hermann, Leafl. W. Bot. 5: 117. 1948. -- TYPE: UNITED STATES. CALIFORNIA: San Bernardino Co.: Bear Valley, San Bernardino Mts., very abundant on wet sandy flats, elev ca 6000', 3-16 Jun 1886, Parish 1859 (Holotype: US!; Isotypes: DS!, F!, GH!, JEPS!, MICH!, MO!, NY!).

Plants 0.3--2 (2.5) cm tall, turning reddish, drying pale reddish or brown; leaves to 0.9 cm long, 1/4--1 times the height of the plant; culms to ca 150, 0.1--1.8 (2.2) cm long (sometimes essentially lacking on otherwise cauline plants), 0.1--0.2 mm thick; bracts (1) 2, ovate (lanceolate), ± acute, usually unpigmented, sometimes brownish at base,

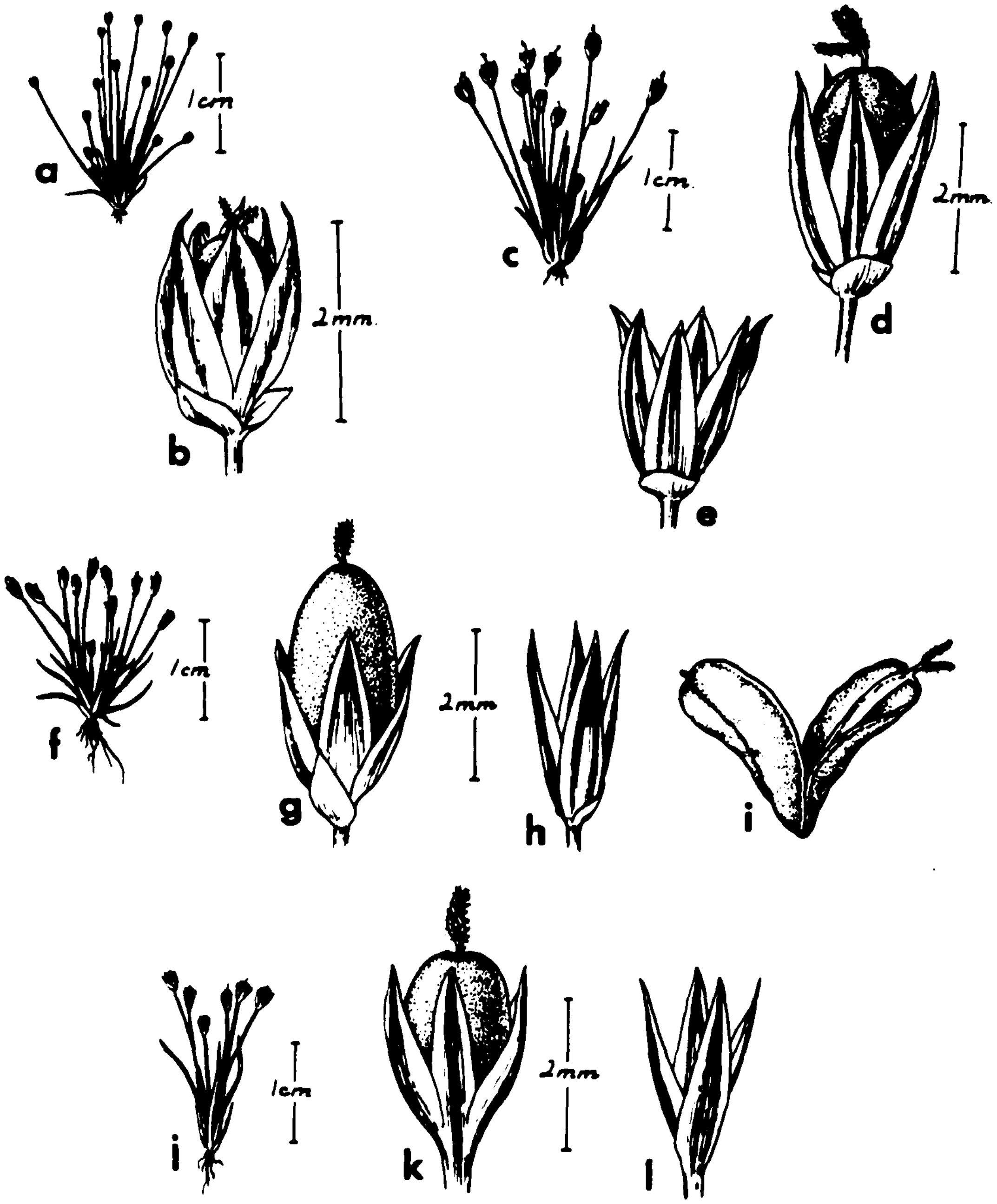

Fig. 26. Illustrations of J. bryoides and members of the "uncialis" group. a-b, J. bryoides. a, habit. b, flower. c-e, J. uncialis. c, habit. d, flower. e, side view. f-i, J. hemiendytus var. hemiendytus. f, habit. g, flower. h, side view. i, open capsule. j-l, J. hemiendytus var. abjectus. j, habit. k, flower. l, side view.

0.3--0.9 mm long, subequal; pedicels to 0.2 mm long; flowers 1, mainly trimerous; tepals (4) 6 (8), lanceolate to acutely oblong, (1) 1.2--2.3 (2.8) mm long, 0.4--0.6 mm wide, subequal or the inner to 0.2 mm longer, acute to acuminate, incurved over the capsule, the central band narrowly tapering, not reaching the apex, 0.05--0.2 mm wide, lustrous, usually turning dark red or brown to almost black with the base sometimes remaining olive-green, not sharply differentiated from the membranous margins, these 0.15--0.25 mm wide, the inner edges concolorous with the center, otherwise unpigmented, the whole often giving a striped aspect to the mature flower); stamens (2) 3 (4), 0.5--0.9 mm long, ca 1/2 the length of the tepals; filaments 0.3--0.6 mm long; anthers 0.15--0.25 mm long, ca 1/3--1/2 the length of the filaments; style lacking or at most 0.1 mm long; stigmas (2) 3, 0.2--0.3 mm long, included at anthesis; capsule ovoid to ellipsoid, (2) 3-valved, terete, rounded, shorter than the tepals by 0.1--0.7 mm, usually concealed by the tepals, (0.7) 1.0--1.9 mm long, 0.5--1.0 mm wide, pale reddish; seeds to 8 per row and ca 40 per capsule, ovoid to globose, somewhat apiculate or umbonulate, 0.3--0.5 mm long (larger extreme in the Sierra Nevada), smooth or faintly transversely lined at 30x (Fig. 6d-f); 2*n* = 38 (± 2).

Widespread, growing in a diversity of habitats such as washes, swales in meadows, and edges of seepage areas on rock outcrops, most frequently on fine sandy soils, occasionally on more clayey soils, sometimes in such abundance as to tinge the ground red, from extreme western Colorado and central Idaho to the mountains of the northern Great Basin in Nevada and Oregon, south through the Wasatch Range and Utah Plateaus to Zion National Park in Utah, and through the

Sierra Nevada to the Sierra San Pedro Mártir of Baja California del Norte, west to Monterey Co., California, from 650 m elevation in the Santa Lucia Range to 3600 m in the White Mountains. Flowering from April to August. (Fig. 27)

Often growing with J. tiehmii, also with both varieties of J. hemiendytus and J. capillaris, rarely with J. luciensis, J. kelloggii, or J. uncialis.

From its original discovery as a component of Bolander's Tuolumne River collection in 1866 to its description by Hermann in 1948, J. bryoides was included within either J. uncialis or J. triformis var. uniflorus. For example, the type collection from Bear Valley (now largely inundated by Bear Lake) had been cited by Parish (1910) as one of the southernmost stations of J. triformis var. uniflorus. Hermann regretted not being able to use the earlier name J. saginoides, which he considered "very appropriate" for this species. Actually, I find his chosen epithet more descriptive of these moss-like plants.

Within the J. triformis complex, J. bryoides has the greatest geographic and altitudinal range as well as the broadest ecological limits. Its geographic range is similar to that of J. tiehmii but extends farther to the east. I suspect that this easily overlooked plant will prove to be more generally distributed in the northern and eastern parts of its range, especially in Utah, than present collections indicate. It most frequently grows in fine sandy soils, often with J. tiehmii, but also grows in more clayey soils with J. hemiendytus. In these mixed populations it is often in the slightly drier microhabitats, for example on higher ground or away from the protection of other plants.

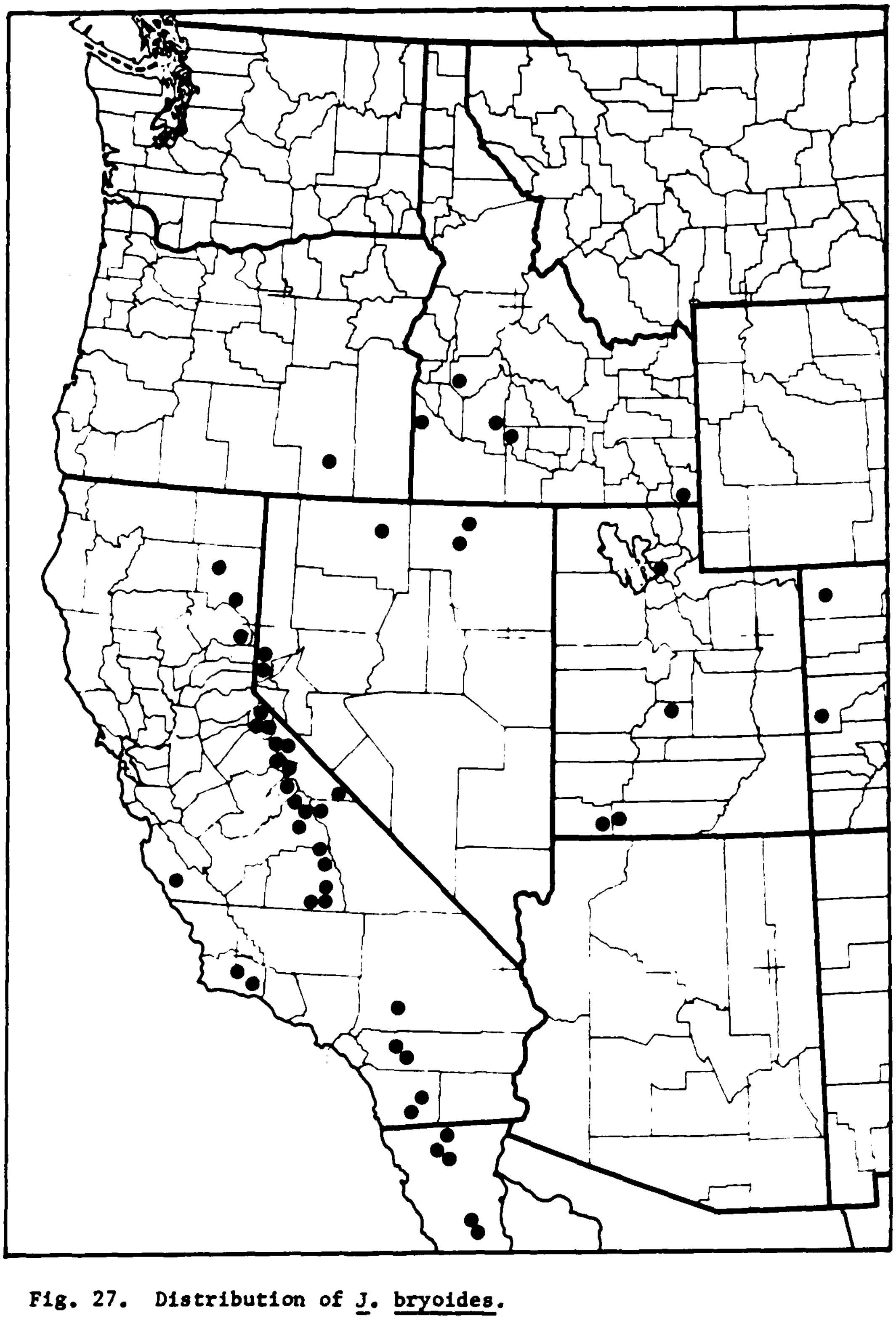

Fig. 27. Distribution of *J. bryoides*.

In light of the relatively broad geographic and ecological limits, one might expect to find some infraspecific subdivisions. There is a certain amount of morphological variation, specifically in the coloration and size of plants and floral parts, but this variation apparently reflects vigor and maturity and has little or no genetic basis. Big green plants are as likely to be represented in collections from Colorado as from Baja California, and the same is true for small reddish ones.

Juncus bryoides is probably the easiest species in the *J. triformis* complex to recognize on sight. Recognition, however, is largely a matter of gestalt, so the distinctiveness of this species is difficult to communicate in descriptions and keys. "Looks like *J. bryoides*" versus "Does not look like *J. bryoides*" is unfortunately not acceptable as a key break. The most diagnostic feature is the inward curvature of the tepals over the ovoid capsule, described by Hermann as "tulip-like in appearance".

Because of this distinctiveness it is difficult to place the species within the complex. The exclusively solitary flowers and smooth seeds would associate *J. bryoides* with the "uncialis" group, but the preferred substrate and the color and shape of the tepals and bracts are more reminiscent of the "kelloggii" group. Probably *J. bryoides* is best interpreted as the lone highly derived end-product of a separate third line, in which the stepwise reduction series from the long-styled, many-flowered ancestral complex displayed by the "kelloggii" and "uncialis" groups has been lost. The species lacks both the ridged seeds of *J. triformis* and the reduced chromosome number of *J. leiospermus*, which means that the "bryoides" line is unlikely to have arisen from either of these two extant species. Instead the seeds have the narrowly transverse honeycomb pattern that I believe comes closest to the primitive condition, while the chromosome number of $2n = 38$ is the closest in the complex to that known for the perennial members of subg. Graminifolii.

If J. bryoides does represent an isolated lineage that diverged from the rest of the complex at an early stage, the question of the fate of the intermediates then arises. It is likely that the same adaptive features that made J. bryoides so successful over such a wide environmental range allowed it to displace any ancestors. Under optimum conditions J. bryoides can form dense enough stands to color the ground red, and could thereby conceivably crowd out any less successful relatives. Furthermore, if inadequate reproductive barriers had developed, the well-adapted J. bryoides genes could have simply swamped those of any less successful relative by introgression.

As a further peculiarity, smut-infected plants occur in certain populations of J. bryoides. The smut infecting the culms and leaf-bases of a few plants in Howell 25452 (= Munz 14054) from Inyo County is apparently a Urocystis related to U. junci Lagerh. (det. by R. E. Halling, 1982). A few plants in Ertter & Strachan 3693 from Mono County and Tiehm 6084 from Elko County, Nevada, are affected with a similar smut. Although all three collections represent mixed populations with J. tiehmii, no infected plants of the latter species have been found. This restriction supports my belief that J. bryoides is phylogenetically isolated from the rest of the complex, although it may be merely coincidence, as only a few plants were infected in each population.

An illustration of J. bryoides appears in Hermann's 1978 treatment of the Rocky Mountain rushes. I am aware of no vernacular names and would therefore suggest Mosslike Dwarf Rush.

Representative specimens: UNITED STATES. CALIFORNIA: **Alpine Co.**: E side Ebbetts Pass, Eastwood & Howell 8496a (CAS, MICH). **Fresno Co.**: Fourth Recess, Howell 22682 (CAS, F, GH, NY, POM, UC, US, UTC, WS); Colby Meadows, Raven 4673 p.p. (CAS). **Inyo Co.**: near Ruby Lake, Rock Creek Lake Basin, Howell 22803 (CAS, GH, NY, US); Cottonwood Creek, Howell 25452 (CAS, NA, US). **Lassen Co.**: 8 mi W of Susanville, Hermann 24752 (CAS, HSC, MICH, US). **Madera Co.**: Garnet Creek to San Joaquin Mt., Howell 16836 (CAS, GH, NA, POM, UC, US). **Mono Co.**: E flank Mt. Conness, head of Slate Creek Valley, Clausen & Kruckeberg 1898a (DS); 4.5 mi E of Sonora Pass on Hwy 108, Ertter & Strachan 3038 (NY); Honeymoon Flat Campground SW of Bridgeport, Ertter & Strachan 3693 (CAS, CHSC, NY, RSA, SFSU, UCSB, UTC); Sonora Bridge Campground, Ertter & Strachan 3922 (CAS, NY); 1/4 mi E of Barcroft Lab, White Mts., Spira 357 (NY). **Monterey Co.**: The Indians, Santa Lucia Mts., Hardham 5342B p.p. (CAS, RSA). **Plumas Co.**: 5.8 mi E of Beckwourth, Howell 37862 p.p. (CAS). **Riverside Co.**: Kenworthy Ranger Station, Hemet Valley, Ertter & Strachan 2972 (CPH, CHR, NA, NY, RSA, UC, UTC); Santa Rosa Mt. Road ca 2 mi S of Hwy 74, Ertter & Strachan 3482 (CAS, R, RSC, K, LA, NSMC, NY, PRE, RSA, SACT, SD, TEX, US). **San Diego Co.**: 1 mi S of road to Cuyamaca on Hwy S1, Ertter & Strachan 3531 (ASU, CAS, MEXU, NY, SD); Moreno Dam, near office, Wiggins 2395 (DS, UC). **Santa Barbara Co.**: Hurricane Deck, Hardham 1981 (CAS); top of Big Pine Grade near road to lookout, Piehl 63586 p.p.

(SBBG). **Tulare Co.**: Chagoopa Plateau, Howell 17571 (CAS, F, GH, MICH, NY); Bakeoven Meadows, S Fork Kern River, Howell 26928 (CAS, DS, NA, US); Fish Creek ca 3.5 mi S of Troy Meadow, Kern Plateau, Howell & True 43003 (CAS). **Tuolumne Co.**: upper Tuolumne River, 1866, Bolander s.n. p.p. (MO); W end Tuolumne Meadows near Tioga Road, Ertter & Strachan 3072 (CAS, NY); mouth of Dingley Creek, Tuolumne Meadows, Ertter & Strachan 3930 (CAS, DAV, HSC, MICH, NY, SBBG); Glen Aulin trailhead, Ertter & Strachan 3932 (NY). **COLORADO: Mesa Co.**: Divide Fork Area, Uncompahgre Plateau, Kelley 06221979-4 (NY). **Moffatt Co.**: 4 mi above Greystone on Zenobia Peak Road, Weber & MacLeod (CAS, DS, MICH, NY, RM, TEX, UC, WS). **IDAHO: Boise Co.**: 0.5 mi SW of Centerville, Ertter & Strachan 3797 (CAS, CIC, NY, RM, WS). **Elmore Co.**: Walker Gulch in Mt. Bennett Hills S of Hill City, Ertter 2438 (BRY, MICH, MO, NY, TEX, UC, WTU), 4180 (CAS, CIC, ID, NY, US, UTC). **Franklin Co.**: Franklin Basin, Bear River Range, Maguire 21628 (NY, UTC). **Gooding Co.**: Davis Mt. road near Bliss - Hill City road, Ertter 220/5 (= BJE 75-186) (BRY, CIC, NY, RSA, UC, UTC, WS, WTU). **Owyhee Co.**: headwaters Jordan Creek E of Silver City, Ertter et al. 4483 (CAS, CIC, ID, NY, OSC, TEX, UTC, WTU). **NEVADA: Elko Co.**: Rt. 11A 1.3 mi S of Bull Run SW of Mountain City, Ertter & Strachan 3778 (BRY, CIC, LE, MARY, MO, MONTU, NY, PH, RENO, RSA, TEX, UTC, WTU); Sunflower Flat N of Wildhorse Reservoir, Ertter & Strachan 3784 (CAS, CIC, NY, UTC); Poorman Creek N of Wildhorse Reservoir, Tiehm & Read 6084 (NY). **Humboldt Co.**: 1 1/2 airmi SE of Canyon Creek summit, Santa Rosa Range, Ertter 4321 (CAS, CIC, GH, ISC, NSW, NY, RENO, UTC, WS). **Washoe Cr.**: Little Valley, E side Carson

Range, Ertter et al. 2771 (BKL, BRY, CAS, GH, MARY, NY, ORE, RSA, UTC); head of Mitchell Canyon, Peavine Mt., Howell et al. 51177 (CAS); Antelope Valley E of Fred's Mt., Tiehm 5744 (NY). **OREGON: Harney Co.:** Steens Mt. 1 mi SE of Fish Lake, Ertter & Strachan 3107 (CAS, CIC, NY, ORE, UTC). **UTAH: Kane Co.:** Clear Creek 2 mi N of Zion Nat'l Park, Ertter & Strachan 2869 (NY). **Salt Lake Co.:** midway between Salt Lake City & Park City, 2 July 1908 Cardiff s.n. (NY). **Sevier Co.:** ca 23 mi E of Salina, Welsh 19584 (NY). **Washington Co.:** Clear Creek Canyon, Zion Park, Eastwood & Howell 9212 (CAS, MICH). **MEXICO: BAJA CALIFORNIA DEL NORTE:** Oak Pasture turnoff, Sierra San Pedro Mártir, Moran 23340 (DAV, MICH, SD); 5 mi W of La Rumorosa, Sierra Juárez, Moran 27013 (NY, SD); 5 mi S of Los Gavilanes, Sierra Juárez, Moran 27501 (SD).

IV. THE "UNCIALIS" GROUP

Plants mostly 0.5--3 cm tall; leaves 1/2--1 1/2 the height of the plant, the blades usually ca 0.3--0.4 mm wide; culms relatively stout, mostly 0.2--0.4 mm thick; bracts 0--2, when 2 the inner often greatly reduced, broadly truncate to rounded to obtusely ovate, rarely acute; flowers strictly solitary, trimerous or dimerous; tepals oblong-lanceolate with nearly parallel sides ending in an obtuse to acute apex, usually erect to recurved; anthers mostly 0.3--0.7 mm long, 1/3 to almost the length of the filaments; style 0.1--0.4 mm long; capsules obovoid or ovid to ellipsoid or oblong, shorter than or to 1 1/2 times the length of the tepals; seeds usually in ca 4 rows per valve, ca 40 per capsule, the longitudinal and transverse lines equally faint, forming a reticulum; $n = 16$. Most frequent on clayey soils. 2 spp.

In the original description of Juncus uncialis Greene (1890) commented, "very unlike our other small annual rushes as to its perianth and seeds", and described the latter as "neither ribbed nor even regularly striate, but marked with transversely elongated quadrate reticulations". Only three years later Brandegee (1893) dismissed the seed coat pattern differences as merely reflecting the degree of maturity and therefore lacking taxonomic significance. She considered J. uncialis to be nothing more than a synonym of J. triformis var. uniflorus (mentioning as an additional synonym a malapropism for J. saginoides). Buchenau (1906) went one step further and treated both J. uncialis and J. triformis var. uniflorus as synonyms of var. brachystylus. Most subsequent authors, however, either followed

Brandegee or did the opposite and treated J. triformis var. uniflorus as a synonym of J. uncialis. Either way only one taxon was used as a catch-all for solitary-flowered dwarf rushes.

Although Greene has a reputation as a notorious splitter, in this instance his emphasis on seed-coat pettern appears to be well-founded. His recognition of the difference in tepals was also correct; those of the "uncialis" group have a distinct color pattern and tend to be blunter and less lustrous than those of other members of the J. triformis complex.

Hermann also recognized the significance of these characters. He not only resurrected J. uncialis but also segregated as two new species the closely related J. hemiendytus and J. abjectus. One of the main features distinguishing the three species concerns the bracts subtending the solitary flowers: a single truncate bract encircling the culm in J. uncialis, one or two ovate bracts slightly clasping the culm in J. hemiendytus, and none at all in J. abjectus. Hermann's two new species are well set off from J. uncialis as well. Both are reddish and predominantly dimerous, in contrast to the greenish, predominantly trimerous J. uncialis. Although Hermann did not place great significance on dimery, Hitchcock (1969) found the dimery in J. hemiendytus noteworthy, and I find this feature to be taxonomically important (see Fig. 3).

At the same time, I do not find the differences between J. hemiendytus and J. abjectus to be nearly as great as those between this pair and J. uncialis. Although the two are indeed distinct and can be found maintaining their identities in most mixed populations, in some populations (especially in the Sierra Nevada) separation becomes rather arbitrary. Plants with relatively slender culm and one highly reduced bract, plants with slender culms and no bracts, and plants with dilated culms and vestigial bracts can all be found. I am accordingly treating *J. abjectus* as a variety of *J. hemiendytus*.

While *J. uncialis* grows primarily in vernal pools at low elevations in the Central Valley of California, the two varieties of *J. hemiendytus* are found in a variety of seasonally moist habitats at middle elevations in northern California, Oregon, southern Idaho, and northern Nevada. Populations of *J. uncialis* mixed with one or both varieties of *J. hemiendytus* may be found in southern Oregon and Lake County, California. Such mixed populations are, however, exceptional, and for the most part the range of *J. uncialis* is reasonably distinct. In contrast, the geographic range of var. *abjectus* is completely included within that of var. *hemiendytus*, differing only in that var. *abjectus* does not occur at low altitudes west of the Sierra-Cascade axis.

The "uncialis" group connects to the ancestral "triformis" group near *J. leiospermus*, especially var. *ahartii*. Both the "uncialis" group and *J. leiospermus* have smooth seeds and a chromosome number of $n = 16$. Furthermore, *J. leiospermus* lies completely within the range of *J. uncialis*, which grows in vernal pools with var. *ahartii*. Significantly this variety differs from var. *leiospermus* in exactly those features that characterize the "uncialis" group: solitary flowers, numerous culms and seeds, short stature, hyaline rounded bracts, and a tendency towards "hypermery". It is quite possible that these similarities reflect the actual evolution of the group, but alternatively the rare var. *ahartii* may have itself been derived from a hybrid of var. *leiospermus* and *J. uncialis*.

Within the group, the trimerous _J_. _uncialis_ is probably the most archaic (except for its single truncate bract) and represents the expression primarily adapted for the Central Valley vernal pools, while the more advanced dimerous _J_. _hemiendytus_ is predominantly montane. The present ranges and mixed populations of the two varieties of _J_. _hemiendytus_ allow for some interesting speculation about their origin. I would suggest that var. _abjectus_ developed from a segment of _J_. _hemiendytus_ isolated in the northern Great Basin during the Pleistocene by the Sierra-Cascade axis. Since that time the ranges of both varieties have expanded, that of var. _hemiendytus_ more successfully. Because both varieties have similar habitat requirements, mixed populations often form. I suspect that in these mixed populations they are reproductively isolated primarily by their self-pollinating tendencies, but that this isolation is not perfect. If so, we have at present two formerly distinct taxa that are in the process of merging, especially in the Sierra Nevada where they would have been in contact longer.

8. JUNCUS UNCIALIS Greene (Fig. 26)

Juncus uncialis (uncialis L., of an inch, in reference to the stature) Greene, Pittonia 2: 105. 1890. -- TYPE: UNITED STATES. CALIFORNIA: Solano Co.: low moist places in fields near Suisun, 5 May 1890, Greene s.n. (Holotype: NDG!; Isotypes: DS!, F!, NA!, NDG!, UC!, US!).

Plants 0.8--3.2 (4) cm tall, yellowish-green or only slightly turning reddish, drying stramineous; leaves to 2.2 cm long, 1/2--3/4 the height of the plant; culms to ca 70, 0.3--2.8 (3.5) cm long, (0.1) 0.2--0.4 (0.5) mm thick, the summit not dilated; bract solitary, broadly truncate, completely enwrapping culm, unpigmented, 0.25--0.9 mm long; pedicels to 0.5 mm long; flowers 1, mostly trimerous; tepals (4) 6 (8), (1.7) 2.1--3.8 (5.3) mm long, 0.6--0.9 mm wide, subequal or the inner to 0.3 (0.7) mm shorter (rarely to 0.3 mm longer) than the outer, usually ± acute, erect to recurved, sometimes slightly incurved, the central band usually remaining green, occasionally turning reddish, 0.2--0.3 mm wide, the membranes unpigmented, 0.15--0.3 mm wide; stamens 2--3, 1.2--2 (3) mm long, 2/3--1 times the length of the tepals; filaments 0.9--1.6 (2.1) mm long; anthers 0.3--0.4 (0.8) mm long, ca 1/3 the length of the filaments; style 0.1--0.3 mm long; stigmas (2) 3 (4), 0.4--1.3 mm long, white, included at anthesis; capsule ovoid to ellipsoid, (2) 3 (4)-valved, terete, retuse, subequalling the tepals or shorter (rarely longer) by up to 0.5 mm, (1.2) 1.8--3.2 (4) mm long, 1.0--2.5 (3) mm wide, remaining greenish or more commonly turning reddish to deep maroon and then strongly contrasting with the tepals; seeds to 12 per row and ca 140 per capsule, ± ovoid, 0.3--0.4 mm long, sometimes apiculate or umbonulate, smooth or reticulate at 30x (Fig. 7a,b); n = 16.

Occasional at the edges of vernal pools and equivalent habitats such as muddy clay edges of stockponds, mainly in the Central Valley of California, extending south to San Diego Co. and north to the Columbia River and the northwestern Great Basin in Oregon, from 45 m elevation in the Sacramento Valley to 1700 m in Nevada. Flowering from March in the Sacramento Valley to July in the Great Basin. (Fig. 28)

Sometimes growing with J. capitatus, J. leiospermus var. ahartii, J. luciensis, and both varieties of J. hemiendytus, rarely with J. bryoides, perhaps also with J. leiospermus var. leiospermus, J. triformis, and J. kelloggii.

Although Greene collected and described J. uncialis while he was a professor of botany at the University of California, most holotypes of his species are in his herbarium (NDG). I am therefore accepting one of the two NDG sheets as the holotype of J. uncialis, even though the word "Type" has been added to the label on the UC sheet in a hand apparently neither Greene's nor Hermann's.

Juncus uncialis is characteristically a component of the Central Valley vernal pool flora of California. Outside the Central Valley it is only occasionally encountered. In San Luis Obispo and Monterey counties it has been twice collected, in vernal pools near Jolon and Estrella, both times with J. luciensis. Only two collections, both meager, are known from the San Diego vernal pools.

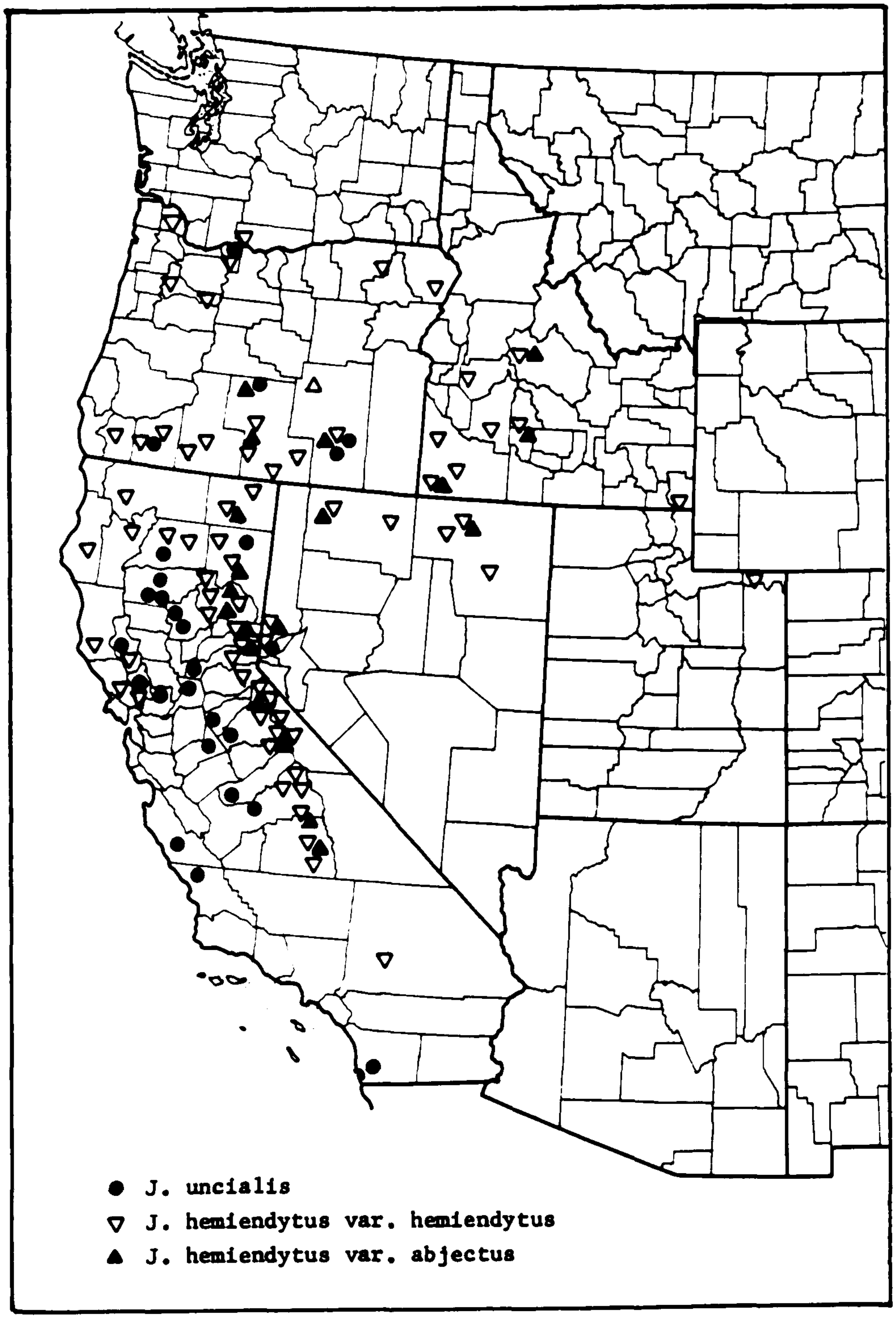

Fig. 28. Distribution of species in the "uncialis" group.

Hermann accepted Lake Merced in Yosemite Park as a location of J. uncialis and Vacaville in the Central Valley as a location for J. triformis, based on Jepson 1205 and Jepson 4414 at US. Vacaville is not far from the type locality of J. uncialis but would be a significant range extension for J. triformis, geographically, altitudinally, and ecologically, while the reverse is true for Lake Merced. Furthermore, the identifications by Coville on the labels match the species one would expect to find in each area instead of the species that are mounted on the sheets. I therefore believe that the labels were accidentally switched on the US sheets, especially since at JEPS comparable labels are matched with the appropriate plants.

The species is represented on the northwestern edges cf the Intermountain Region by scattered collections. Leiberg 375 from Button Springs in Lake County, Oregon, is an old collection of J. uncialis mixed with J. hemiendytus var. abjectus. I visited what I believe to be the site in 1980 and found it converted into a stock pond with no sign of dwarf rushes. The only place I found the species in Oregon was on the edge of a cattle-trodden stock pond on Steens Mountain. Although this was a healthy population, I would recommend that J. uncialis be placed on the Oregon watchlist, and it may even qualify for state threatened status. Only one collection is known from Nevada, so the species should be similarly list in that state. Its habitat is being whittled away in California, but the species does not appear to be in immediate danger of extinction.

The illustration of J. triformis var. uniflorus in Jepson (1922, 1923) is based on the JEPS sheet of Jepson 1205, although the single truncate bract is not obvious. In the illustration of J. uncialis in Abrams and

Coville (1923), the bracts are decidedly acute and therefore not representative of *J. uncialis* s.s. Abrams and Coville (1923) dubbed this species the Inch-High Dwarf Rush, an appropriate vernacular name, shortened by Peck (1961) to Inch-High Rush.

Specimens examined: UNITED STATES. CALIFORNIA: **Butte Co.**: Ahart Ranch NE of Honcut, 11 Apr 1974, Ahart 363, 364 (Ahart herb.), 24 Apr 1974, Ahart 422 (CAS, Ahart herb.), 6 Jun 1974, Ahart s.n. (CAS), 10 Apr 1978, Ahart 1626 (Ahart herb.), 1 May 1978, Ahart 1695 (CAS, Ahart herb.), 1 May 1982, Ahart 3401 (F, LA, NY, OBI, SD), 9 May 1982, Ahart 3428 (MICH, NY, PH, SBBG, UC, US); Thermalito, 4 May 1980, Ahart s.n. (NY); Vina Plains N of Munjar Road & E of Meridian Road, Holland 386 (Holland herb.); 1/4 mi S of jct Hwy 162 on Hwy 99, Jokerst 0121 (CHSC); SE of Chico, along Skyway, Schlising 3517 (CHSC); 1/4 mi S of jct Hwy 162 to Oroville & Hwy 99, Schlising 3551 (CHSC). **Calaveras Co.**: 2 mi N of Jenny Lind, Breedlove 4762A p.p. (CAS). **Fresno Co.**: ca 12 mi S of Friant, Ferris & Bacigalupi 12389 (UC). **Lake Co.**: Kelseyville & Lower Lake Hwy 4.3 mi S of Adams Springs Road, Baker 9889 (=Kock 873) p.p. (CAS, MICH); 1.5 mi E of Loch Lomond, Smith & Anderson 2983 (UC). **Lassen Co.**: 5.6 km S of Madeline on Hwy 395, Holmgren & Holmgren 9469 (NY). **Madera Co.**: 7 mi NE of Madera on Hwy 145, Ertter & Strachan 3069 (NY, TEX); 7 mi NE of Madera, Howell 41096 (CAS). **Mariposa Co.**: W of Chapman Place, Congdon 84 (GH). **Merced Co.**: Ryer, Hoover 2095 (OBI, UC). **Monterey Co.**: ca 5 mi N of Jolon, Howell 31141A (CAS). **Napa Co.**: 3-4 mi E of Angwin's, Tracy 1611 1/2 p.p. (UC). **Placer Co.**: N outskirts of Lincoln, Howell & True 7079 (CAS). **Sacramento**

Co.: Sacramento Junior College, 17 Apr 1935, Copeland s.n. (SACT), 19 May 1938, Copeland 1566 (GH, JEPS, SACT, SBBG, UC); E of Sacramento, 2 Apr 1936, Copeland s.n. (SACT); Keithly Ranch, Rio Linda, Crum 1602 (UC). **San Diego Co.**: Montgomery Air Field, Holland 348 (Holland herb.); Camp Kearney Mesa, Purer 7242 (POM, SD). **San Luis Obispo Co.**: near Estrella, Eastwood & Howell 4197 (CAS, GH, MICH, NY, US). **Shasta Co.**: 3 mi NE of Redding, Wheeler 3387 (US). **Solano Co.**: near Violet Station N of Vacaville, Jepson 1205 (JEPS, US); 8 mi SE of Fairfield, Lin 61 (SFSU). **Stanislaus Co.**: 4 mi S of Oakdale, Hoover 490 (OBI, UC). **Tehama Co.**: 5 mi NE of Red Bluff, Ahart s.n. (NY); Vina Plains, Lassen Road 0.55 mi W of Singer Creek, Holland 402 (Holland herb.); 6 mi S of Corning, Howell 29190 (CAS, DAV, NY, RSA, UC, US, WTU). **Tuolumne Co.**: 2 mi W of Chinese Camp, Jepson 18070a (JEPS). NEVADA: **Washoe Co.**: Virginia Range E of Little Washoe Lake, Tiehm & Williams 7140 (NY). OREGON: **Harney Co.**: 4 mi S of Steens Mt. Loop Road 9.4 mi W of Blitzen Crossing, Ertter 4430 (BRY, CAS, CHR, CIC, GH, MO, NY, ORE, RENO, RM, RSA, TEX, UTC, WTU); 5 mi S of head of Wild Horse Creek, Steens Mt., Peck 14042 p.p (WTU). **Jackson Co.**: Lower Table Rock NW of Medford, Chambers 2453 p.p (OSC). **Lake Co.**: 4 km N of Button Springs, Leiberg 375 p.p. (NY, ORE, US). **Wasco Co.**: The Dalles, Peck 9976 (WILLU).

9. JUNCUS HEMIENDYTUS F. J. Hermann (Fig. 26)

Plants (0.2) 0.3--3.6 cm tall (the short extreme at high altitudes in the Sierra Nevada, usually turning reddish, drying pale reddish or stramineous; leaves to 1.8 cm long, 1/2--1 1/3 the height of the plant; culms to ca 50, 0.1--3.2 cm long, 0.1--0.5 mm thick; flowers 1, usally dimerous; tepals 4 (6), (0.8) 1.9--3 (3.5) mm long, 0.5--1.2 mm wide, all equal or the inner shorter, rounded to acute, usually recurved or erect, the central band usually turning reddish, 0.2--0.5 mm wide, the membranes usually unpigmented, 0.1--0.3 mm wide; stamens 2 (3), (0.7) 1--1.8 mm long, ca 1/2--3/4 the length of the tepals; filaments 0.5--1.4 mm long; anthers (0.2) 0.3--0.7 mm long, 1/3 the length of to almost equalling the filaments; style 0.1--0.4 mm long; stigmas 2 (3), 0.3--1 mm long, white, included at anthesis; capsule obovoid to ellipsoid or oblong, 2 (3)-valved, usually flattened, rounded to distinctly retuse, slightly less than to 1 1/2 times the length of the tepals, (1) 1.9--3.5 mm long, (0.9) 1.1--2 mm wide, usually turning reddish at maturity, not contrasting strongly with the tepals; seeds to 12 per row and ca 70 per dimerous capsule, ovoid to oblong, 0.3--0.55 mm long, often apiculate, sometimes umbonulate as well, the longitudinal and transverse lines equally prominent or faint, smooth or faintly reticulate at 30x (Fig. 7c-f).

Various damp open habitats such as vernally moist depressions, streambeds, and swales in sagebrush flats, forest clearings,and alpine meadows, most frequently in clayey soils, from the Uinta Mountains of Utah west through central Idaho and the mountains of the northern Great Basin in Nevada to Klickitat Co., Washington, and the Willamette

Valley of Oregon, south to the North Coast Ranges and through the Sierra Nevada to the San Bernardino Mountains of California, from 400 to 3400 m elevation. (Fig. 28)

9a. JUNCUS HEMIENDYTUS F. J. Hermann var. HEMIENDYTUS

Juncus hemiendytus (*hemi-* Gr., half, *endytus* Gr., clad, in reference to the capsule only partly covered by the tepals) F. J. Hermann, Leafl. W. Bot. 5: 118. 1948. -- TYPE: UNITED STATES. CALIFORNIA: Trinity Co.: Big Flat [head of Coffee Creek, NE side of Trinity Alps, elev. ca 1500m], 21 Jul 1937, *Howell 13213* (Holotype: CAS!; Isotypes: DS!, GH!, MICH!, NY!, RSA!, UC!, US!).

Juncus triformis Engelm. var. γ *uniflorus* (*uniflorus* L., one-flowered) Engelm., Trans. Acad. Sci. St. Louis 2: 493. 1868. [This name supersedes *J. saginoides* (resembling *Sagina*, Caryophyllaceae), introduced in anticipation of formal publication but not described by Engelmann in Trans. Acad. Sci. St. Louis 2: 436. 1866]. -- *J. brachystylus* (Engelm.) Piper var. *uniflorus*, comb. attrib. to Engelm. by M. E. Peck, Man. Higher Pl. Oregon, 183. 1941. -- LECTOTYPE: UNITED STATES. CALIFORNIA: Mendocino Co.: Long Valley, poor damp sandy soil, in a grove of *Pinus ponderosa*, 6 May 1866, *Bolander 4691b* (distributed as *Herb. Norm. 32*) (Lectotype: MO!; Isolectotypes: CAS!, F!, GH!, ISC!, MICH!, MO!, NY!, RSA!, US!).

Plants (0.2) 0.8--3.6 cm tall; *culms* to ca 50, (0.1) 0.5--3.2 cm long, 0.1--0.3 mm thick, the summit not dilated; *bracts* 1--2, rounded to obtusely ovate (acute), not sheathing culm, unpigmented, seldom brownish near the base, to 2 mm long (occasionally greatly reduced or lacking on depauperate plants or individual flowers of otherwise bracteate plants), rarely tepaloid to 5 mm long; pedicels to 0.3 mm long; tepals (0.8) 1.9--3 mm long, 0.5--0.9 mm wide, all equal (or the inner to 0.7 mm shorter), rounded to acute, commonly recurved, the central band 0.2--0.3 mm wide, the membranes normally unpigmented, rarely brownish, 0.1--0.3 mm wide; anthers (0.2) 0.3--0.5 mm long, ca 1/3 the length of the filaments; style 0.1--0.2 mm long; capsule (ovoid) elliptic to oblong, rounded to slightly retuse, usually 1--1 1/2 times the length of the tepals, (1) 2--3.5 mm long, (0.9) 1.2--1.9 mm wide, usually turning reddish at maturity; seeds to 12 per row and ca 70 per dimerous capsule, elliptic-ovoid, 0.3--0.5 mm long, smooth or faintly reticulate at 30x (Fig. 7c,d); n = 16.

Range of the species, from 400 to 3200 m elevation. Flowering from April to September.

Often growing with var. abjectus, J. tiehmii, J. bryoides, and J. kelloggii, occasionally with J. uncialis, J. capillaris, and J. luciensis.

Engelmann in essence applied the name J. triformis var. uniflorus to all solitary-flowered members of the complex. The three representative collections he cited were "Sierra Nevada, among mosses, Hillebrand; upper Tuolumne River, Bolander, and in the lowlands, Anderson Valley, the same, Hb. n. 32". The Hillebrand collection would be Hillebrand 2333 from the Calaveras Big Trees, referable to J. capillaris. The Tuolumne River collection is a mixture of J. tiehmii and J. bryoides. The widely distributed Herb. Norm. 32 consists of J. hemiendytus var. hemiendytus. Although the Geological Survey sheet at UC referable to this last collection is numbered 4691, the two sheets from Engelmann's herbarium at MO are numbered 4691b, with 4691 reserved for J. kelloggii from the same location. Apparently Bolander 4691 represents a mixed collection that Engelmann separated into its components, the larger of which was distributed as Herb. Norm. 32.

As with Herb. Norm. 30 and Herb. Norm. 31, there is a discrepancy between the location on Bolander's label (Long Valley) and in the protologue (Anderson Valley). Bolander's field book does not list the collections in strict chronological order, but as 4691 is adjacent to other collections from near Longvale on Long Valley Creek north of Ukiah, I believe that Long Valley is the correct location.

In Hermann's understanding, var. uniflorus was based on a mixture of J. bryoides and J. capillaris. He cited J. triformis var. uniflorus, pro parte, in the synonymy of both species but did not use any of the specimens cited by Engelmann as the type of either. Furthermore, he cited Hillebrand 2333 under J. capillaris and Bolander, Herb. Norm. 32 under J. hemiendytus, but did not cite any of the syntypes under J. bryoides or make any mention of Bolander's Tuolumne River collection.

Hermann apparently did not intend to lectotypify J. triformis var. uniflorus, and nothing in his revision effectively does so. Lectotypification is therefore still necessary. The Tuolumne River collection can quickly be eliminated because it is a mixed collection, and nothing can be gained by using it as a lectotype. Choosing between the other two possibilities is more difficult. The Hillebrand collection was the only one available to Engelmann when he first formed his concept of J. saginoides, which Engelmann himself stated was to be replaced by J. triformis var. uniflorus. Although it would be fitting to emphasize the continuity between J. saginoides and var. uniflorus, such a move is not required.

Instead *Herb. Norm. 32* is the better choice. Not only does this represent a truly one-flowered taxon, but it is also the collection that Engelmann distributed to represent *J. triformis* var. *uniflorus*, similar to the types of var. *stylosus* (*Herb. Norm. 30*) and var. *brachystylus* (*Herb. Norm. 31*). I have therefore designated as lectotype of *J. triformis* var. *uniflorus* a sheet of *Bolander 4691b* in Engelmann's herbarium at MO. Although this sheet does not have a *Herb. Norm. 32* label or brown paper labels bearing Bolander's handwriting, it is nevertheless annotated by Engelmann in the same fashion as the lectotype of var. *stylosus* and the holotype of var. *brachystylus*.

Buchenau (1890) believed that the solitary-flowered condition was probably not taxonomically significant and therefore treated var. *uniflorus* as simply a depauperate extreme of var. *brachystylus* with the words:

> Forma minima, depauperata, capitulo *unifloro*, flore *dimero* varietatis *brachystyli* non raro occurrit. Haec forma a cel. Engelmann nomine: *J. triformis* var. *uniflorus* . . . salutatur.

and again (1906):

> In var. *brachystilo* haud raro formae occurrunt perpusillae, uniflorae, *floribus* dimeris. Hasce formas cel. Engelmann . . . nomine *Junc*. (subgenus *Juncellus*) *saginoides* salutavit, sed . . . sub nomine var. γ *uniflorus* ad *Junc. triformem* reduxit.

Buchenau was apparently not using the word "forma" to denote a formal taxonomic rank, and therefore no new combination was made (ICBN Art. 53.1). Jepson (1922), however, cited it as such in his synonymy of *J. triformis* var. *uniflorus*, ascribing the combination to Buchenau. Because this combination was cited only in synonymy, it is not validly published (ICBN Art. 34.1d). Buchenau's inclusion of the variety within var. brachystylus, incidentally, was not followed by subsequent authors.

The epithet also appeared in a different combination in Peck (1941), who used the name J. brachystylus (Engelm.) Piper var. uniflorus Engelm. without explicit reference to the basionym. Several other new combinations made in the same work were later published with basionym (Peck, 1945), but this combination was not among them. Nonetheless, his intended meaning is obvious, and because the combination was made before 1953, Art. 33.2 of the ICBN does not apply. In my understanding the combination is therefore validly published.

The next collection of J. hemiendytus var. hemiendytus after Bolander's was Watson 1200 from the Clover Mountains (= East Humboldt Range) in Elko County, Nevada, made in 1868 in conjunction with King's survey of the fortieth parallel. This collection was mentioned by Watson (1871) as "a starved, stunted form" of J. triformis var. uniflorus. Coville's (1925) inclusion of J. uncialis (considered by him a synonym of var. uniflorus) in Tidestrom's Flora of Utah and Nevada was undoubtedly based on this specimen. Hermann's annotations indicate that he did not see Watson's collection until 1942, which explains why he excluded J. uncialis from his 1940 treatment of the Nevada Juncaceae with the statement: "Juncus uncialis Greene is ascribed to Nevada by Coville . . . but no specimens have been located to substantiate this report". It is a revealing commentary on the history of botanical collecting in Nevada that no additional collections of the J. triformis complex were made in Nevada for 107 years after

Watson's discovery, at which time a mixed population of both varieties of *J. hemiendytus* and *J. bryoides* was found near Reno by Howell and members of the Northern Nevada Native Plant Society. It is now apparent that all three taxa and *J. tiehmii* can be found in appropriate habitats throughout northern Nevada.

Juncus hemiendytus var. *hemiendytus* is the most successful member of the "uncialis" group, extending from the Columbia River of Washington and the Uinta Mountains of Utah to the San Bernardino Mountains of California. As such it is in no way endangered, but it could qualify as rare in Washington (known only from turn-of-the-century Suksdorf collections) and Utah (one collection).

An excellent illustration of the variety appears in Buchenau (1906, p. 258, fig M-Q), based on *Herb. Norm. 32*. It has also been well illustrated in Hitchcock (1969). This is the same illustration used for Cronquist's (1977) all-inclusive *J. kelloggii*. The dimerous nature of the flower is clearly shown in both illustrations.

Peck (1961) gives Herman's [sic] Dwarf Rush as a vernacular name. Hitchcock and Cronquist (1973) use merely Dwarf Rush. Hermann's Dwarf Rush is perfectly suitable (much better than Half-clad Dwarf Rush!)

Representative specimens: UNITED STATES. CALIFORNIA: **Alpine Co.**: 0.5 m W of Monitor Pass, *Howell 39752* (CAS). **Butte Co.**: 0.1 mi S of jct Humboldt Road & Skyway, *Jokerst & Schlising 0841* (CHSC). **El Dorado Co.**: 3 mi SW of Twin Bridges, *Howell 39879* (CAS). **Fresno Co.**: E of entrance to Graveyard Lakes Basin, *Quibell & Quibell 4621*

(FSC, RSA). **Humboldt Co.**: Buck Mt., Tracy 4168 (UC, WTU). **Lake Co.**: W of Putah Creek bridge, Mason 14037 (DS, NY, UC, US). **Lassen Co.**: Big Valley Mts. SW of Nubieber, 11 Jun 1940, Eastwood & Howell s.n. (CAS). **Mariposa Co.**: 6 mi E of Porcupine Creek on Tioga Road, Ertter & Strachan 3074 (CAS, FSC, NY). **Modoc Co.**: Dismal Swamp, Warner Mts., Wheeler 3739 (CAS, MICH, NY). **Mono Co.**: Sonora Bridge Campground, Ertter & Strachan (NY). **Napa Co.**: 3-4 mi E of Angwin's, Tracy 1534 (UC, US, UTC). **Nevada Co.**: Small Lake on Bowman Lake Road, True & Howell 4079 (CAS). **Placer Co.**: Chambers Lodge, Tahoma, Howell 39833 (CAS). **Plumas Co.**: Milford - Beckwourth Road, Ertter & Strachan 3880 (CAS, NY, RSA), 3884 (NY, UC). **San Bernardino Co.**: Road 2N10 2 mi S of Hwy 18, Ertter & Strachan 3004 (CAS, NY, RSA, SD). **Shasta Co.**: Hatchet Mt. between Montgomery Creek & Burney, Eastwood & Howell 7902 (CAS, MICH). **Sierra Co.**: Mitchell Canyon Road, Dog Valley, Ertter et al. 2765 (BKL, CHR, CHSC, CPH, DAV, FSC, HSC, K, MARY, MICH, NY, OBI, PH, PRE, RSA, SACT, SBBG, SD, SFSU, TEX). **Siskyou Co.**: W of Upper English Lake, Salmon Mts., Oettinger & Thorne 1266 (HSC, MICH, RSA, UC). **Sonoma Co.**: summit of Bennett Valley Road, Eastwood & Howell 7865 (CAS, MICH). **Tulare Co.**: Sky Parlor Meadow, Chagoopa Plateau, Howell 17522 (CAS, F, GH, MICH, NY, SFSU); Bubbs Creek Canyon, Howell 25018 (CAS, DS, NA, NY, UC, US). **Tuolumne Co.**: Tuolumne Meadows, Ertter & Strachan 3925 (CAS, NY), 3929 (NY, RSA, UC), 3933 (NY, RSA, TEX, UTC); between Sugar Pine & Long Barn, Howell 30262 (CAS). **Yuba Co.**: cemetary near Brownsville, Ahart 2352 (CAS, CHSC, NY). IDAHO: **Boise Co.**: 1/2 mi SW of Centerville, Ertter & Strachan 3798 (CIC, NY). **Custer Co.**: Elk Meadows, N end Stanley

Basin, Ertter ST-223 (CIC). **Elmore Co.** Walker Gulch, Mt. Bennett Hills S of Hill City, Ertter 4179 (CAS, CIC, ID, NY, OSC, US, UTC, WTU). **Franklin Co.**: Franklin Basin, Bear River Range, Maguire 21628 p.p. (NY). **Gooding/Camas Co. line**: 19 mi N of Gooding, Ertter 4200 (BRY, CIC, MO, MONTU, NY, ORE, RM, WS). **Owyhee Co.** headwaters of Jordan Creek E of Silver City, Ertter et al. 4485 (CAS, CIC, NY, UTC). NEVADA: **Elko Co.**: Jack Creek Road, Independence Mts., Ertter & Strachan 3770 (CAS, CIC, MICH, NY, RENO, TEX, UTC); 1.3 mi S of Bull Run, SW of Mountain City, Ertter & Strachan 3779 (CAS, CIC, NY, UTC); W side Sunflower Flat N of Wildhorse Reservoir, Ertter & Strachan 3783 (BRY, GH, NY, ORE, UC, WS); Clover Mts. = East Humboldt Mts., Watson 1200 (GH, NY, US). **Humboldt Co.**: 1 1/2 mi S of Canyon Creek Summit, Santa Rosa Mts., Ertter 4323 (CAS. CIC, NY); SE side Rock Spring Table, Sheldon Wildlife Refuge, Tiehm & Rogers 4482 p.p. (NY, RENO, UTC). **Washoe Co.**: Little Valley, Carson Range, Ertter et al. 2773 (ASU, GH, ISC, LE, MEXU, NA, NSMC, NSW, NY, UC, UTC, WTU); Mitchell Canyon, Peavine Mt., Howell et al. 51178 (CAS). OREGON: **Columbia Co.**: St. Helen, May 1887, Howell s.n. p.p. (F, MO, NA, NY, OSC, ORE, UC, US). **Harney Co.**: Steens Mt. between Fish Lake & Frenchglen, Ertter & Strachan 3113a (NY). **Jackson Co.**: Lower Table Rock NW of Medford, Chambers 2453 p.p. (DS, NY, OSC). **Josephine Co.**: Grant's Pass, 24 Jun 1884, Howell s.n. p.p. (F, ORE, WTU). **Klamath Co.**: 27.5 mi N of Klamath Falls, Maguire & Holmgren 26506 (NY, UC, US, UTC, WTU). **Lake Co.**: Indian Springs, Hart Mt. Antelope Refuge, Ertter 4403 (NY); Mill Creek 4 mi NW of Paisley, Peck 15660 (DS, UC, WILLU). **Marion Co.**: Salem to Silverton, Hall 543 (F, GH, LA, MICH, MO, NY, RM, UC, US). **Umatilla Co.**: Green Mt. ca 10 mi NNE of La Grande, Wagner 2512 (ORE). **Wallowa Co.**: Target Springs area, Mason 7774 (ORE). **Wasco Co.**: Clear Lake, Peck 15902 (DS, WILLU). UTAH: **Daggett Co.**: 5 mi S of Carter Cr on Rt. 44, Maguire 12397 (NY, UTC). WASHINGTON: **Klickitat Co.**: Falcon Valley, Suksdorf 6987 (CAS, DS, MO, NA, NY, PH, UC, WS).

9b. JUNCUS HEMIENDYTUS var. ABJECTUS (F. J. Hermann) Ertter

Juncus abjectus (abjectus L., cast away, by way of abject, wretched, in reference to the "dispirited or dejected appearance" [Hermann, pers. comm.]) F. J. Hermann, Leafl. W. Bot. 5: 120. 1948. -- TYPE: UNITED STATES. OREGON: Harney Co.: 7 mi W of Riley, dry stream bed, 22 Jun 1925, M. E. Peck 13893 (Holotype: F!; Isotypes: CAS!, MICH!).

Plants 0.3--2.5 cm tall; culms to ca 20, 0.1--2.2 cm long, 0.2--0.5 mm thick, the summit dilated at the base of the flower; bracts lacking; tepals (1.2) 2--3 (3.5) mm long, 0.5--1.2 mm wide, all equal or the inner slightly shorter, obtuse or acute, erect or rarely slightly incurved, the central band 0.2--0.5 mm wide, the membranes unpigmented, 0.2--0.3 mm wide; anthers 0.4--0.7 mm long, 1/2 the length of or almost equalling the filaments; style 0.1--0.4 mm long; capsule obovoid to oblong, distinctly retuse, most often slightly less than but sometimes to 0.5 mm longer than the tepals, (1) 1.9--3.2 mm long, 1.1--2 mm wide, often turning brick-red at maturity; seeds to 10 per row and ca 60 per dimerous capsule, ovoid to oblong, 0.4--0.55 mm long, finely reticulate at 30x (Fig. 7e,f).

Central Idaho west to central Oregon, south to the mountains of the northern Great Basin in northern Nevada and through the Sierra Nevada to Tulare Co., California, from 1450 to 3400 m elevation. Flowering from May in the Great Basin to August in the Sierras.

Frequently growing with var. hemiendytus, less often with J.

bryoides, J. tiehmii, and J. capillaris, rarely with J. uncialis and J. luciensis.

This variety was first collected in Oregon as part of Leiberg 375, a mixture of var. abjectus and J. uncialis identified by Coville as J. saginoides. The plants are immature but still identifiable by their bracts (or lack thereof). Buchenau (1906), who rejected both J. triformis var. uniflorus and J. uncialis as distinct, nevertheless suggested that Leiberg's collection might represent a new species:

> Planta Leibergi . . . caules praebet unifloros, flores plerumque dimeros, saepe perfecte eprophyllatos, tepala fructu immaturo longiora, obtusa, dorso viridiuscula, apice interdum rubescentia. An species propria?

The illustrations accompanying these words verify that Buchenau was concentrating on that portion of the collection referrable to var. abjectus.

When Hermann published his revision he was aware of var. abjectus from only two locations, both in Harney County, Oregon. He annotated and cited Leiberg's collection only as J. uncialis. A collection of var. abjectus from the Sierra Nevada (Howell 20449) was annotated and cited as J. hemiendytus.

In my understanding J. hemiendytus var. abjectus is that member of the complex most specifically adapted to the northern Intermountain Region. The seeds of var. abjectus are the most difficult to germinate in the complex, which suggests that complicated controls have been developed to allow the variety to thrive under the unreliable climate of the northern Intermountain region.

This variety, as J. abjectus, has been included on the state lists of rare, threatened, and endangered plants in both Oregon and California. It was placed on the 1979 Oregon review list (Siddall et al., 1979) pending further evaluation of Cronquist's reduction of all short-styled members of the J. triformis complex under J. kelloggii (Gruber et al., 1979). In both the 1974 (Powell) and 1980 (Smith et al.) editions of the California inventories, J. abjectus is coded as rare but in no immediate danger. Apparently the variety is not particularly common anywhere, but it is not presently threatened, either.

The only previous illustration is that of Leiberg 375 in Buchenau (1906). Peck (1961) has used Least Dwarf Rush as a suitable vernacular name.

Specimens examined: UNITED STATES. CALIFORNIA: **Alpine Co.**: Hope Valley, 23 Jun 1982 Best s.n. (NY); 3.2 mi N of Markleeville, Breedlove 3579-A p.p. (CAS); 0.5 mi W of Monitor Pass, Howell 38753 (CAS). **Lassen Co.**: Harvey Valley near Cone Springs, Norris et al. 19271A (HSC). **Modoc Co.**: 7 mi S of Hackamore, Eastwood & Howell 8278 p.p. (CAS, MICH). **Mono Co.**: Slate Creek, Munz 20041 (CAS, NY, RSA, TEX). **Nevada Co.**: 5.2 mi N of Boca, Howell & True 7131 (CAS); W side Donner Pass, Howell 18392 p.p. (CAS, NA); jct Boca - Hobart road & Dry Creek road, True & Howell 7719 p.p. (CAS); 4 mi SE of Hirschdale, True et al. 7906 p.p. (CAS); 1/2 mi NW of Summit Lake, True & Howell 7977 (CAS). **Plumas Co.**: Milford - Beckwourth Road, Ertter & Strachan 3882 (NY), 3884a (NY), 3891 (CAS, NY, RSA, UTC); 3/4 mi SW of Beckwourth, 18 Jun 1962, Howell s.n. p.p. (CAS). **Sierra Co.** Dog Valley, Mitchell Canyon Road, Ertter et al. 2765a (NY);

0.6 mi N of Dog Valley NW of Verdi, Ertter & Strachan 3695 (CHSC, DAV, LA, NY, SACT, SBBG, SD, SFSU, UC). **Tulare Co.**: Center Basin, Howell 24145 (CAS, NA); same, Munz 12580 (RSA); Rock Creek, Howell 25666 (CAS, NA, RSA, US); Crabtree Meadows, Raven 7511 (CAS). **Tuolumne Co.**: Glen Aulin trailhead, Tuolumne Meadows, Ertter & Strachan 3933a (NY); Glen Aulin trail, Howell 20449 (CAS, GH, LL, US). **IDAHO: Custer Co.**: Bonanza Guard House, Smith 58 (UTC). **Gooding Co.**: 19 mi N of Gooding, Ertter 4201 (CAS, CIC, ID, NY, WTU), same, Ripley & Barneby 10659 (CAS, NA). **Owyhee Co.**: Mudflat Road SE of Jordan Valley, Rosentreter 1786 p.p. (CIC). NEVADA: **Elko Co.**: Sunflower Flat N of Wildhorse Reservoir, Ertter & Strachan 3782 (CAS, CHR, CIC, GH, MICH, NY, PH, PRE, RENO, RM, RSA, TEX, US, UTC, WS). **Humboldt Co.**: Sheldon Nat'l Wildlife Refuge, SE side Rock Spring Table, Tiehm & Rogers 4482 p.p. (NY, RENO, UTC). **Washoe Co.**: Mitchell Canyon, Peavine Mt. near Reno, Howell et al. 51176 (CAS), Williams & Tiehm 75-82-24 p.p. (CAS, RENO); Big Meadows SE of Verdi, Howell 53239 (CAS), Tiehm et al. 4581 (NESH, NY, UTC); W Fork Gray Creek below Rose Knob, Tiehm 1447 p.p. (RENO); Little Valley, Carson Range, Tiehm 2135 (CAS, RENO). **OREGON: Harney Co.**: Steens Mt. Loop Road near Fish & Lily lakes, Ertter 4424 (BRY, MO, NY, OSC, UC), Ertter & Strachan 3106 (CIC, NY), 3113 (CAS, CIC, NY, ORE, UTC); Steens Mt., 5 mi S of Wildhorse Creek, Peck 14042 p.p. (DS, F, WILLU, WTU). **Lake Co.**: 4 km N of Button Springs, Leiberg 375 p.p. (DS, NY, ORE, US); near Button Springs, Jul 1894, Leiberg s.n. (WS); 9 mi W of Lakeview, Peck 25449 p.p. (UC, WILLU).

[The NY sheet of Suksdorf s.n., 25 Jun 1881, from Falcon Valley, Klickitat Co., Washington, has 1 plant of var. abjectus in a packet of var. hemiendytus, but I take this to be an accidental inclusion as no other duplicates include var. abjectus.]

EXSICCATAE

abj = *J. hemiendytus* var. *abjectus*
aha = *J. leiospermus* var. *ahartii*
bry = *J. bryoides*
cap = *J. capillaris*
hem = *J. hemiendytus*
kel = *J. kelloggii*
lei = *J. leiospermus* var. *leiospermus*
luc = *J. luciensis*
tie = *J. tiehmii*
tri = *J. triformis*
unc = *J. uncialis*

Ahart 192, 15 Apr 1973 (aha); **363**, 11 Apr 1974 (unc); **364**, 11 Apr 1974 (unc); **422**, 24 Apr 1974 (unc); **423**, 24 Apr 1974 (aha); **s.n.**, 5 Jun 1974 (aha); **s.n.**, 6 Jun 1974 (unc); **891**, 16 Jul 1975 (hem); **1620**, 26 Mar 1978 (aha); **1626**, 10 Apr 1978 (unc); **s.n.**, 13 Apr 1978 (aha); **1644**, 17 Apr 1978 (lei); **1645**, 17 Apr 1978 (lei); **1648**, 18 Apr 1978 (aha); **1661**, 21 Apr 1978 (aha); **1692**, 1 May 1978 (aha); **1695**, 1 May 1978 (unc); **1702**, 2 May 1978 (lei); **1703**, 2 May 1978 (lei); **s.n.**, 25 Apr 1979 (lei); **s.n.**, 25 Apr 1979 (unc); **1854**, 30 Apr 1979 (lei); **1857**, 7 May 1979 (lei); **s.n.**, 10 May 1979 (lei); **1895**, 29 May 1979 (lei); **s.n.**, 4 May 1980 (unc); **2238**, 10 May 1980 (aha); **2240**, 11 May 1980 (kel); **2263**, 13 May 1980 (kel); **2352**, 25 May 1980 (hem); **2474**, 20 Jul 1980 (tri); **3401**, 1 May 1982 (unc); **3402**, 1 May 1982 (aha: type of *J. leiospermus* var. *ahartii*); **3428**, 9 May 1982 (unc); **3434**, 14 May 1982 (aha).

Applegate 4347a (hem).

Austin s.n., Jun 1879 (hem).

Baker 9889 (hem, unc); **10418** (hem, kel).

Baker & Nutting s.n., 26 May 1894 (lei).

Best s.n., 23 Jun 1982 (abj).

Bolander 4646 = Herb. Norm. 31 (kel: type of *J. triformis* var. *brachystylus*); **4691**, 6 May 1866 (kel); **4691b = Herb. Norm.**

32 (hem: lectotype of *J. triformis* var. *uniflorus*); 4864 = Herb. Norm. 30 (tri: lectotype of *J. triformis* var. *stylosus*); 6034, 8 Jul 1866 (cap); s.n., 8 Jul 1866 (tri); s.n., Apr 1866 (kel); s.n., Ft. Bragg (kel); s.n., Tuolumne R. (bry, tie).

Bolander & Keller s.n., 1872 (hem).

Brandegee, K., s.n., May 1884 (kel).

Brandegee, T., 3375 (tri); s.n., 16 May 1893 (tie).

Breedlove 3579-A (hem, abj); 3579-B (bry); 4726A (unc, aha).

Brock 233 (tri).

Campbell s.n., 30 Jul 1983 (tri).

Cardiff s.n., 2 Jul 1908 (bry).

Chambers 2453 (hem, 1 unc); 3991 (hem).

Clausen & Kruckeberg 1898a (bry).

Congdon 84 (unc); s.n., 13 Apr 1902 (tri); s.n., 15 Jun 1902 (tri); s.n., 19 Apr 1903 (tri).

Copeland 1566 (unc); s.n., 17 Apr 1935 (unc); s.n., 2 Apr 1936 (unc); s.n., 15 Jul 1947 (cap, hem).

Coville 617 (hem).

Crum 1602 (unc).

Day & Campbell 62-22 (hem).

Diehl s.n., 17 Jun 1902 (kel); s.n., 18 Jun 1902 (kel).

Dunn 282A (tri).

Eastwood 4136 (luc, kel); s.n., 1-13 Jul 1899 (tri).

Eastwood & Howell 4197 (unc); 4198 (luc); 5454 (tri); 7865 (hem); 7866 (kel); 7902 (hem); 8111 (tie); 8278 (hem, abj); 8496a (bry); 9212 (bry); s.n., 11 Jun 1940. (hem).

Ertter ST-223 (hem); 220/5 = BJE 75-186 (bry); 2438 (bry); 4179 (hem); 4180 (bry); 4200 (hem); 4201 (abj); 4321 (bry); 4322 (tie); 4323 (hem); 4403 (hem); 4424 (abj); 4430 (unc).

Ertter & Strachan 2869 (bry); 2971 (tie: type of *J. tiehmii*); 2972 (bry); 2987 (tie); 2995 (tie); 3004 (hem); 3005 (tie); 3028 (tie); 3029 (cap); 3038 (bry); 3060 (tri); 3064 (tri); 3069 (unc); 3070 (tri); 3072 (bry); 3073 (cap); 3074 (hem); 3075 (cap); 3076 (cap); 3086 (hem); 3106 (abj); 3107 (bry); 3113 (abj); 3113a (hem); 3333 (kel); 3365 (luc); 3366 (luc: type of *J. luciensis*); 3369 (kel); 3369a (luc); 3378 (luc); 3379 (kel); 3380 (luc); 3381 (kel); 3394 (luc); 3395 (kel); 3396 (luc); 3397 (tie); 3398 (luc); 3439 (tie); 3481 (tie); 3482 (bry); 3517 (tie); 3518 (tie); 3518a (bry); 3520 (tie); 3521 (tri); 3522 (tie); 3529 (luc); 3530 (tie); 3531 (bry); 3538 (tri); 3541 (tie); 3693 (bry); 3694 (tie); 3695 (abj); 3770 (hem); 3776 (tie); 3777 (hem); 3778 (bry); 3779 (hem); 3781 (hem); 3782 (abj); 3783 (hem); 3784 (bry); 3786 (tie); 3792 (tie); 3796 (tie); 3797 (bry); 3798 (hem); 3880 (hem); 3881 (luc); 3882 (abj); 3884 (hem); 3884a (abj); 3885 (luc); 3886 (luc); 3887 (tie); 3891 (abj); 3891a (hem); 3896 (cap); 3896a (tie); 3897 (cap); 3897a (tie); 3921 (tie); 3922 (bry); 3923 (hem); 3924 (tie); 3925 (hem); 3926a (hem); 3927 (tie); 3928 (cap); 3928a (tie); 3929 (hem); 3930 (bry); 3931 (hem); 3932 (bry); 3933 (hem); 3933a (abj); 3934 (cap); 3934a (tie); 3935 (tri); 3942 (tri).

Ertter et al. 2765 (hem); 2765a (abj); 2766 (tie); 2771 (bry); 2772 (hem); 2773 (hem); 3267 (aha); 3309 (lei); 4289 (tie); 4483 (bry); 4484 (tie); 4485 (hem).

Ferris 11182 (bry).

Ferris & Bacigalupi 12389 (unc).

Gander 1189 (tri); 3392 (tri); 3706 (tri); 4064 (tri); 5834 (tie); 6341 (tie); 7215 (tri).

Greene s.n., May 1886 (kel); s.n., 5 May 1890 (unc: type of *J. uncialis*).

Grimes et al. (bry).

Haid s.n., 4 Jul 1967 (tie).

Hall 543 (kel, hem).

Hall & Chandler 558 (tri: type of *J. megaspermus*).

Hardham 1981 (bry); 2410 (hem); 2416 (hem); 3094 (luc); 3100 (luc, kel); 3680A (tri); 4519 (luc, tie); 5342B (luc, kel, bry); 5433 (luc, kel, bry); 5573 (kel, luc); 5896 (tie); 5896A (luc); 5899 (tie); 10707 (luc), 12090 (tie, tri); 21566 (lei); 21821b (cap).

Heller 12326 (lei: type of *J. leiospermus*).

Heller & Kennedy 8695 (luc, hem).

Henderson 812 (kel); 1029 (kel); 13033 (kel).

Hermann 24752 (bry); 24775 (hem).

Hesse 599 (kel); 614 (kel); 2071 (tie); 2326 (tie); 2326a (cap); 2353 (cap); 3342 (kel).

Hilend 171 (hem).

Hillebrant 2333 (cap).

Holland 289 (lei); 348 (unc); 386 (unc); 402 (unc); 500 (lei).

Holmgren & Holmgren 9469 (unc); 9587 (hem).

Hoover 490 (unc); 2095 (unc); 2270 (lei); 3444a (tri); 8472 (luc, tie); 9907 (tie).

Howell, J.T., 13213 (hem: type of of *J. hemiendytus*); 15564 (cap);

15904 (cap); 16354 (kel); 16651 (tie, bry); 16710 (bry); 16836 (bry); 17328 (cap, tie); 17336 (cap); 17522 (hem); 17571 (bry); 17925 (kel); 18031 (hem); 18033 (kel); 18392 (abj, hem); 19891 (tie); 19892 (cap); 20441 (cap, tie); 20449 (abj); 20487 (cap); 20785 (kel); 21980 (kel); 22490 (bry); 22673 (bry); 22683 (bry); 22803 (bry); 25018 (hem, bry); 25145 (abj); 25337 (kel); 25452 (bry); 25453 (tie); 25666 (abj); 25667 (bry); 25682 (cap); 25731 (bry); 26927 (tie); 26928 (bry); 27135 (tie, bry); 27956 (cap); 29190 (unc); 30262 (hem); 31141A (unc); 33948 (cap); 34874 (hem); 35814 (hem); 37820 (hem); 37862 (tie, bry); 38282 (tie); 38539 (tie); 39752 (hem); 39753 (abj); 39754 (bry); 39833 (hem); 39879 (hem); 41096 (unc); 41192 (tri); 42549 (kel); 44151 (tie); 47248 (tie); 50538 (luc); 52836 (lei); 53239 (abj); 53801 (tie); s.n., 18 Jun 1962 (hem, abj, tie).

Howell, J. T., & Barneby 29354 (tri); 29369 (tri).

Howell, J. T., & True 7079 (unc); 7131 (abj); 41731 (tie); 42844 (tie, bry); 43003 (bry); 43004 (tie); 43131 (tie); 43196 (tie); 43197 (bry); 45586 (tie); 46288 (hem); 46348 (tie); 46722 (tie); 46862 (bry); 46863 (tie); 47129 (tie); 47160 (tie, hem); 48567 (tie).

Howell, J. T., & Wagnon 53616 (hem).

Howell, J. T., et al. 51178 (hem); 51176 (abj); 51177 (bry).

Howell, T., 307, 24 Jun 1884 (kel, hem); s.n., May 1887 (hem, kel).

Iverson 5 (tri).

Jepson 1205 (unc); 4414a (tri); 12835a (tri); 18070a (unc).

Johnston 2888 (tie).

Jokerst 0121 (unc); 0481 (lei); 0594 (lei); 0699 (lei); 0830 (tri).

Jokerst & Schlising 0841 (hem).

Keck 1225 (tri).

Keck & Clausen 5289 (cap).

Kelley 06221979-4 (bry).

Kellogg s.n., 22 Apr 1866 (kel: type of J. kelloggii).

Kellogg & Harford 1039 (kel).

Knight et al. 1999 (hem).

Koch 873 (hem, unc).

Lathrop 5451 (luc).

Leiberg 375 (abj, unc); **2525** (cap, tie); **5170** (hem); s.n., Jul 1894 (abj).

Leschke s.n., 1 Aug 1942 (hem); s.n., 29 Apr 1945 (kel).

Lin 51 (unc).

Maguire 12397 (hem); **21628** (bry; 1 hem).

Maguire & Holmgren 26506 (hem).

Mason 7774 (hem); **11939** (tri); **11981b** (tri); **14037** (hem).

Mathias 880 (tie).

McGregor 139 (tie).

Moran 16150 (tie); **16333** (tie); **22024** (tie); **23340** (bry); **24415** (tie); **25693** (bry); **25700** (bry); **27013** (bry); **27031** (bry); **27464** (tie); **27464 1/2** (bry); **27501** (bry); **27521** (tie); **27700** (tie); **27740** (tie).

Moran & Thorne 14302 (tie); **14452** (tie).

Munz 5473 (bry, tie); **7364** (tri); **9676** (bry); **10531** (hem, tie); **10862** (tie); **12533** (bry, hem); **12580** (abj); **12632** (hem); **14054** (bry, tie); **14195** (bry); **15203** (bry); **15203 A** (tie); **20041** (abj).

Nelson 645 (hem); **4863** (kel).

Norris et al. 19271A (abj).

Oettinger 1386 (hem); 1520 (hem).

Oettinger & Thorne 1266 (hem).

Orcutt 1166 (tie).

Ornduff 6144 (tri); 6154 (kel).

Orr & Orr s.n., 25 Jun 1980 (hem).

Packard 71-161 (hem).

Parish 1859 (bry: type of *J. bryoides*); 3701 (tie, bry); 10815 (tie).

Parry 343?, Jun 1881, (cap: type of *J. capillaris*).

Peck, M.E. 5145 (hem); 9976 (unc); 13718 (kel); 13893 (abj: type of *J. abjectus*); 14042 (abj, hem, 1 unc); 15098a (hem); 15660 (hem); 15902 (hem); 16292 (kel); 25449 (hem, abj).

Peirson 1645 (tie); 3105 (tie).

Piehl 63586 (bry, 1 luc).

Pollard s.n., 16 May 1956 (luc); s.n., 22 May 1956 (luc).

Purer 7242 (unc).

Purpus 5683 (tri).

Quick 48-61 (tri); 52-232 (tri); 52-239 (tri).

Quibell 1190 (hem); 4821 (cap).

Quibell & Brock 2 (tri).

Quibell & Quibell 2565 (cap, tie); 2587 (tie); 2588 (hem); 4621 (hem).

Quick & London 52-252A (cap).

Raven 3235 (cap); 3375 (cap); 4278 (bry); 4299 (tie, hem); 4299a (tie); 4673 (bry, cap?, hem?); 5676 (cap); 5802 (cap); 6020 (tie, cap, hem, bry); 7142a (tie); 7191 (hem); 7191 (bry); 7342 (cap); 7511 (abj); 7892 (bry); 8339 (cap); 9764 (hem).

Reed 2481 (tie).

Reveal 536 (tie).

Ripley & Barneby 10659 (abj).

Rosentreter 1786 (hem, abj).

Schlising 3517 (unc); 3551 (unc).

Sharp s.n., 21 May 1951 (hem).

Sharsmith 2171 (cap).

Simontacchi 815a (tie, bry, 1 hem).

Smiley 363a (tri); 739 (tri).

Smith 58 (abj).

Smith & Anderson 2983 (unc).

Spira 357 (bry).

Suksdorf 265, 1880 (hem); s.n., 15 Jun 1881 (hem); 427, 19 Jun 1882 (kel); s.n., 5 Jun 1883 (hem); s.n., May 1885 (kel); s.n., 12 Jun 1890 (hem); s.n., 27 Jun 1892 (hem); 2524, 28 May 1895 (kel); 2571, 3 Aug 1894 (kel); 6987, 11 May 1910 (hem).

Thorne et al. 38115 (tie).

Tiehm 985 (bry); 1332 (hem); 1447 (hem, abj); 1517 (bry, hem); 1531 (hem); 2135 (abj); 5392 (tie); 5744 (bry).

Tiehm & Read 6084 (bry); 6089 (tie).

Tiehm & Rogers 4482 (hem, abj).

Tiehm & Williams 7140 (unc); 7142 (bry).

Tiehm et al. 4581 (abj, hem); 5267 (bry).

Tracy 1534 (hem); 1534a (kel); 1555 (kel); 1555 1/2 (hem); 1611 1/2 (hem, unc); 4168 (hem); 4431 (kel); 16592 (kel).

Trowbridge 4012 (hem).

True 3645 (hem).

True & Howell 3947 (hem); 4079 (hem); 5410 (hem); 6601 (kel); 7284 (tie); 7719 (hem, abj); 7977 (abj).

True et al. 7906 (abj, hem).

Twisselmann 8690 (tie); 10961 (tie); 11351 (tie); 13406 (bry); 17847 (tie).

Wagner 2512 (hem).

Watson 1200 (hem).

Weber & MacLeod 12561 (bry).

Welsh 19584 (bry).

Welsh et al. 367 (bry).

Wheeler 3387 (unc); 3739 (hem).

Wiggins 2395 (bry); 9884 (tie).

Williams & Tiehm 75-82-22 (bry); 75-82-24 (abj, hem).

APPENDICES

APPENDIX I. Synopsis of subgenera in Juncus.

Beginning with Buchenau (1875), Juncus has been divided into eight to 12 subgenera or sections on the basis of inflorescence morphology, leaf structure, seeds characters, and duration. Most of these subgenera fall into one of two informal groups: 1) the prophyllate rushes having flowers arranged in one-sided cymes (drepania) with two bracteoles ("prophylls") subtending each flower; and 2) the eprophyllate rushes with flowers arranged in heads and lacking bracteoles.

The following brief synopsis of the subgenera is drawn mainly from Buchenau (1906), the last monograph of the entire genus. Subgenus Ensifolii is Snogerup's (1978) adaptation of one of Rydberg's (1917) unranked infrageneric subdivisions; all other subgenera are Buchenau's.

Snogerup (1963) and Index Nominum Genericorum (Farr et al, 1979) accepted Britton and Brown's (1913) lectotypification of Juncus L. on J. acutus L., which then requires that Buchenau's subg. Thalassi be renamed subg. Juncus. However, the arbitrary nature of Britton and Brown's lectotypification (see example to ICBN Art. 8.1), combined with Buchenau's earlier use of a subg. Genuini (which also contains Linnaean species), suggests that that the question of lectotypification of Juncus should be re-examined. For the purposes of this paper Buchenau's names have been retained.

I. Prophyllate subgenera.

A. Poiophylli: annual or perennial (or perennials separated as subg. Pseudotenageia); pith aerenchymatous; leaves mostly cauline, flat or canaliculate, not septate; flowers in drepania; fruit usually 3-locular; seeds not tailed. About 25 spp., cosmopolitan, centered in N. America. J. bufonius, J. tenuis, J. gerardii, etc.

B. Genuini: perennial; pith aerenchymatous; leaves culm-like on special short shoots or reduced to cataphylls at base of culm; inflorescence appearing pseudolateral because lowest bract appears as extension of culm; flowers in drepania; fruit usually 3-locular; seeds sometimes tailed. About 30 spp., cosmopolitan, centered in Pacific America and Australasia. J. effusus, J. balticus, J. drummondii.

C. Subulati: similar to subg. Genuini but with parenchymatous pith; leaves terete on culms. 1 sp., J. subulatus, Mediterranean.

II. Eprophyllate subgenera.

D. Thalassi (= subg. Juncus fide Snogerup): perennials; leaves basal, terete but not septate, pungent, auricles lacking; flowers in heads; stamens 6; fruit 3-locular; seeds apiculate to caudate. 10 spp., cosmopolitan, mainly coastal. J. acutus, J. maritimus, etc.

E. Alpini: perennials; leaves basal or cauline, mostly canaliculate, indistinctly septate, auricles usually conspicuous; flowers in 1-few heads, sometimes intensely colored; stamens 6, often exserted; fruit usually 1-locular; seeds usually distinctly tailed. 25 spp., mountains of northern hemisphere. J. biglumis, J. castaneus, etc.

F. Septati: perennials or annuals; leaves mostly cauline, terete, septate, auricles usually present; flowers in heads; stamens usually 6; fruit usually 1-locular; seeds variable. The largest subgenus of ca 100 spp., cosmopolitan. J. articulatus, J. nevadensis, J. nodosus, J. mertensianus, J. bulbosus, etc.

G. Ensifolii: similar to subg. Septati but leaves laterally flattened, equitant, incompletely septate, auricles often lacking. 8 spp. of western N. America. J. ensifolius, J. xiphoides.

H. *Graminifolii*: perennials or annuals (annuals sometimes separated as subg. *Juncinella*); leaves basal or cauline, flat or canaliculate, not septate, auricles present or absent; flowers usually in heads; stamens 6 or 3 (2); fruit 1- or 3-locular; seeds rarely tailed. 40 spp., mostly in N. America and S. Africa. *J. triformis*, *J. marginatus*, *J. capitatus*, *J. capensis*, *J. planifolius*, etc.

I. *Singulares*: often included in subg. *Graminifolii*, differs in the laterally compressed leaves. 1 rare sp., *J. singularis*, of S. Africa.

APPENDIX II. Collection of the complex before 1900.

Hillebrand 2333	1863	CA: Calaveras Co.	cap
Kellogg s.n.	22 Apr 1866	CA: San Francisco	kel
Bolander s.n.	1866	CA: Fort Bragg	kel
" 4646	May 1866	CA: Ukiah	kel
" 4691	6 May 1866	CA: Mendocino Co.	hem, kel
" 4864	10 Jun 1866	CA: Mariposa Co.	tri
" 6034	8 Jul 1866	CA: Yosemite	cap
" s.n.	8 Jul 1866	CA: Yosemite	tri
" s.n.	1866	CA: Tuolumne River	tie, bry
Kellogg & Harford 1039	1868-9	CA: no location	kel
Watson 1200	Sep 1868	NV: Clover Mts.	hem
Hall 543	Jun 1871	OR: Salem	kel, hem
Bolander & Keller	1872	CA: Sierra Valley	hem
Austin s.n.	Jun 1879	CA: Butte or Lassen Co.	hem
Parry s.n.	Jun 1881	CA: Yosemite	cap
Suksdorf 138	25 Jun 1881	WN: Falcon Valley	hem
" s.n.	19 Jun 1882	WN: Klickitat Co.	kel
Henderson 812	28 Jun 1882	OR: Hood River	kel
Suksdorf s.n.	5 Jun 1883	WN: Falcon Valley	hem
K. Brandegee s.n.	May 1884	CA: Lakeport	kel
T. Howell s.n.	24 Jun 1884	OR: Grants Pass	kel
Orcutt 1166	9 Jul 1884	MEX: Baja Calif.	tie
Greene s.n.	May 1883	CA: Suisan	kel
Parish 1859	Jun 1886	CA: Bear Valley	bry
Henderson 1029	24 Jun 1886	OR: Grants Pass	kel
T. Howell s.n.	May 1887	OR: St. Helens	kel, hem
Greene s.n.	5 May 1890	CA: Suisan	unc
Suksdorf s.n.	27 May 1892	WN: Falcon Valley	hem
T. Brandegee s.n.	16 May 1893	MEX: Baja Calif.	tie
Baker & Nutting s.n.	26 May 1893	CA: Shasta Co.	lei
Leiberg 375	30 Jun 1894	OR: Lake Co.	unc, abj
Suksdorf 2751	3 Aug 1894	WN: Bingen	kel
Parish 3701	Jun 1895	CA: Bear Valley	tie, bry
Leiberg 2525	5 Jul 1896	OR: Steens Mt.	cap, tie
Coville 617	26 Jul 1896	OR: Lake Co.	hem
Congdon 84	27 Apr 1897	CA: Mariposa	unc
Purpus 5683	Jun 1897	CA: Tule River	tri

APPENDIX III. Seed coat patterns from Balslev and Clemants. For key to abbreviations see Table 1.

PROPHYLLATE

subg. *Poiophylli*

J. bufonius	- c/b	a	Balslev, Clemants
J. dudleyi	- c	p	Clemants
J. gerardii	- c/b	p	Clemants
J. greenei	- c/a	p	Clemants
J. interior	- c	p	Clemants
J. tenuis	- c	p	Balslev, Clemants
J. uruguensis	+ c	p	Balslev
J. vaseyi	- dv	p	Clemants

subg. *Genuini*

J. arcticus			
var. *andicola*	+ ?	p	Balslev
J. balticus	± c	p	Clemants
J. effusus	± c	p	Balslev, Clemants
J. filiformis	± a?	p	Clemants
J. procerus	- c	p	Balslev

EPROPHYLLATE

subg. *Thalassi*

J. roemerianus	+ ?	p	Balslev

subg. *Alpini*

J. stygius	+ a	p	Clemants

subg. *Septati*

J. alpinus	+ d	p	Clemants
J. articulatus	- dv	p	Clemants
J. brachycarpus	- d	p	Clemants
J. brachycephalus	- dv	p	Clemants
J. brevicaudatus	- dv	p	Clemants
J. canadensis	- dv	p	Clemants
J. ebracteata	- d/c	p	Balslev
J. ecuadorensis	- dv	p	Balslev
J. leibmannii	- c	p	Balslev
J. microcephalus	- d	p	Balslev
J. nodosus	- d	p	Clemants
J. pallescens	- d/b	p	Balslev
J. pelocarpus	- d	p	Clemants
J. stipulatus	- d	p	Balslev
J. torreyi	- dv	p	Clemants

subg. *Ensifolii*			
J. ensifolius	- d	p	Balslev
subg. *Graminifolii*			
J. cyperoides	- d	p	Balslev
J. marginatus	- b	p	Balslev
"	- dv	p	Clemants
J. longistylus	- dv	p	Clemants
J. planifolius	- a	p	Balslev

APPENDIX IV. Somatic chromosome numbers in *Juncus*. (Compiled mostly from Index to Plant Chromosome Numbers. Counts made in conjunction with present study marked with an asterisk*).

subg. *Poiophylli*

perennials:

J. compressus	40, 44
J. dichotomus	80
J. dudleyi	80
J. greenei	80
J. gerardii	80, 84
J. interior	80
J. squarrosus	40, 42
J. tenuis (=*macer*)	30, 32, 40, 80, 84
J. trifidus	30

annuals:

J. ambiguus	34
J. bufonius	30, 34, ca 54, ca 60, 70, ca 72, 80, 100-110
J. foliosus	26
J. hybridus	34
J. ranarius	30, 32, 34, 60, 80, 120
J. sphaerocarpus	36
J. sorrentinii	28

subg. *Genuini*

J. arcticus	74
J. balticus	40, 80
J. conglomeratus	40, 42
J. coriaceus	80
J. drummondii	120
J. effusus	5, 40, 42, 80
J. filiformis	40, 70, 80
J. glaucus	40
J. haenkei	74
J. inflexus	20, 40, 80

subg. *Subulati*

J. subulatus	42

subg. *Thalassi*

J. acutus	ca 42, 46, 48
J. maritimus	40, 48

subg. *Alpini*

J. albescens	ca 130, ca 134
J. biglumis	100, 120, ca 130
J. castaneus	40, 60
J. membranaceus	60, 120
J. triglumis	50, ca 130

subg. *Septati*

J. acuminatus	40
J. acutiflorus	40
J. alpigenus	40
J. alpinus	40,80
J. anceps	40
J. articulatus	ca 60, 80
J. atratus	40
J. atricapillus	40
J. brachycarpus	44
J. brachycephalus	80
J. brevicaudatus	80
J. bulbosus	40
J. canadensis	80
J. elliottii	40
J. lamprocarpus	ca 60, 80
J. mertensianus	40, 80
J. nevadensis	40*
J. nodosus	40
J. nodulosus	30, 40, 80
J. oreganus	ca 60, 100-120, ca 112
J. pelocarpus	40
J. prismatocarpus	44, 76
J. pygmaeus	40
J. rugulosus	40
J. scheuzcherioides	40
J. scirpoides	44
J. subnodulosus	40
J. subtilis	40
J. supiniformis	56
J. supinus	40

J. thomasii	40
J. torreyi	40
J. trigonocarpus	40
J. validus	40
subg. *Ensifolii*	
J. ensifolius	ca 38*, 40
J. xiphoides	40
subg. *Graminifolii*	
perennials:	
J. biflorus	40
J. covillei	38
J. dregeanus	ca 35, ca 40
J. filipendulus	40
J. marginatus	38, 40
annuals:	
J. capitatus	18, ca 20*
J. bryoides	ca 38*
J. capillaris	36*
J. hemiendytus	32*
J. kelloggii	34*
J. leiospermus	32*
J. luciensis	32*
J. tiehmii	34*
J. triformis	36*
J. uncialis	32*

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