SVEN SNOGERUP

A revision of *Juncus* subgen. *Juncus (Juncaceae)*

Abstract

Snogerup, S.: A revision of *Juncus* subgen. *Juncus (Juncaceae)*. – Willdenowia 23: 23–73. 1993. – ISSN 0511–9618.

A revision of *Juncus* subgen. *Juncus* is presented and the following taxa are treated: *Juncus acutus* subsp. *acutus* and subsp. *leopoldii*, *J. littoralis*, *J. heldreichianus* subsp. *heldreichianus* and subsp. *orientalis*, *J. maritimus*, *J. rigidus*, *J. socotranus*, *J. roemerianus*, *J. cooperi*, *J. kraussii* subsp. *kraussii*, subsp. *australiensis* and subsp. *austerus*; three of these names are new combinations. The morphological characteristics and ecological tendencies of the subgenus are discussed. A key and distribution maps are given and the presence of gynodioecism and dioecism is discussed.

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1. Introduction

The two large genera in the family *Juncaceae*, *Juncus* and *Luzula*, differ in a combination of characters that must reflect one of the first dichotomies in the phylogeny of the family. *Luzula* has a three-seeded capsule with basal placentation, closed sheaths and hairs, whereas *Juncus* has a many-seeded capsule with different degrees of marginal to central placentation, usually open sheaths and no hairs.

There are two other character differences that also probably mark basal dichotomies in the family. One is the difference between several-flowered and one-flowered inflorescences and concerns the mono- or polyphyletic origin of the Antarctic-Andean small genera. The other is the divergence between single bracteolate flowers and the certainly derived state with discrete heads of bracteole-less flowers. The latter dichotomy divides between groups of subgenera of *Juncus*, and constitutes such a complicated combination of changes that the group of headed forms must be presumed to be monophyletic. I am not convinced that all the small genera *Prionium, Rostkovia, Marsippospermum, Oxychloe, Patosia* and *Distichia* represent lines more distinct than the subgenera of *Juncus*. Especially the present genus *Prionium* will probably have to be placed with changed rank among the headed subgenera of *Juncus*. I think it is advisable to await thorough DNA investigations before trying to decide between different possible phylogenetic trees or making changes in the generic or subgeneric delimitations.

The subgenus *Juncus* is one of the most easily delimited subgenera in the genus. It is recognized by the unique derived features of pungent leaf tips and terete leaves with marrow of rounded parenchyma cells, and by the additional characters of flowers in bracteole-less heads, tailed seeds, trilocular or triseptate capsules and many, small chromosomes (2n = 46, 48).

2. Material

For this revision living material, in nature and in cultivation, has been studied for all taxa except *J. kraussii* subsp. *austerus*. More than 9000 herbarium specimens have been checked for descriptions and distribution maps.

Material has been seen from the following herbaria: ANK, ATH, ATHU, B, BG, BM,

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BOL, BOLO, C, CAI, CAIM, CAM, CAS, CGE, CGG, E, EGE, FI, G, GAT, GB, H, HUJ, JEPS, K, L, LD, LE, LINN, M, MANCH, NPG, O, PR, PRE, RSA, S, SAM, STE, TAU, TUR, UC, W, WU, ZT and the private herbaria of A. Huber-Morath, F. Sorger, A. Baytop, K.-P. Buttler, J. Zaffran, W. Greuter and K. H. Rechinger.

3. Typification of *Juncus*

The first formal typification of *Juncus*, with *J. acutus* L., was made by Coville in Britton & Brown (1913: 465) but generally the typifications by Britton & Brown have been dismissed as founded entirely on a mechanical principle. Nevertheless the typification of *Juncus* with *J. acutus* has been repeated by subsequent authors without being challenged. According to present rules my indication of J. acutus as type of the name *Juncus* L. (Snogerup in Rechinger 1971) is to be regarded as the valid selection of this type. Later Novikov (in Fedorova 1976) selected *J. inflexus* L., a selection further defended by Novikov (1990) for which I see no justification. My earlier typification of *Juncus* L. has also been accepted recently in the "List of Linnaean generic Names and their Types" (Jarvis et al. 1993).

4. Morphology and anatomy

4. 1. Mode of branching

All species of this subgenus are long-lived perennials and develop innovation shoots from the base of the old individual. This is, however, effected in different ways in different groups of species.

In the *J. maritimus* group and in *J. kraussii* and *J. roemerianus* the rhizome is well developed, branching, with internodes of varying length. The culms develop in a series from the rhizome and are unbranched. Thus, the whole plant is matforming to laxly caespitose and a single individual may propagate vegetatively to form extensive stands.

In the *J. acutus* group and *J. socotranus* the rhizome is extremely abbreviated. Branching is effected by intravaginal shoots in the axils of the lower sheaths of culms. This results in the formation of a dense tussock which eventually becomes more or less hemispherical. The individual produces many flowering culms but forms only a tussock of limited although considerable size and age and does not propagate vegetatively.

The two modes of branching are rarely combined, although in the species with creeping rhizomes, new rhizomes are sometimes generated from the lowest axils of the culm, which break through the sheath laterally and sometimes produce a new culm close to the old one. Such events are often observed after a resting period, e.g. after winter in northern localities, or after dry periods in desert localities. Only *J. cooperi* has both types of branching described above, thus forming both dense tussocks and wide stands.

4. 2. Leaves

In all species of *Juncus* subgen. *Juncus* the leaves are arranged basally, and are born on extremely abbreviated internodes of the culm base. They may appear as deviating at different heights only because of successively longer sheaths of later leaves.

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The leaf tip is pungent, sclerenchymatous and sharply pointed. This type of leaf tip is not found in other subgenera of *Juncus*. The leaf tips of some species of *Juncus* subgen. *Genuini* are only superficially similar.

Auricles are never present at the delimitation between sheath and lamina as it is commonly observed in other subgenera.

The medulla of young leaves consists of rounded parenchyma cells with only small intercellular spaces between them (Fig. 1). The size of the cells is gradually larger towards the center of the leaf. In mature or old leaves the cells of the center are dead and empty, and may partly collapse, thus obscuring the original build-up of the medulla. The vascular bundles are distributed over most of the cross section, the largest ones occurring near the leaf center. Terete leaves are also found in some other subgenera of *Juncus* but in these all vascular bundles occur in a marginal parenchyma layer or in parenchymatous walls dividing the leaf into several tubes. The medulla is also different in these cases, consisting of either asterisciform or completely degenerated cells in mature leaves. Thus, the terete leaves of *Juncus* subgen. *Juncus* are only superficially similar to those of subgenera *Genuini, Subulati, Septati* and *Alpini*. They probably represent a separate phylogenetic line of the terete leaf form from the flat leaves which are considered primitive for both the family and genus (Fig. 1).

The stomata are found in longitudinal rills of the culms and leaves (Fig. 1) and are arranged between the weakly developed ridges.

The first very small leaves of the seedling are more or less U-formed in cross section but the third and later leaves are usually similar to those of the adult plants.

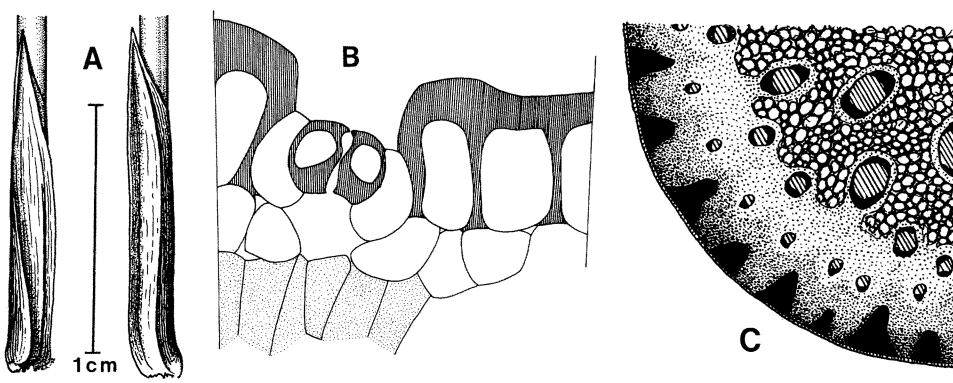

Fig. 1. A: *J. rigidus*, two-ridged bracteols from inflorescence branchings. – B: *J. acutus*, stoma from leaf. – C: *J. maritimus*, schematic part of leaf transect.
Material: A: Sinai, Wadi Talaa, Snogerup et al. 2827 (LD). – B: Greece, Naxos, *Snogerup cult. no. 1246* (LD. – C: Sweden, Blekinge, *Lövkvist* (LD).

4. 3. Inflorescence

The inflorescence is composed of a variable number of heads each usually few-flowered. Rarely, some flowers occur singly but this most probably reflects a reduction of few-flowered

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to one-flowered heads. Just as in the other subgenera with heads, there are never any simple involucral bracteoles like those found in the subgenera *Subulati, Genuini, Poiophylli* and *Pseudotenageia.*

The branches of the inflorescence, like all branches of the culms in this genus, appear in the axil of a bract and start with a basal, adaxial, two-ridged structure, here called prophyll. If each culm is regarded as an inflorescence, this structure may be explained as first or only bracteole of a present or potential top flower of the branch. The prophyll has two conspicuous keels or low wings and is often double-tipped but at the uppermost branches it is smaller and more variable in form (Fig. 1). Sometimes this prophyll functions as the bract of a second branch and this may even be repeated one or a few times, leading to a very compact inflorescence. In the heads, only a single bract per flower is present but never any bracteoles.

Comparison with other genera of the family indicates that the condition with three bracteoles to each flower is basic in *Juncaceae*. Therefore, the bracteole-less head as a flowering unit is a complicated, derived feature which *Juncus* subgenus *Juncus* shares with subgenera *Septati, Alpini, Graminifolii* and *Juncinella* and the genus *Prionium.*

The inflorescence is a raceme. Its main axis has short internodes so that the side branches usually overtop it. The presence of an apical head gives the impression of a 'cymose' inflorescence. However, the axis proceeds through the head with a series of flowers originating laterally. These flower in a sequence which indicates that their number is not strictly fixed. The main axis finally produces some reduced, more or less rudimentary flowers, consequently there is never any true apical flower. Thus, the bracteole-less head has to be regarded like the entire inflorescence as racemose.

All inflorescences in the genus *Juncus* are probably best explained as racemes with all flowers in a lateral position, as pointed out by Engelmann (1868). Novara (1976) states that only the headed subgenera have a racemose inflorescence, while that of the bracteole-flowered subgenera is cymose. If this interpretation is supported by further studies it will strengthen the difference between these two groups within *Juncus.*

4. 4. Flower

The floral parts are usually arranged in a conspicuous vertical sequence, and the capsule is shortly stipitate. The uppermost part of the short pedicel is often incrassate and more or less spongy, coalescent with the thickened and dorsally ridged bases of the outer tepals which are often inserted only slightly below the inner ones.

The tepals, especially those of the *J. acutus* group, have auricle-like, scarious apical parts often combined with a lamina-like mucro. Such tepals resemble a leaf sheath with reduced lamina. Similar tepal forms are found in most other subgenera as well, supporting the theory of such a homology of the *Juncaceae* tepal. The tepals are always persistent in fruit.

The filaments are broad at the base and inserted at the bases of the tepals. The anthers are two to several times as long as the filaments. The stamens are also persistent in fruit.

The capsule is clearly trilocular in most species, but in the *J. acutus* group it is variably triseptate. In some of the species with a trilocular capsule placental parts of neighbouring carpels form wings protruding into the locules of the capsule. In *J. roemerianus* these placental folds are incrassate and fill a large part of the capsule.

In all species except *J. roemerianus* and *J. kraussii* all flowers are hermaphrodite and usually conspicuously protogynous. *J. roemerianus* is gynodioecious with some individuals having perfect flowers and others functionally female flowers with rudimentary stamens;

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rarely both types of flowers occur on the same individual. Eleuterius (1984) reported a ratio of female to hermaphrodite plants of 1:2 in a progeny raised from seeds harvested from natural stands. As the seeds used for his experiments were harvested from mixed stands, this result implies that the inheritance of sex is complicated in *J. roemerianus*. My studies of plants collected in Florida, USA, indicate that Eleuterius probably collected most or all seeds from hermaphrodite plants.

Among five plants of *Juncus roemerianus* derived from transplanted rhizomes from the same locality there were two with female flower only, one with hermaphrodite flowers only, and two with both hermaphrodite and female flowers. The two plants with mixed flower types may of course be derived from the same clone.

Two other individuals of *Juncus roemerianus* with mixed flower types were found in seed progenies of females from two other localities. In these two progenies females, hermaphrodites and plants with mixed flower types occurred in the ratio of 5:3:1 and 4:2:1 individuals respectively. Three plants derived from seeds from a fourth locality were females. After free flowering the progeny of one of these consisted of 12 females and four plants with hermaphrodite flowers only.

The above figures suggest that the female status is determined by several complementary genes. The presence of female individuals in *J. roemerianus* was first noted by Engelmann (1868).

In *J. kraussii* subsp. *kraussii*, some individuals have female flowers with only rudimentary anthers, others have functionally male flowers with degenerating or reduced ovary and stigmas. In *J. kraussii* subsp. *australiensis* most populations contain hermaphrodite individuals only. Functionally female flowers were reported for this taxon by Buchenau (1890: 258), but until now I have observed only hermaphrodite flowers. The material of *J. kraussii* subsp. *austerus* studied has been limited, but all individuals examined were hermaphrodite.

4. 5. Chromosomes

A chromosome number of 2n = 48 was found in all taxa investigated for this revision but also 2n = 46 has been reported for *J. rigidus* (B. Snogerup 1985) and *J. acutus* (S. Snogerup 1958, Borgen 1969, Dalgaard 1986). However, my own earlier report of 2n = 46 for *J. acutus* should probably be regarded as a miscount. I have examined some of the slides on which B. Snogerup's report of 2n = 46 for *J. rigidus* was based and find the interpretation correct.

It is not known whether x = 24 or x = 23 is the original basic number in *Juncus* subgen. *Juncus*. The diffuse centromeric function may allow for a persistent dimorphism between x = 23 and x = 24 without disturbances of the meiotic functions in the heterozygotes. At least the *J. rigidus* plant with 2n = 46 has one pair of heterochromatic chromosomes longer than seen in the 2n = 48 plants of the subgenus.

Several other numbers published earlier by different authors can probably be regarded as miscounts due to the special difficulties of the material. All chromosomes in usual Navashin-fixed root tip mitoses are smaller than 1 µm, usually 0.1–0.5 µm; mitoses can only be interpreted after concentrated study with the help of good optical equipment. Four to eight of the largest chromosomes usually appear to stain differently but no chromosome pairs can be identified and no satellites have been observed. A few recent reports which I regard as probably correct and my own counts are summarized in Tab. 1.

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Tab. 1: Counts of chromosome numbers in *J.* subgen. *Juncus*

Taxon	2n	Locality
J. acutus	48	France, Bouche-du-Rhone, Badet 7 km N Les Stes Maries, 1957, *Snogerup* – S. Snogerup (1963)
—	48	Italy, 3 km N Livorno, 1957, *Snogerup* – S. Snogerup (1963)
—	48	Greece, Kikladhes, Naxos, S of the town, 1958, *Snogerup* – S. Snogerup (1963)
—	46	Italy, Emilia, 6 km S Porto Garibaldi, 1957, *Snogerup* – S. Snogerup (1958)
—	46	Borgen (1969)
—	46	Dalgaard (1986)
J. acutus × *littoralis*	48	Greece, Kikladhes, Naxos, S of the town, 1958, *Snogerup* – New count
J. heldreichianus subsp. *heldreichianus*	48	Greece, Kikladhes, Naxos, ESE of S Procopi, 1958, *Snogerup* – New count
—	48	Greece, Kikladhes, Naxos, 3 km N Mitria, 1958, *Snogerup* – New count
J. littoralis	48	Greece, Kikladhes, Naxos, S of the town, 1958, *Snogerup*, – New count
J. maritimus	48	Sweden, Blekinge, 1958, *Lövkvist cult.* – S. Snogerup (1963)
—	48	Sweden, Öland, Borgholm, 1959, *Snogerup* – S. Snogerup (1963)
—	48	Greece, Kikladhes, Ios, S of the harbour, 1957, *Runemark* – S. Snogerup (1963)

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5. Ecological specialization

Most species of *Juncus* subgen. *Juncus* occur in saline seashore habitats or in ecologically similar localities in desert and steppe areas such as wadis and depressions. The common ancestor of the subgenus probably evolved from the early *Juncus* forms by an adaptation to localities with high water stress. This is reflected in obviously adaptive characters such as the hard leaf and culm surfaces with stomata in rills, the tough, deep-growing roots and the strong, perennating basal parts of the large plants.

In deserts and other dry areas the few comparatively wet places, like depressions, wadis and salt marshes, are subject to intensive grazing. Especially during extended dry periods with no growth of annuals the perennial species will be severely overgrazed. Therefore, it can be expected that the perennials of such areas develop various methods of protecting themselves against grazing animals. In *Juncus* subgen. *Juncus* the pungent leaf tips represent such an adaptation. Their effects is further strengthened in the *J. acutus* group where the dense tussocks have pungent bracts pointing in all directions. The rather peculiar, salty and bitter taste may also serve as a protection. When the species of subgen. *Juncus* grow mixed with stands of other *Juncus* species, e.g. *J. subulatus*, the latter are always taken first by the animals.

J. heldreichianus is found in the same habitats as the other species but also in permanently moist localities like streams and fresh-water swamps. *J. socotranus* is also predominantly found in moist fresh-water habitats. As the closely related forms of the *J. acutus* group are more typical seashore and desert plants, the former cases probably reflect later reverse specializations.

An important feature of the life cycle of *Juncus* subgen. *Juncus* is the tendency to start flowering long before the plant has reached its final size, often with considerably smaller inflorescences than those in the adult plant. This may be a way to combine the benefit of a tall perennial habit with the possibility of quickly securing a seed reserve against the chance of catastrophic drought. This tendency is especially conspicuous in *J. cooperi*. It begins flowering a few months after germination while still resembling a small annual. Only after about two years the plant has reached its full size, and not till then it develops a tussock and spreading rhizomes.

6. Hybridization in *Juncus* subgen. *Juncus*

In most cases of hybridization in other subgenera of *Juncus*, the hybrids are almost completely seed sterile and secondary hybrid products are rarely observed in nature (cf. Nilsson & Snogerup 1971, 1972, Riebe 1978, Snogerup 1969, Stace 1975). In *J.* subgen. *Juncus* the hybrids often set some seed and introgression or formation of hybrid swarms cannot be excluded. However, I have observed several localities where species of the *J. acutus* group grow together and there were usually no or very few plants which appeared to be hybrids. Thus, the hybrids are probably less viable than the parental types.

The populations consist of a small to moderate number of very large and long-lived plants so that establishment of new ones from seedlings must be considered as very rare in spite of the high seed output. A very hard selection must take place at the seedling stage, allowing the establishment of plants from only one of some million seeds. Even if some random factors are involved in this large-scale elimination, such as the moisture at the site of germination, most of the losses must be regarded as selective. Hybrids with any degree of reduced viability will stand a great chance of being eliminated completely in one or a few generations.

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There are, however, some observations which indicate that introgression can take place. Thus, in the Caspian area some *J. acutus* specimens show wide inflorescences combined with dark capsules and sometimes a more pyramide-shaped capsule top than usual in this species. This combination of characters may be taken as indicative of introgression from *J. littoralis* with which *J. acutus* frequently occurs in mixed stands in this area. Presumably introgressive *J. acutus* specimens are found in other places, e.g. near Athens, Greece. *J. acutus* and *J. littoralis* have about the same flowering period, so cross-pollination can easily occur. Hybrids of this parental combination have been identified in Greece and in Israel. The seed set is often 25–50% in the Greek hybrids whereas much less in those from Israel.

J. acutus and *J. heldreichianus* frequently occur together in the Aegean area but their flowering times are so different that there is little chance of hybridization. When intermediates are occasionally found, they are rather fertile, thus the isolation between these two species is probably mainly maintained by seasonal isolation. The type collection of *J. heldreichianus* happens to contain some probable hybrid specimens but a suitable lectotype to maintain current usage could be selected.

On the W coast of Naxos, Kikladhes, four species, i.e. *J. acutus, J. littoralis, J. heldreichianus* and *J. maritimus*, grow together in large numbers over several square kilometers of sand fields. A thorough search for hybrid individuals was made in these mixed stands. Most individuals showed no sign of hybridity and were fully fertile. Some individuals growing 1–2 km S of the town of Naxos, could be interpreted as hybrids of the parental combinations *J. acutus* × *heldreichianus*, *J. acutus* × *littoralis* and *J. heldreichianus* × *littoralis*. The populations of the presumed parents seemed, however, quite uneffected so that only a small number of hybrid tussocks occurred without upsetting the distinction between the parental species.

J. heldreichianus specimens with unusually obtuse capsules occurring in some places in the Aegean should probably not be interpreted as being of hybrid origin. Such a capsule form is characteristic of the eastern subsp. *orientalis* and may occur locally further W as a variation within pure *J. heldreichianus*.

J. heldreichianus has repeatedly been misdetermined by collectors as a hybrid between *J. acutus* and *J. maritimus*. I have, however, found no indications that hybridization has occurred between species of the *J. acutus* and *J. maritimus* groups.

J. maritimus and *J. rigidus* are no doubt very closely related. In areas where they meet or may have met, forms of probable hybrid origin have been observed. Thus, many *J. maritimus* individuals from the Atlantic area have much longer anthers than usual, which could be interpreted as indicating ancient introgression from *J. rigidus*. The forms from Turkestan and adjacent regions appear problematic and were described as a separate species, i.e. *J. nevskii,* by Kreczetowicz & Gontscharov (1935). Typical *J. maritimus* has been seen from Buchara but other material from the area has large anthers and has been classified as *J. rigidus*. An early collection with large anthers is the holotype of *J. nevskii;* consequently I have listed *J. nevskii* as a synonym under *J. rigidus*, but the entire material from the area may contain both species as well as intermediates and requires further investigation.

7. Germination and viability of seeds

The seeds of all *Juncus* species studied by me require constant moisture for at least several weeks in order to germinate and establish seedlings. They germinate best when placed on the soil surface. When covered with a layer of sand or other soil most seeds do not germinate in spite of watering. In older seeds the best germination rate was achieved when sown on filter paper or sand and supplied with sufficient artificial light.

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The highest germination rate was obtained with fresh water but species of *J.* subgen. *Juncus* germinate also with moderately salty water. Zahran (1975) tested the germination of *J. acutus* and *J. rigidus* seeds watered with salt water containing up to 3% NaCl. Both species showed a reduced germination rate in salt concentrations above 0.5% but the *J. acutus* seeds still germinated at 1% and those of *J. rigidus* at all concentrations tested. Even with a salt concentration of 3% still 80% of the seeds germinated if the temperature was kept at 10°–20° C during the experiment, while at temperatures varying between 20° and 35° C, the same salt concentration totally inhibited the germination.

The germination of seeds harvested the same or the previous year is usually 95–100% which means that a seed reserve can build up in the surface layer only if the soil is constantly dry or contains high salt concentrations. The requirements of light for germination, however, indicate that seeds buried in the soil may stay as a seed reserve. 22 year old seeds of *J. rigidus* kept in the herbarium germinated in one case to more than 50%; thus it can be assumed that a seed bank is effective at least if the seeds are buried in constantly dry soil. In several cases, seeds of other *Juncus* species belonging to different subgenera have been found to germinate after 20–30 years storage in the herbarium.

8. Actual and potential uses

Eleuterius (1979) analyzed the amino acids of *J. roemerianus* and considered it to be one of the most nutritious and productive marsh plants. He did not present data about actual grazing. The species of *J.* subgen. *Juncus* are usually avoided by grazing animals, not only because of their pointed leaves but also because of a peculiar taste.

J. rigidus has been used for making mats and this is still practised in the Bahariya oasis in Egypt, and probably elsewhere. Such mats have to some extent been used as prayer mats and sometimes been transported into regions far outside the distribution area of the species.

J. rigidus has also been proposed as a possible source for paper making (Zahran, Kamal El-Din & Boulos 1972). No doubt an acceptable paper can be produced although *J. rigidus* has never been used commercially. The main difficulty would be to organize the harvest of sufficiently pure material in the large quantities necessary for industrial use. *J. rigidus* fibres are among the plant materials proposed for improvement of the stability of concrete (Zahran pers. comm.).

In ancient Egypt *J. rigidus* leaves and/or culms were used as pens for writing on papyrus.

9. *Juncus* subgen. *Juncus*

≡ *J.* sect. *Marsippospermum* E. Mey., Syn. Junc. 8, 52 (1822) p.p.
≡ *J.* sect. *Steriocaulos* Griseb., Spicil. Fl. Rumel. 2: 405 (1845).
= *J.* [unranked] *acuti* Fr., Summa Veg. Scand. 1: 66 (1845) ≡ *J.* sect. *Acuti* (Fries) Rouy, Fl. France 13: 229 (1912) – Typus: *J. maritimus* Lam.
≡ [*Juncastrum* Fourr. in Ann. Soc. Linn. Lyon, ser. 2, 17: 122 (1869) nom. nud.] ≡ *J.* sect. *Juncastrum* Fourr. ex Post & Kuntze, Lex. Gen. Phan. 303 (1903) ≡ *J.* subgen. *Juncastrum* (Post & Kuntze) Krecz. & Gontsch. in Komarov, Fl. URSS 3: 543 (1935).
≡ *J.* subgen. *Thalassici* Buchenau in Abh. Naturwiss. Vereine Bremen 4: 406 (1875).
≡ *J.* sect. *Pungentes* Cout. in Bol. Soc. Brot. 8: 96 (1890).
≡ *J.* subgen. *Thalassii* Buchenau in Engler, Pflanzenr. 25: 100 (1906) ≡ *J.* sect. *Thalassii* (Buchenau) Vierh. in Engler & Prantl, Nat. Pflanzenfam. ed. 2, 15a: 216 (1930).

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= *J.* subgen. *Maritimus* Engelm. in Trans. Acad. Sci. St. Louis 2: 425 (1866), 433 (1868) ≡ *J.* sect. *Maritimi* (Engelmann) Rouy, Fl. France 13: 230 (1912) – Typus: *J. maritimus* Lam.

Tall, rigid perennials. Leaves basal except for the bracts of inflorescence branches, terete, non-septate, pungent, medulla of rounded cells, vascular bundles distributed over most of the leaf cross section, auricles lacking. Stomata in longitudinal rills. Flowers in heads, bracteoles not present with individual flowers. Seed with a persistent seed-coat forming appendages.

I give lists of specimens studied only for the rare or local taxa and in some cases for special areas where a species is rare or little collected. The rest of the information is expressed in the maps. All specimens examined have been provided with determination slips and are to be found in the herbaria listed above. For more precise information on minor areas or individual taxa please do not hesitate to contact the author.

Lectotypes have been selected in all cases where appropriate material has been seen. The few cases where the exact typification remains to be effected I hope this will be made by fellow botanists after seeing this paper. The only names in use to which this applies are *J. roemerianus* Scheele and *J. cooperi* Engelmann. The correct application of both names is beyond doubt, but the original material has not yet been found. As there is good hope that it still exists, I find it unnecessary to select neotypes. The following important synonyms are also waiting for a lecto- or neotypification: *J. multibracteatus* Tineo, *J. acutus* var. *sphaerocarpus* Engelm., *J. acutus* β *microcarpus* Loret & Barrandon and *J. pseudacutus* Pau.

Key to the taxa recognized

1. Rhizome inconspicuous, plants densely caespitose, branching by intravaginal shoots only 2
– Rhizome stout, creeping, producing dense or elongated rows of culms 7
2. Inner tepals with a wide, scarious apical part but not notched . . . . 4. *J. socotranus*
– Inner tepals with wide apical auricles, thus conspicuously notched (*J. acutus* group) 3
3. Capsule 4–6 mm, with 80–120 seeds, conical or obtuse at apex 4
– Capsule 2.5–4 mm, with 25–75 seeds, conical or pyramide-shaped at apex, or rarely blunt and then inflorescence of several separate groups of heads 5
4. Capsule with a conical apex, light to dark brown, inflorescence usually condensed . . . . . 1a. *J. acutus* subsp. *acutus*
– Capsule with a blunt apex, usually dark, inflorescence usually lax . . . . . 1b. *J. acutus* subsp. *leopoldii*
5. Capsule dark brown, pyramide-shaped at apex . . . . . 2. *J. littoralis*
– Capsule conical to blunt at apex, light or rarely dark brown 6
6. Capsule blunt, inflorescence of a few heads or groups of heads . . . . . 3b. *J. heldreichianus* subsp. *orientalis*
– Capsule apically conical, inflorescence elongated, of usually numerous small heads . . . . . 3a. *J. heldreichianus* subsp. *heldreichianus*
7. Seeds 1.25 mm or longer, anthers 3 mm or longer, intravaginal shoots frequent . . . . . 9. *J. cooperi*
– Seeds at most 0.9 mm long, anthers at most 2.5 mm long, intravaginal shoots rare . 8

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8. Capsule trigono-ovoidal or narrowly so, usually attenuate or pyramide-shaped at apex, light brown with longest appendages 0.2 mm or usually much longer (*J. maritimus* group) 9
– Capsule trigono-ellipsoidal to obovoidal, blunt, dark brown to chestnut-coloured, with appendages 0.1 mm or shorter (*J. kraussii* group) 10
9. Capsule not or slightly exceeding tepals, obtuse or abruptly attenuate, anthers up to 2.5 times as long as filaments . . . . . 5. *J. maritimus*
– Capsule exceeding tepals, ± narrowly pyramide-shaped at apex, anthers 3–5 times as long as filaments . . . . . 6. *J. rigidus*
10. Seed-coat forming two conspicuous though small appendages, capsule considerably longer than broad, trigono-ellipsoidal to obovoidal 11
– Seed-coat very tight, appendages inconspicuous, capsule broadly trigono-ellipsoidal to almost sphaeroidal . . . . . 8. *J. roemerianus*
11. Flowers functionally male or female on separate individuals, inflorescence wide . . . . . 7a. *J. kraussii* subsp. *kraussii*
– Most or all flowers hermaphrodite, inflorescence various 12
12. Inflorescence elongate, capsule exceeding tepals . 7b. *J. kraussii* subsp. *australiensis*
– Inflorescence wide, capsule equalling tepals . . . . . 7c. *J. krausssi* subsp. *austerus*

9. 1. ***J. acutus*** L., Sp. Pl. 325 (1753) – Fig. 2.
≡ *Juncastrum acutum* (L.) Fourr. in Ann. Soc. Linn. Lyon ser. 2, 17: 171 (1869).
≡ *J. acutus* L. var. *conglobata* Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 480 (1878).
≡ *J. acutus* L. var. *conglomeratus* Buchenau in Bot. Jahrb. Syst. 12: 250 (1890).
Typus: Lectotype (selected here): LINN 449: 1, left hand specimen (!).

Perennial, densely caespitose by intravaginal shoot formation. Rhizome extremely abbreviated, inconspicuous. Young plants often with some vegetative shoots. Leaves terete, pungent. Auricles lacking. Inflorescence of various form, composed of many, few-flowered, often confluent heads. Inner tepals with prominent, scarious, auricle-like apical parts, thus notched.

Total distribution: Fig. 3.

9. 1a. ***J. acutus*** subsp. ***acutus***
= *J. spinosus* Forssk., Fl. Aegypt.-Arab. 75, xxiv, lxv (1775) – Typus: Lectotype (selected here): *Hb. Forsskål no. 29, Cent. III, no. 38* (C!).
= *J. multibracteatus* Tineo in Gussone, Fl. Sic. Prodr. Suppl. 105 (1832) ≡ *J. acutus* L. var. *effusus* Buchenau in Bot. Jahrb. Syst. 12: 250 (1890) – Typus: In humentibus Castronuovo, *Todaro 556* (BM!, FI!, K!, W!).
[= *J. macrocarpus* Nees in Linnaea 20: 243 (1847) nom. nud.].
= *J. karelini* Steud., Syn. Pl. Glumac. 297 (1855) – Typus: Lectotype (selected here): Astrabad, *Karelin* (LE!).
= *J. acutus* L. var. *longibracteatus* Buchenau in Boissier, Fl. Orient. 5: 354 (1882) – Typus: Tell Afar inter Sindschar et Mosul, 1867, *Haussknecht 978* (G-BB!).

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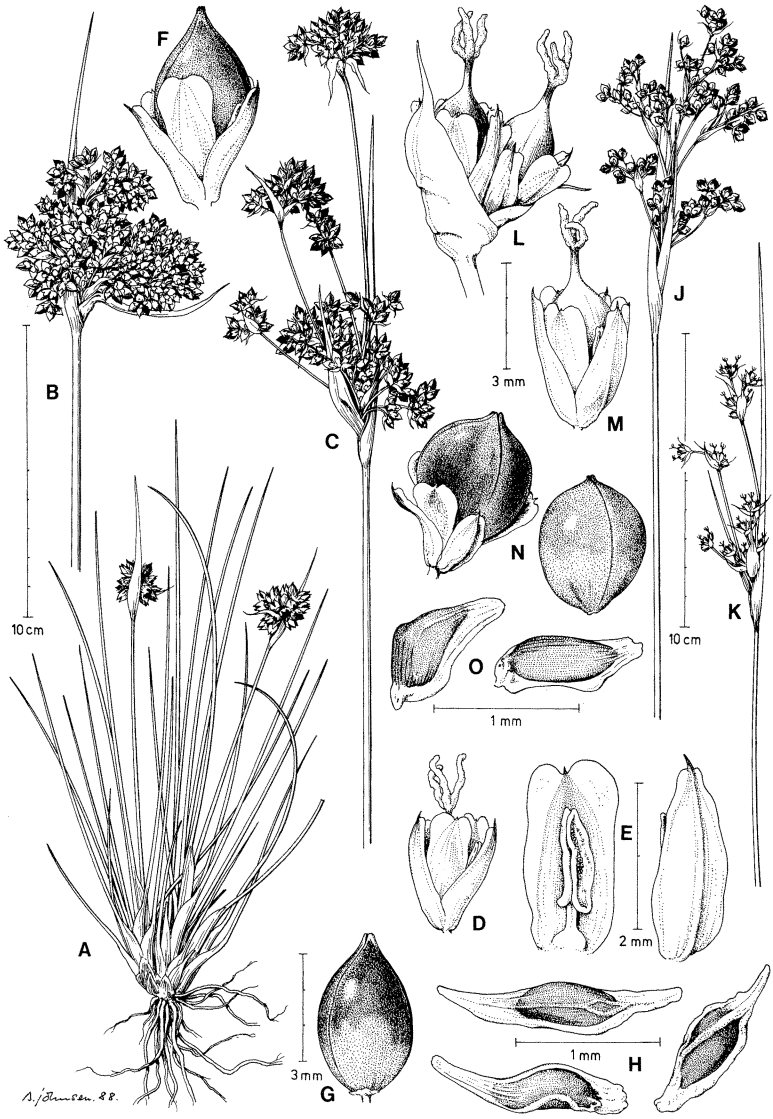

Fig. 2. *J. acutus*. A–H: subsp. *acutus*. – A: Habit of young plant with depauperate inflorescence. – B, C: Inflorescences. – D: Flower. – E: Inner and outer tepals with stamens. – F: Flower with ripe fruit. – G: Ripe capsule. – H: Seeds. – J–O: subsp. *leopoldii*. – J, K: Inflorescences. – L: Head in late flower. – M: Flower with young fruit. – N: Flower with ripe fruit and capsule. – O: Seeds.
Material: A: Egypt, El Dikheila, 24. 8. 1952, *El Hadidi* (LD). – B: Greece, Peleponnesos, Loutra Kiafa, *Snogerup 1473* (LD). – C, F, G, H: Greece, Kerkyra, *Snogerup 23608* (LD). – D, E: France, Bouches-du-Rhone, N Les Stes Maries, *Snogerup cult. no. 360* (LD). – J, N, O: Gran Canaria, *Wängsjö 231* (LD). – K, L, M: USA, California, Los Angeles Co., *Snogerup cult. no. 3850* (LD).

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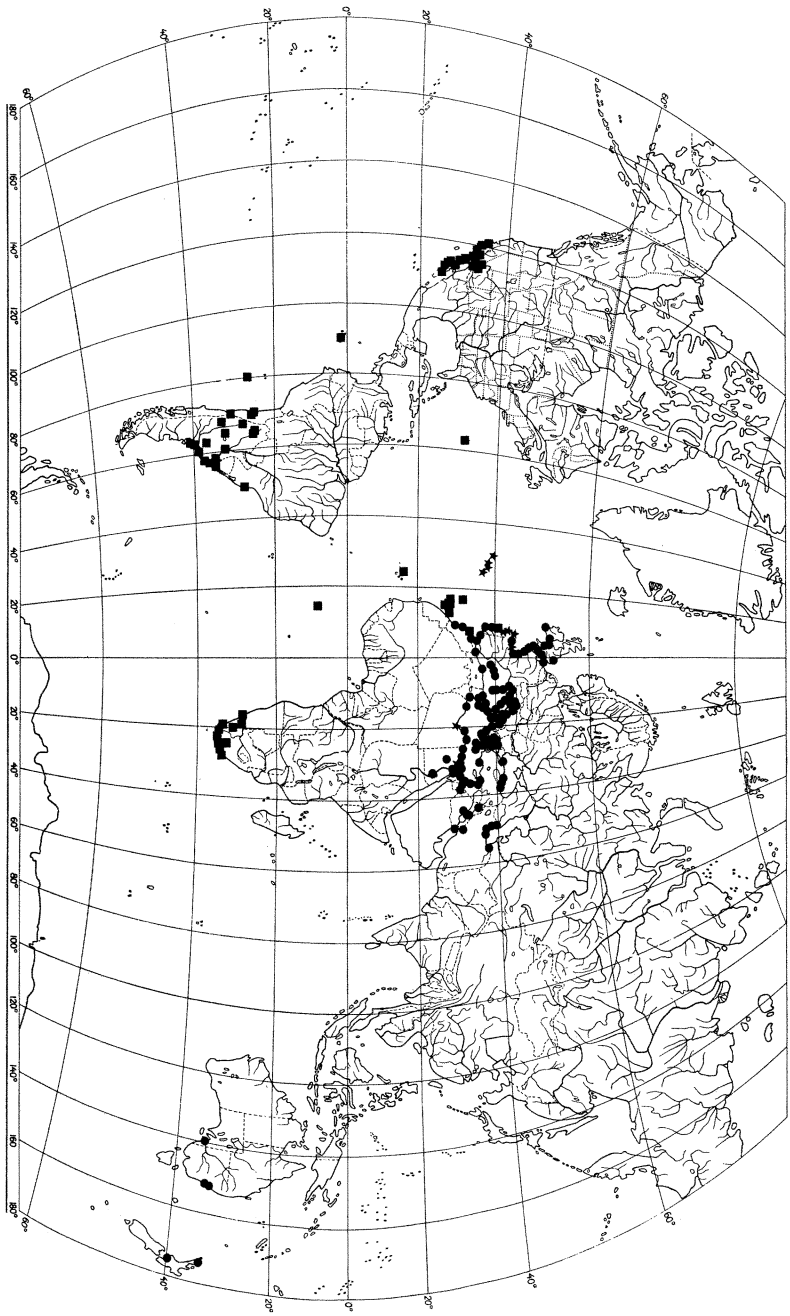

Fig 3. *J. acutus*, total distribution according to revised material. – Dots: subsp. *acutus*. – Squares: subsp. *leopoldii*. – Stars: intermediates.

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Culms 50–150 cm, rigid, 2–4(–6) mm thick, with a few small basal sheaths and 1–5 basal leaves. Leaves (10–)30–80(–120) cm long or sometimes the first very short, 1.5–4 mm thick. Inflorescence 5–15 × 3–7 cm, usually dense, almost sphaerical, rarely lax, elongated or wide, many-flowered, with (10–)50–100(–200) heads. Lowest two bracts leaf-like, pungent, the first (4–)7–25(–40) cm long, including the (2–)3–5(–10) cm long sheath, forming an apparent prolongation of the culm, the second 2–5(–8) cm, including the 1–4 cm long sheath, erecto-patent; upper bracts gradually smaller, with a broad, sheath-like, amplexicaul base, cuspidate but not pungent, those of the heads non-herbaceous, amplexicaul, ovate, pointed, usually light brown. Heads (1–)2–3(–4)-flowered; uppermost part of pedicel thick. Tepals (2.8–)3.5–4(–4.5) mm, usually equal, oblong, usually light brown to straw-coloured with darker, brown to chestnut-coloured margins of the herbaceous part, with broad hyaline margins, outer tepals slightly cymbiform, basally ± keeled, obtuse, with an up to 0.3 mm long mucro, when young with small scarious wings apically, inner with broad hyaline auricles and thus notched. Stamens 6, equalling tepals or slightly shorter, anthers 1.5–1.8(–2.0) mm, 2.5–4 times as long as filaments, usually red when young. Style 0.5–0.8 mm, stigmas 1.5–2 mm, light to dark purplish brown. Capsule 4–6 mm, much exceeding tepals, spheroidal to ovoidal with a conical top, mucro very short, glossy, straw-coloured to dark brown, triseptate, normally containing 80–120 seeds. Seeds 0.8–1.1 mm, including the seed-coat 1.8–2.5 mm, ellipsoidal to narrowly ovoidal, c. 25-striate, light brown with two darker tips; seed-coat forming two equal or subequal appendages.

Chromosome number: 2n = 48, chromosomes very small.

Distribution: W Europe, the Mediterranean, through Jordan and Iraq to the Persian Gulf, coasts of the Black Sea and the S Caspian area. Introduced and apparently established in Australia and New Zealand. Fig. 4 shows the main distribution area.

Ecology: *J. acutus* subsp. *acutus* occurs mainly in sand fields, sand dunes and salt marshes. Occasionally it also grows in river-beds, in fresh-water marshes and near wells. It is mostly found from sea level to about 10 m, but occasionally up to 900 m altitude.

9. 1b. ***J. acutus*** subsp. ***leopoldii*** (Parl.) Snogerup in Bot. Not. 130: 187 (1978).
≡ *J. leopoldii* Parl. in Giorn. Bot. Ital. 2: 324 (1846) ≡ *J. acutus* var. *leopoldii* (Parl.) Buchenau in Abh. Naturwiss. Vereine Bremen 4: 421 (1875) – Typus: Lectotype (selected here): South Africa, Sommerset, Stellenbosch, *Ecklon & Zeyher 4308* (FI!, iso- S!, W!).
= *J. acutus* L. var. *sphaerocarpus* Engelm. in Wheeler, Rep. U.S. Geogr. Surv. 100th Merid., Bot. 6: 376 (1878) ≡ *J. robustus* S. Watson in Proc. Amer. Acad. Arts 14: 302 (1879) – Typus: California, S. Barbara (not traced; material from type locality seen).

Culms (50–)80–150(–200) cm, rigid, usually 1.5–2.5 mm thick, sometimes up to 6 mm, with some small and 1–2 larger basal sheaths and 3–4(–5) basal leaves. Leaf sheaths wide and often up to 25 cm long. Leaves 40–100 cm long, 1.5–3 mm thick. Inflorescence 5–30(–40) cm long, 2–6(–8) cm broad, lax or rarely congested, with (10–)35–100(–250) heads, heads often densely aggregated into ± large groups. Lowest two bracts leaf-like, pungent, the first 3–20(–35) cm, including the 3–6(–10) cm long sheath, often shorter than inflorescence, forming an apparent prolongation of the culm, the second 2–7(–10) cm, including the 2–3(–5) cm

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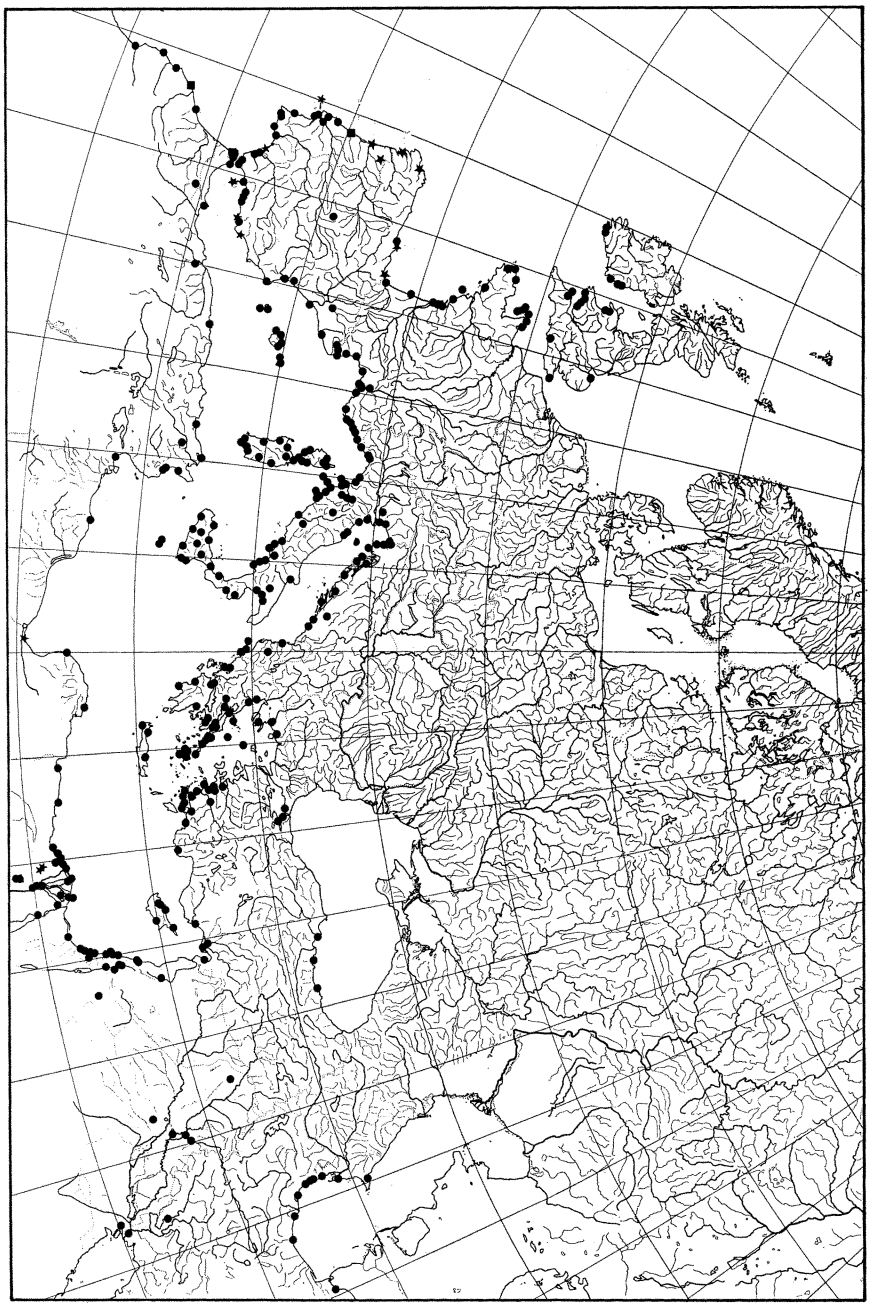

Fig. 4. *J. acutus*, distribution in Europe, N Africa and SW Asia according to revised material. – Dots: subsp. *acutus*. – Squares: typical subsp. *leopoldii*. – Stars: intermediates.

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long sheath; upper bracts gradually smaller, usually only the lowest with conspicuous laminas, but in Californian material sometimes even the upper with small pungent laminas, those of the heads usually shorter than flowers, rarely in Californian material some exceeding with large tips, non-herbaceous, amplexicaul, ovate, usually mucronate, dark brown to straw-coloured. Heads (1–)2–4-flowered; uppermost part of pedicels thickened, more than in subsp. *acutus*, especially in fruit stage, and outer tepals inserted slightly below the rest. Tepals 2.2–3.7 mm, equal or inner higher (because of higher insertion), oblong with broad hyaline margins, non-scarious parts light to dark brown, usually with a darker marginal zone, outer tepals cymbiform with small auricle-like expansions apically and usually with mucro up to 0.5 mm long, inserted lower than the inner and ± keeled basally, inner tepals with broad hyaline auricles apically and thus notched. Stamens 6, slightly shorter than tepals, anthers 1.4–1.8 mm, (2–)2.5–4 times as long as filaments, usually red when young, rarely yellow. Style 0.6–1.3 mm, stigmas 1.5–2.5 mm, reddish. Capsule (3–)3.5–5 mm, much exceeding tepals, obovoidal, apically usually blunt, with an 0.2–0.6 mm long mucro, rarely with a small conical projection, usually chestnut-coloured to dark or rarely light brown, basally lighter, trilocular or when ripe triseptate, normally containing 95–120 seeds. Seeds 0.7–0.8(–0.9) mm, including the seed-coat 1.1–1.4 mm long, ellipsoidal to obliquely ovoidal, 20–25-striate; seed-coat forming two equal or subequal appendages.

Chromosome number: 2n = 48, chromosomes very small.

Distribution: The total distribution is shown in Fig. 3, the distribution in N America in more detail in Fig. 22. Typical plants of this subspecies are found in the Atlantic Islands, W Africa, S Africa, Argentina, Chile, Uruguay, S Brazil, W coast of Mexico, California, Nevada, and Bermuda. The mapped occurrence on the Galapagos Islands was probably based on mislabelled material.

The few and mainly intermediate populations in SW Europe might be the results of recent introductions; those in Egypt were found mainly in some places most untouched by human influence, thus it can be assumed that they are probably relicts of a formerly more continuous distribution of *Juncas acutus* subsp. *leopoldii* in Africa.

Important specimens examined from N Africa and Europe:

M o r o c c o : Pr. opp. Tanger, 15. 7. 1926, *Lindberg 1532* (H).

L i b y a : Cyrenaica, 40 km E of El Agheila, 19. 8. 1957, *Guichard Cyr. 57/36* (BM).

E g y p t : Wadi Natroun, lake Beda, 7. 5. 1968, *El Hadidi* (CAI, LD); ibid., lake Goabar, 11. 10. 1942, *Täckholm et al.* (CAI); ibid., lake Umm Risha, 24. 12. 1944, *Davis 8094* (K); Cairo-Alex. desert road, 25. 1. 1978, *Abdel Wahab* (CAI); Ain Murun, kl. Oase, 26. 4. 1876, *Ascherson 513* (CAI, G-BOIS, K, M, W, WU).

P o r t u g a l : Buarcos, 1877, *?Neottez 548* (G, K); shore of Oporto, 1. 7. 1887, *Murray* (BM); Praia de Vieira, 10. 1881, *Barros Gomez 180 Fl. Lus. Soc. Brot.* (BM); in arenosis ad lacun Albufeira, 8. 5. 1844, *Willkomm Pl. hisp. exs. 7a* (BM); Estremadura, Sacavém, marg. Rio Trancão, 27. 10. 1943, *Foules & Rainha 15381* (S).

S p a i n : Guipuzeoa, S. Sebastian, 6. 1895, *Gandoger 290* (E); Almeria, edge of lagoon on the Llanos de Almeria, 6. 5. 1960, *Glanville 315* (BM); Prov. de Almeria, Roquetas de Mar, Punta del Sabinal, 21. 7. 1950, *Roivainen* (H, S); Gerona, N of Ampuiras, 26. 6. 1969, *Verdcourt 4700* (K); Andalusia, Fuengirola, near sea level, 10. 12. 1967, *Kraft* (LD); Fuengirola, Rio de las Pasadas, 18. 7. 1952, *Erlandsson* (S); Arenas Gordas, 21. 4. 1910, *Raunkier*

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691 (C); Santander, 10. 10. 1852, *Lange* (C); La Coruna, 2. 10. 1852, *Lange* (C, GB); Galecia, prov. Pontevedra, isthmus El Grove, 9. 7. 1930, *Buch* (H).

Ecology: Seashores, especially in sand dunes and sand fields, salt marshes. Saline places inland, river-beds and other permanently or seasonally wet spots with fresh water, in the Atlantic Islands often on volcanic materials. From sea level to at least 1400 m in S Africa, to 1000 m in W North America, to 200 m in the Azores, to 510 m in the Canary Islands.

J. acutus* × *heldreichianus

Usually a moderate-sized plant. Inflorescence slightly elongate, capsules often light coloured with a long conical tip, looking unfilled. Seed set irregular, from 0% up to at least 30% in the best developed capsules. Pollen almost 100% staining.

Specimens examined:
G r e e c e : Euboea, N of Akr. Mantili near the shore, 21. 6. 1958, *Runemark & Snogerup 11655C* (LD); Naxos, sand dunes S of the town of Naxos, 25. 5. 1958, *Snogerup cult. nos. 1676, 1707, 1728* (LD); pr. Korinthum in aren. marit., 26. 4. 1885, *Haussknecht* (W).

J. acutus* × *littoralis

Usually a tall plant forming large tussocks. Inflorescence and flowers like those of *J. littoralis*. Capsules differently developed, the large ones with conical top. Seed set irregular, from 0% to c. 50% in the best developed capsules. Pollen almost 100% staining.

Specimens examined:
I t a l y : Toscana, palude di Arno vecchio, 10. 9. 1916, *Savelli 239* (FI).
G r e e c e : Nom. Kavalas, in maritime sand 4 km SSW of Pontolivadon, c. 15 km E of Kavala, 0–2 m, 1. 7. 1971, *Snogerup 530* (LD); Euboea, Chalkis in planitie litorea, 6. 9. 1966, *Rechinger 37917* (W); Naxos, sand dunes S of the town of Naxos, 29. 5. 1958, *Snogerup cult. no. 1684* (LD).
I s r a e l : Philistean Plain, S of Ascalon, 11. 7. 1979, *Berliner* (HUJ); Acre Plain, Qishon river, 12. 4. 1925, *Smoly* (HUJ, S, W); Negev, S of Gaza, banks of Nahal Gaza, 28. 3. 1942, *Zohary* (HUJ, S).

9. 2. ***J. littoralis*** C. A. Mey., Verz. Pfl. Casp. Meer 34 (1831) – Fig. 5.
≡ *J. acutus* L. var. *littoralis* (C. A. Mey.) Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 480 (1878).
Typus: Lectotype (selected in Snogerup 1971: 6): Insula Sara, 26. 6. 1830, *C. A. Meyer 138* (LE!, iso- G!, G-BOIS!, W!).
= *J. tommasinii* Parl., Fl. Ital. 2: 315 (1852) ≡ *J. acutus* L. subsp. *tommasinii* (Parl.) Arcang., Comp. Fl. Ital. 715 (1882) ≡ *J. acutus* L. var. *tommasinii* (Parl.) Buchenau in Bot. Jahrb. Syst. 12: 250 (1890) – Typus: Lectotype (selected here): Nei paludi presso Monfalcone, Grado, *Tommasini* (FI!).

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Fig. 5. *J. littoralis.* – A: Base of culm and inflorescence. – B, C, D: Inflorescences. – E: Two-flowered head. – F: Flower. – G: Tepals with stamens. – H: Flower with ripe fruit. – K: Capsule. – L: Seeds.
Material: A: Israel, coastal Negev, *Naftolsky 13455* (HUJ, LD). – B, C, D, H, K, L: Greece, Naxos, ***Snogerup cult. nos. 1727, 1697, 1702*** (LD). – E, F, G: Italy, Emilia, Valli di Commachio, 24. 5. 1957, ***Snogerup s. n.*** (LD).

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= *J. acuto-maritimus* E. Mey. in Ledebour, Fl. Ross. 4: 234 (1853) nom. illeg. (orig. superfl.).
= *J. acutus* L. β *microcarpus* Loret & Barrandon, Fl. Montpellier, ed 2: 512 (1886) ≡ *J. acutus* L. var. *microcarpus* (Loret & Barrandon) Husn., Joncées 9 (1908) – Typus: (not traced).
= *J. acutus* L. [unranked] *tyraicus* Pacz., Fl. Chers. 1: 381 (1914) ≡ *J. tyraicus* (Pacz.) V. Krecz. & Gontsch. in Komarov, Fl. URSS 3: 544 (1935) – Typus: Lectotype (selected here): In maritimis subhumidis arenosis salsis in insula ad ostia Tyrae fluv. copiose, 9./22. 6. 1906, *Paczoski* (LE!, iso- G!).

Perennial, densely caespitose by intravaginal shoot formation. Rhizome extremely abbreviated, inconspicuous. Culms 50–100 cm, rigid, usually 2–4 mm thick, with several basal sheaths and 2–6 basal leaves. Leaves 25–100 cm long, 1.5–3 mm thick, terete, pungent. Auricles lacking. Inflorescence 5–20(–40) cm long, 2–7 cm broad, lax, rather broad, rarely condensed or elongated, many-flowered, with (10–)50–200 heads. Lowest two bracts leaf-like, pungent, with wide sheaths, the first 4–15(–20) cm, including the 2–4(–7) cm long sheath, usually shorter than inflorescence, forming an apparent prolongation of the culm, erecto-patent, the second 2–4(–6) cm, including the 1–3 cm long sheath; upper bracts gradually smaller, mostly without laminas, with broad, sheath-like, amplexicaul bases, non-herbaceous, those of the heads shorter than flowers. Heads (1–)2–3(–5)-flowered; uppermost part of the pedicel incrassate. Tepals 2.5–3 mm, inner usually higher, usually light brown in basal and central part, margins and apical parts dark brown to chestnut-coloured, with broad scarious margins, outer tepals ovate, ± cymbiform, basally ± keeled and thickened by a spongy tissue when young with narrow scarious wings apically, obtuse, often with an up to 0.4 mm long mucro, inner tepals oblong, with broad, light apical auricles and thus notched, usually with a very short mucro. Stamens 6, equalling tepals, anthers 1.2–1.9 mm, 4–5 times as long as filaments, yellow to purple when young. Style 0.8–1.3 mm long, stigmas 1.5–2 mm long, contorted. Capsule 2.5–3.5(–4) mm long, exceeding tepals, spheroidal to trigono-ovoidal with a pyramide-shaped top and an 0.2–0.5 mm long mucro, dark brown to chestnut-coloured apically, basally lighter, triseptate, normally containing 25–60 seeds. Seeds 0.8–1.1 mm, including the seed-coat 1.5–2.0 mm long, faintly reticulate with 25–30 inconspicuous longitudinal striae; seed-coat forming two equal or sub-equal appendages.

Chromosome number: 2n = 48, chromosomes very small.

Distribution: N shores of the Mediterranean from NE Spain eastwards, E Mediterranean shores, also inland in a few localities as in Egypt southwards to Abu Qurqas, to the Black Sea coasts and the shores of S Caspian area (Fig. 6).

Important specimens examined:
S p a i n : Barcelone, Castelldefels, 11. 6. 1920, *Sennen* (K, G-BB).
E g y p t : Minia, Abu Qurqas, 13. 3. 1952, *Täckholm* (CAI, LD).

Ecology: Almost exclusively a plant of moving sand, rarely occurring in stabilized sand fields or on canal banks, on sea shores and in the SE of its area also in more or less saline inland localities from sea level to 450 m.

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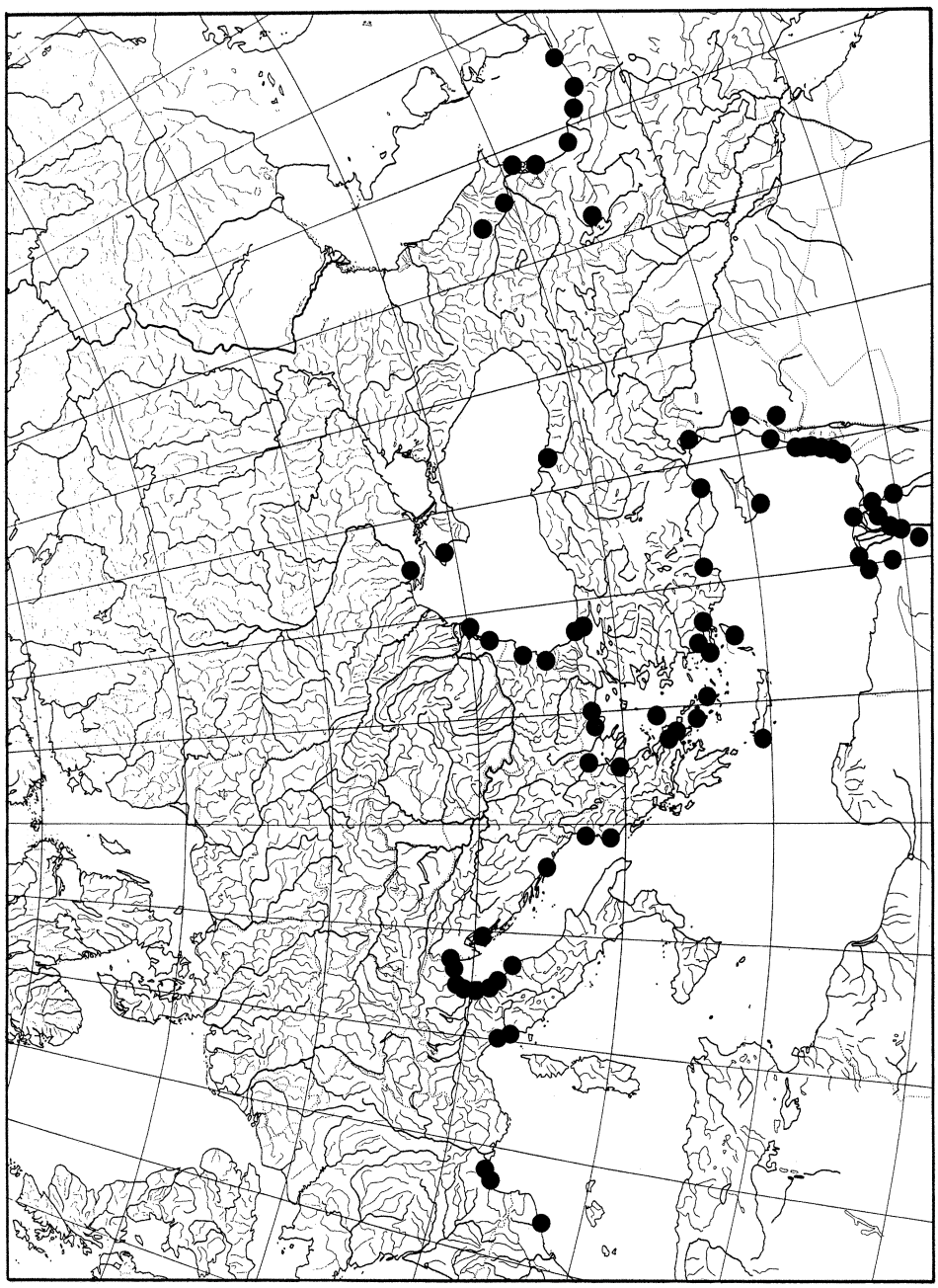

Fig. 6. *J. littoralis*, distribution according to revised material. One locality S of the map in the Nile valley at Abu Qurqas.

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9. 3. ***J. heldreichianus*** Marsson ex Parl., Fl. Ital. 2: 315 (1852).
≡ *J. acutus* L. var. *heldreichianus* (Parl.) Halácsy, Consp. Fl. Graec. 3: 280 (1904).
Typus: Lectotype (selected in Snogerup 1971: 6): *Heldreich 1993* (FI!, iso- FI!, G-BOIS!, K!).

Perennial, densely caespitose by intravaginal shoot formation. Rhizome extremely abbreviated, inconspicuous. Leaves terete, pungent, auricles lacking. Inflorescence lax, of various forms, with 8–200 heads, usually even upper bracts with small laminas. Inner tepals with prominent scarious, auricle-like apical parts and thus notched. Flowers light brown. Capsule 2.8–4(–4.5) mm long, ovoidal to spheroidal with a conical to blunt top, light to dark brown, containing 40–75 seeds.

9. 3a. ***J. heldreichianus*** subsp. ***heldreichianus*** – Fig. 7.

Culms 40–100(–150) cm, rather rigid but usually compressed and ± arcuate, usually 1.5–2.5 mm thick, with a few basal sheaths and 3–6 basal leaves. Leaves (10–)40–100(–150) cm long, 1.5–3 mm thick. Inflorescence 10–40 cm long, 3–5 cm broad, lax, elongated, many-flowered, with (10–)40–100(–200) heads, heads sometimes in several clusters. Lowest two bracts leaf-like, pungent, with large sheaths, the first 6–40 cm including the (2–)4–6(–10) cm long sheath, usually shorter than inflorescence, forming an apparent prolongation of the culm, the second 3–7 cm including the (1–)2–3(–5) cm long sheath, erecto-patent; upper bracts gradually smaller, many of them usually with small, pungent laminas, with a broad, sheath-like, amplexicaul base, those of the heads non-herbaceous, amplexicaul, ovate, pointed, usually light brown. Heads (1–)2–5(–8)-flowered; uppermost part of pedicel slightly incrassate and winged. Tepals 3–4 mm long, equal or subequal, oblong with broad hyaline margins, non-scarious part straw-coloured to light brown, in marginal and apical parts darker brown, outer tepals slightly cymbiform, not or little keeled basally, when young with small scarious wings apically, obtuse, mucronate, inner tepals with broad scarious, light apical auricles and thus notched, usually with a very small mucro; tepals and bracts often brown to reddish brown punctulate-striatulate. Stamens 6, c. 3/4 as long as tepals, anthers 1.5–2.2 mm long, 5–8 times as long as filaments, red when young. Style 0.8–1.5 mm long, stigmas 1–1.5 mm long, soon contorted. Capsule 3–4(–4.5) mm long, up to 1.5 times as long as tepals, ovoidal or rarely subspheroidal, apically conical or rarely obtuse or slightly angular, mucro very short, light or rarely darker brown, basally lighter, triseptate, normally containing 40–75 seeds. Seeds 0.8–0.9 mm, including the seed-coat 1.0–1.5 mm long, 20–25-striate; seed-coat forming two slightly unequal appendages.

Chromosome number: 2n = 48, chromosomes very small.

Distribution: Southern and coastal parts of Greece, especially common in the Aegean area, W, S and C parts of Anatolia and Cyprus (Fig. 9).

Ecology: Sand dunes, sand fields, salt marshes. Also common near fresh-water, e.g. streamsides, marshes and near wells, from sea level to 1700 m. Flowering usually March to May.

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Fig. 7. *J. heldreichianus* subsp. *heldreichianus*. – A: Culm with depauperate inflorescence from young tussock. – B, C: Inflorescences. – D: Head. – E: Tepals with stamens. – F: Flower with ripe fruit. – G: Capsule. – H: Seeds.

Material: A: Greece, Naxos, *Snogerup cult. no. 2637* (LD). – B, G: *Snogerup cult no. 1784* (LD). – C, E: Greece, Ikaria, *Runemark & Snogerup 6566* (LD). – D: Greece, Andros, *Snogerup & v. Bothmer 31749* (LD). – F, H: Greece, Kimolos, *Runemark & Bentzer 29945* (LD).

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9. 3b. ***J. heldreichianus*** subsp. ***orientalis*** Snogerup in Rechinger, Fl. Iranica 75: 7, t. 2 (1971) – Fig. 8.
Typus: 94 km N Khvoy inter Shahabad et Maku, *Rechinger 32735* (holo- W!).
= *J. tenax* Banks & Sol. in Russel, Nat. Hist. Aleppo ed. 2, 2: 251 (1794) p.p., nom. illeg., non Sol. in Forster (1786).

Note: The name *J. tenax* Banks & Sol. was published with a very vague description which does not even place it into a subgenus and was based on mixed material. In Snogerup (1971) it was only given as a synonym of *J. inflexus* because I had found only one of the two original specimens at BM. The other specimen is *J. heldreichianus* subsp. *orientalis*. As the name is illegitimate being a later homonym I find a formal typification meaningless.

Culm 30–70 cm, rigid, erect, usually 1.5–2.5 mm thick, with a few basal sheaths and usually 4–5 basal leaves. Leaves (10–)20–45 cm long or probably sometimes longer, 1.5–3 mm thick. Inflorescence 4–10 cm long, 2–5 cm broad, lax, wide, with 8–30 discrete, well separated heads. Lowest two bracts leaf-like, pungent, with wide sheaths, the first 3–7(–15) cm, including the 1.5–2.5 cm long sheath, longer or slightly shorter than inflorescence, forming an apparent prolongation of the culm, the second usually inconspicuous, 1.5–4 cm, including the 1–2 cm long sheath, erecto-patent; upper bracts gradually smaller, usually with no or only small laminas, with a broad, sheath-like, amplexicaul base, those of the heads equalling or exceeding flowers, non-herbaceous, ovate, amplexicaul, light brown, pointed. Heads (3–)4–5(–8)-flowered; uppermost part of pedicels incrassate. Tepals 2.5–3.5 mm, equal or subequal, oblong with broad scarious margins, non-scarious part herbaceous or later straw-coloured to light brown, apically and marginally darker to reddish brown, rarely more evenly dark-coloured, outer tepals cymbiform, keeled and thickened by spongy tissue basally, when young with small scarious wings apically, obtuse, with an 0.1–0.3 mm long mucro, inner tepals with broad, scarious, light apical auricles and thus notched; tepals and bracts usually brown to reddish-brown punctulate-striulate. Stamens 6, 3/4–4/5 as long as tepals, anthers 1.4–2.0 mm long, 4–8 times as long as filaments, yellow when young, later turning red. Style 1–1.5 mm long, stigmas 1–1.5 mm long, soon contorted. Capsule 2.8–3.5 mm long, equalling or slightly exceeding tepals, spheroidal with a blunt or shortly conical top, mucro c. 0.2 mm long, apically dark or rarely light brown, basally lighter, triseptate, normally containing 40–65 seeds. Seeds 0.75–0.8 mm, including the seed-coat 1.2–2.0 mm long, obliquely ovoidal, c. 25-striate and faintly reticulate; seed-coat forming two much unequal appendages.

Distribution: C and E Anatolia, Syria, N Iran, S Caucasus area and Turkestan (Fig. 9).

Ecology: In various permanently or seasonally wet places as fens, streamsides and moist pastures, with fresh as well as saline water, 800–1700 m, probably also both lower and higher.

Comments: The two subspecies of *J. heldreichianus* differ in several characters such as inflorescence form, upper bracts, tepals, form and colour of fruit. Their typical forms from Greece and N Iran are so different that a species status might be proposed. There are, however, several intermediate or less typical populations in Anatolia, and fruit forms similar to those of subsp. *orientalis* have been observed as far W as the C Aegean; thus I find subspecific rank necessary. Fig. 9 probably shows more the difference in investigation intensity than the actual frequency of the plant.

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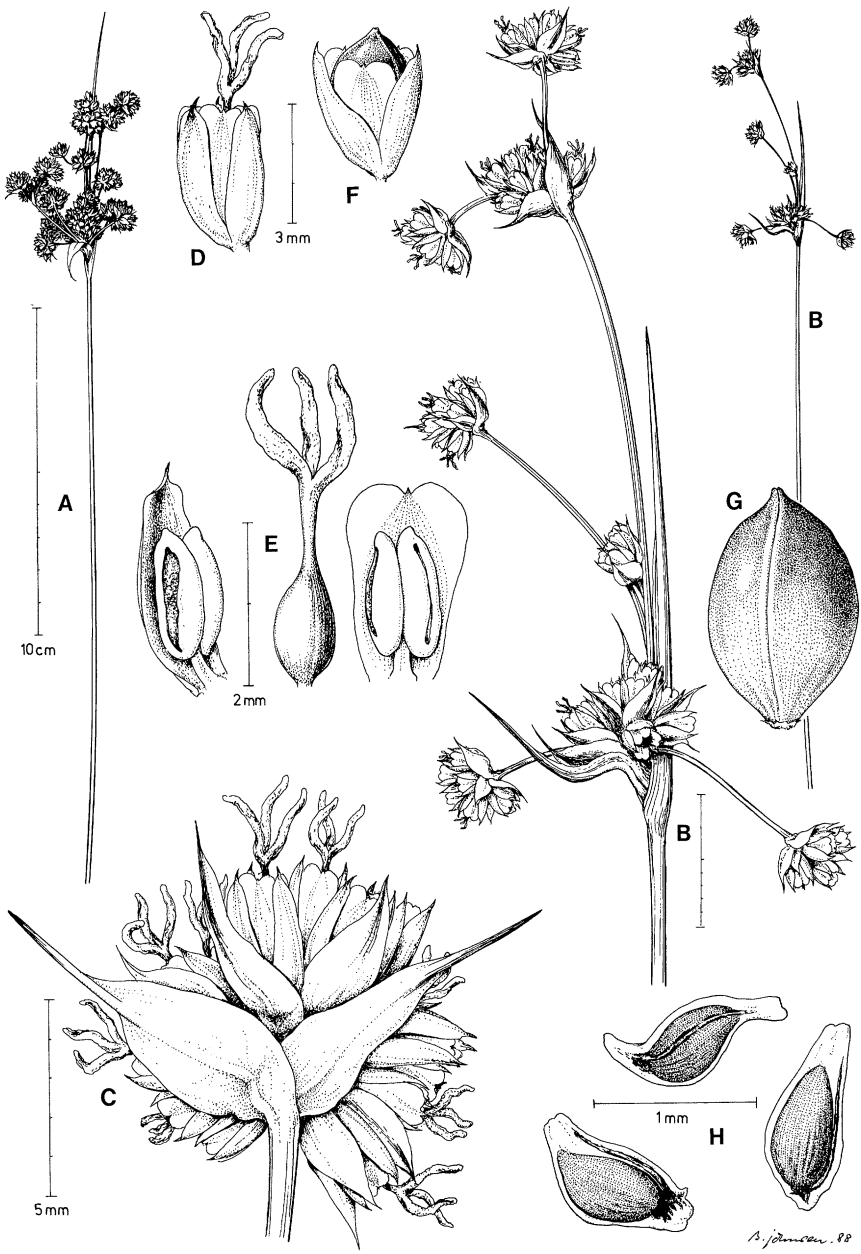

Fig. 8. *J. heldreichianus* subsp. *orientalis*. – A, B: Inflorescences. – C: Head. – D: Flower. – E: Tepals and pistil. – F: Flower with ripe fruit. – G: Capsule. – H: Seeds.
Material: A: Turkey, Agri, Diyadin, *Hewitt 258* (E). – B, C, D, E: Turkey, Eskisehir, *Secmen et al. 3442* (LD). – F, G, H: Turkey, Konya, Ak Göl, *Secmen & Leblebici 3076* (LD).

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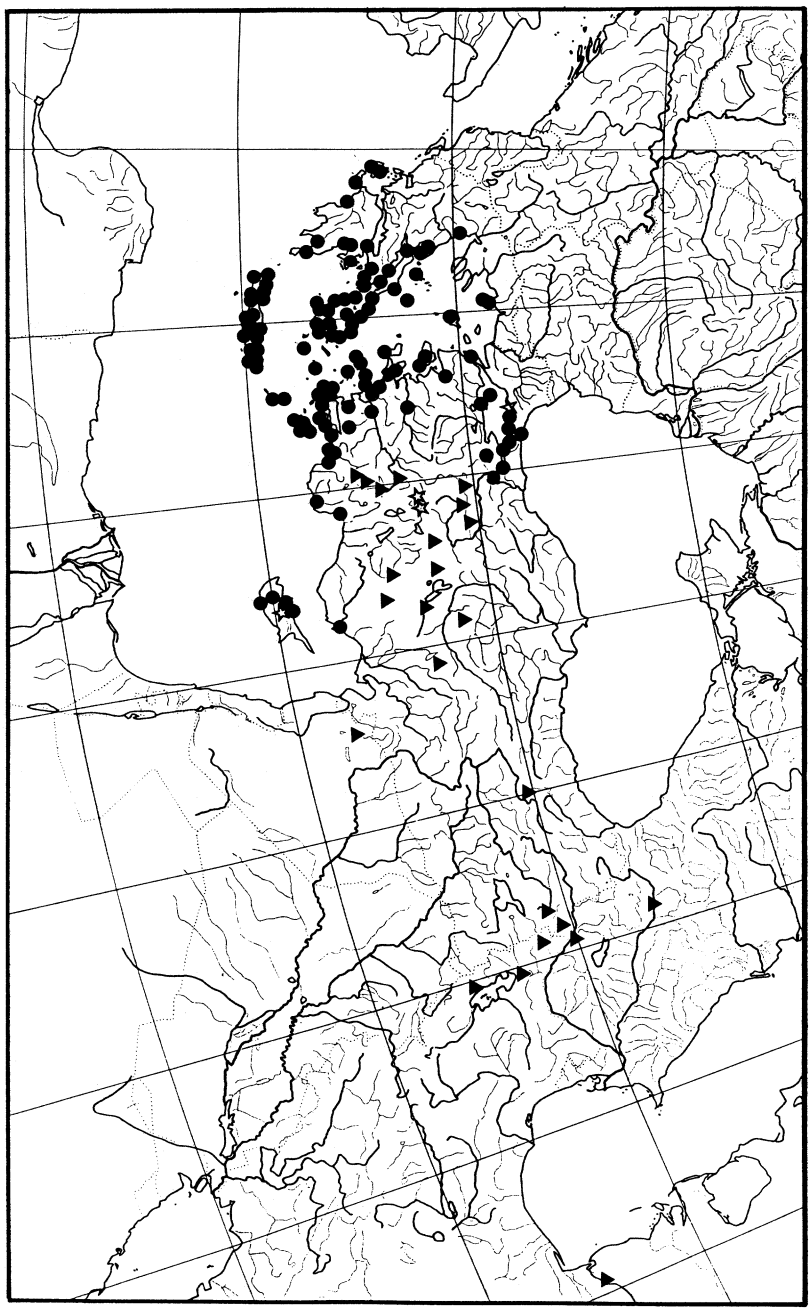

Fig. 9. *J. heldreichianus*, distribution according to revised material.

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J. heldreichianus* × *littoralis

In habit like moderately tall *J. heldreichianus*. Inflorescence variable, often with long ± erect branches and dense groups of heads. Capsules small and blunt, dark above. Most seeds degenerated, good seeds often few, but in the best capsules at least up to 30%. Pollen 80–95% staining and normal.

Specimens examined:
Greece: Naxos, sand dunes S of the town of Naxos, 29. 5. 1958, *Snogerup cult. nos. 1681, 1690, 1691, 1694, 1713, 1718, 1736* (LD).

9. 4. ***J. socotranus*** (Buchenau) Snogerup, **comb. nova** – Fig. 10.
≡ *J. maritimus* Lam. var. *socotranus* Buchenau in Bot. Jahrb. Syst. 12: 258 (1890).
Typus: Socotra, Kishen, 1000–600 met., 29. 4. 1881, *Schweinfurth 604* (holo- K!, iso- WU!).

Perennial, densely caespitose, branching by intravaginal shoots, rhizome inconspicuous. Culms 80–150(–200) cm, 2–4(–6) mm thick, terete and when fresh circular in transect, with a few basal sheaths and up to 10 basal leaves, leaf sheaths broad, basally brown, forming a thick cover around the base. Leaves 25–110 cm long or probably sometimes longer, 2-4 mm thick, terete, pungent, auricles lacking. Inflorescence (13–)20–40 cm long, (2–)5–10(–15) cm broad with erect to erecto-patent branches, often divided into two or more separate parts above each other, with (60–)200–500 or more heads. Lowest bracts leaf-like, pungent, the first 8–25(–40) cm, including the 4–8 cm long sheath, usually much shorter than inflorescence but occasionally longer, forming an apparent prolongation of the culm, the second 4–10 cm, including the 2–4 cm long sheath, erecto-patent; upper bracts small, amplexicaul, with small, stiffly pointed laminas, those of the heads considerably shorter than flowers, ovate, acuminate, in central part herbaceous but major part scarious. Heads (1–)2–4(–6)-flowered; pedicel apically incrassate. Tepals 2.2–3 mm, equal or the inner slightly longer, with a scarious margin, non-scarious part when young herbaceous, later straw-coloured to light brown or rarely darker and ± reddish brown, sometimes with a darker marginal zone, outer tepals narrowly ovate to oblong, pronouncedly cymbiform, scarious margin slightly broader apically, with an arista up to 0.2 mm long, inner tepals oblong, obtuse, with a wide, silvery hyaline, when young, cucullate apical part, not or slightly notched. Bracts and tepals ± conspicuously red punctulate-striulate. Stamens 6, 2/3–3/4 as long as tepals, anthers 1.1–1.7 mm long, (2.5–)4–6 times as long as filaments, yellow when young, filaments broad, 0.35–0.5 mm long. Style 1–1.5 mm, stigmas 1.5–2.5 mm long. Capsule 2.5–3 mm long, exceeding tepals, trigono-ovoidal to spheroidal, abruptly contracted to an (0.1–)0.3–0.6 mm long mucro, dark and ± reddish brown, trilocular with placental wings, containing 25–35 seeds. Seeds 0.6–0.8 mm, including the seed-coat 0.85–1.5 mm long, 0.25–0.35 mm broad, rather variable in form, well developed seeds usually obliquely narrowly ovoidal, c. 20-striate; seed-coat wide, forming two ± unequal appendages.

Distribution: Socotra, S and W Saudi Arabia, Yemen, Oman and Iran (Fig. 11). Distribution probably still imperfectly known.

Specimens examined:
Socotra: Kishen, 1000-600 met., 29. 4. 1881, *Schweinfurth 604* (K, WU); ibid., 2080′,

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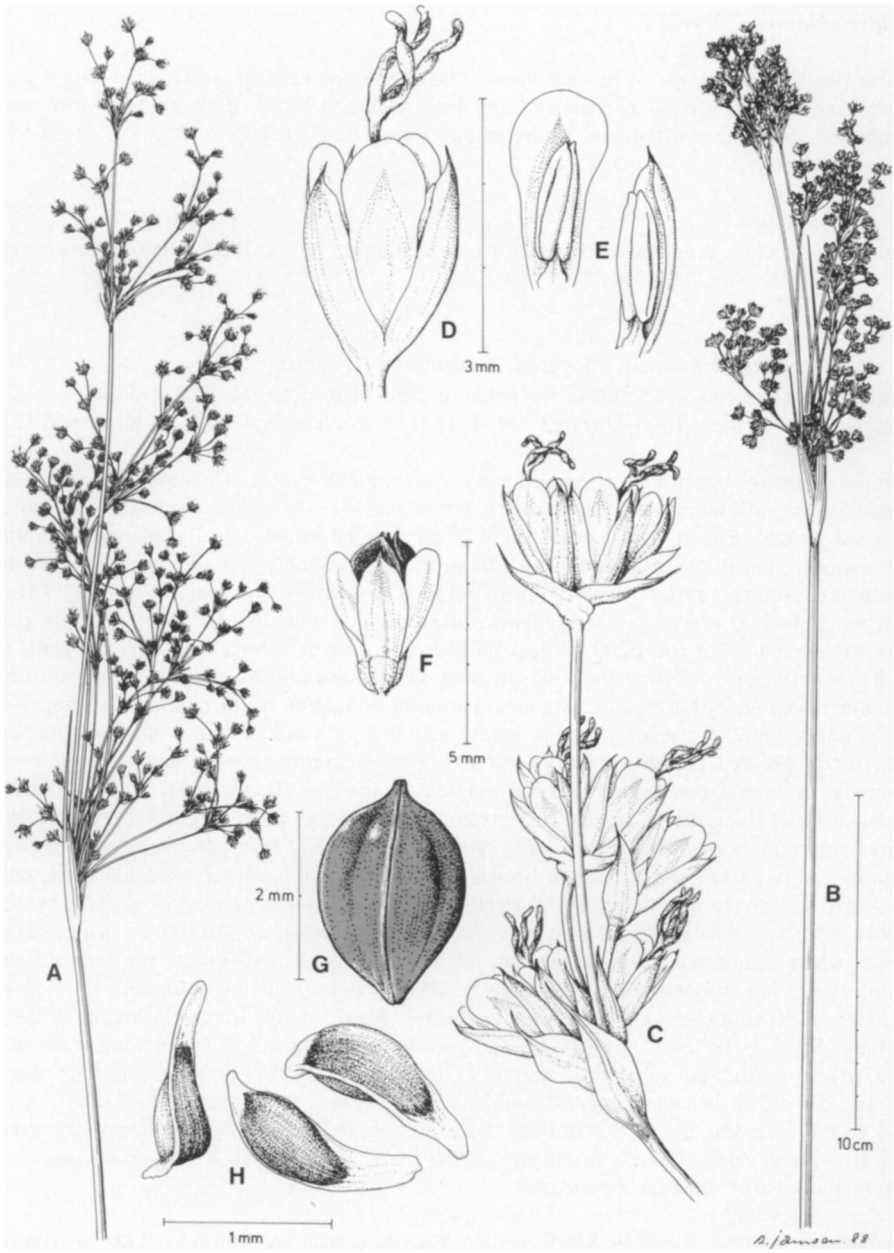

Fig. 10. *J. socotranus*. – A, B: Inflorescences. – C: Detail of inflorescence. – D: Flower. – E: Tepals with stamens. – F: Flower with ripe fruit. – G: Capsule. – H: Seeds.
Material: A: Saudi Arabia, Khaybar, *Popov 71/64* (BM). – B, C, D, E: Socotra; Hijama, *Popov GP/SO/256* (BM). – F, G, H: Saudi Arabia, Khaybar, *Zeller 16403* (BM).

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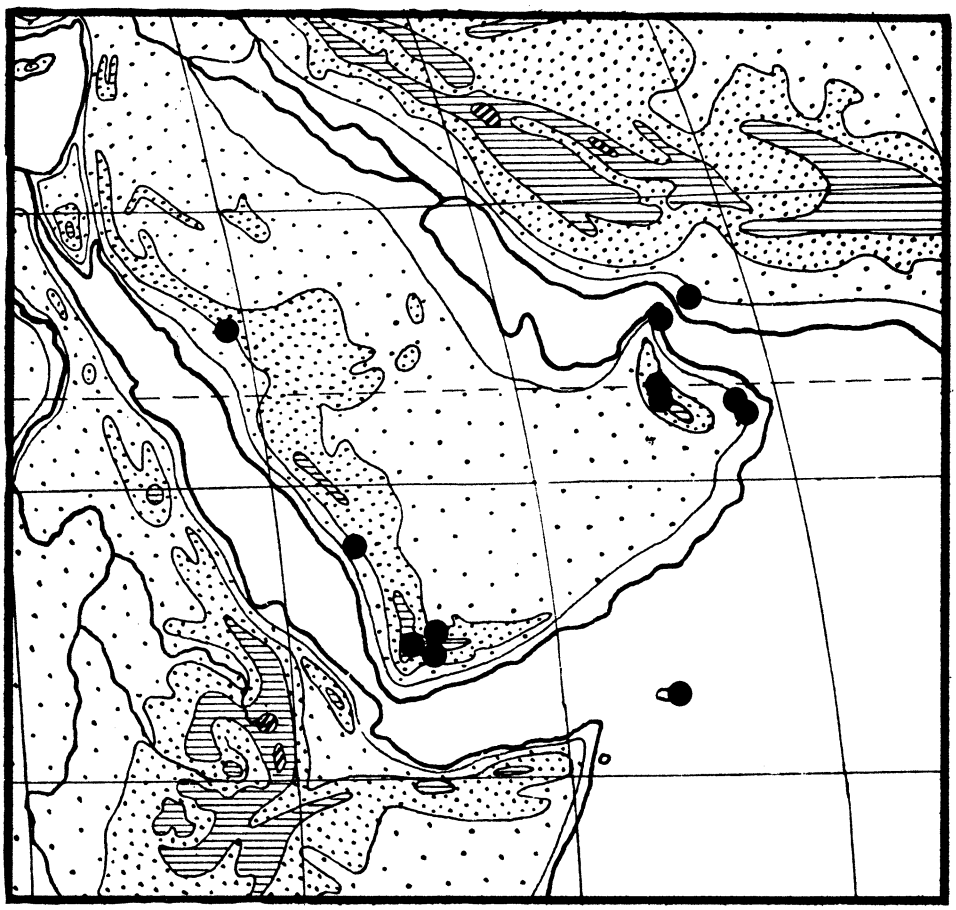

Fig. 11. *J. socotranus*, distribution according to revised material.

common, 20. 8. 1956, *Gwynne 84* (BM); Adhein, 3000′, very common in stream, 29. 8. 1956, *Gwynne 194* (BM); Hijama, 15. 3. 1953, *Popov 256* (BM).

S a u d i A r a b i a : Khaybar, 25°45′N, 39°10′E, 19. 5. 1962, *Zeller 16403* (BM); ibid., 13. 4. 1971, *Popov 71/64* (BM); in a stream below the camp at Nejd-El-Khubair, 19. 11. 1975, *coll. ignot.* (HUJ); Bashawat Shimran, 1. 8. 1975, *Al-Sheik 528E, 544–3* (CAI); Asir, Dalaghan Nat. Park, 30 km SE Abha, 1. 3. 1981, *Hillcoat 57* (BM).

Y e m e n : In marsh by a pond E of Dhamar, 2500 m, 22. 3. 1978, *Wood 2283* (K); abundant in marsh c. 10 km W of Dhamar, 2500 m, 17. 10. 1979, *Wood 2986* (BM, K); 20 km N of Rada, by salty stream, 23. 11. 1979, *Wood 3088* (BM, K); Wadi Walan, 2300 m, marshy meadow, 12. 11. 1978, *Wood 2613* (K); Hamman Damt, 1900 m, 16. 6. 1978, *Wood 2422* (BM, K).

O m a n : before 1899, *Jayakar 85* (BM); ad rivulos Mascate, *Aucher-Eloy 5475* (K); Amlah near Ibri, Nadi al Ayn, 500 m, 12 .1. 1978, *Whitcombe 71* (E); top of Wadi Beni Habib nr.

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Syq, 1850 m, 29. 7. 1980, *Whitcombe 909* (E); W. Hajar mts., Wadi Bani Kharus, 5 km N of Subaykah, UTM EA6889, 250 m, 2. 3. 1980, *Edmondson 3210* (E); N Oman near Yangul, 23°45′N, 56°45′E, 16. 3. 1980, *Lawton 2274* (BM); Al Bidaya, in wadi watercourse, fresh running water, 22°08′N, 58°25′E, 19. 1. 1982, *Maconochie 3101* (E); Wadi Bani Khalid, Sharqiyah, 22°34′N, 59°06′E, 550 m, 1984, *Gallagher 673312* (E); near Yangul, northern Darow, 23°45′N, 56°45′E, 16. 3. 1980, *Lawton 2274* (BM); Jabal al-Akhdar and adjacent areas, Wadi Qid, 23°12′N, 58°37′E, 1500–1700 feet, 21. 4. 1975, *Mandaville 6716* (BM).
F u j a i r a h E m i r a t e : between Khatt and Dibla, 25°55′N, 56°14′E, beside wadi, 455–1065 m, 21. 5. 1982, *Western 19* (E).
I r a n : Bandar-Abbas, 35 km from Senderk to Araghin Deh-e-Ziaraton (EQ3), 1000 m, 9. 5. 1983, *Mozaffarian 44488* (LD).

Ecology: Margins of water-courses, between 600 and 1000 m.

Use: According to collectors' information used for making baskets.

9. 5. *J. maritimus* Lam., Encycl. 3: 264 (1789) – Fig. 12.
≡ *Juncastrum maritimum* (Lam.) Fourr. in Ann. Soc. Linn. Lyon, ser. 2, 17: 171 (1869).
Typus: (P-LA, photo 657!).
= *J. acutus* L. ß. [unnamed variety] Sp. Pl. 325 (1753).
[= *J. hoppii* Noë in sched. (1834) nom. nud.].
= *J. broteri* Steud., Syn. Pl. Glumac. 2: 297 (1855) – Typus: *Welwitsch, It. Lusit. 330* (BM!, G!, K!).
= *J. ponticus* Steven in Bull. Soc. Imp. Naturalistes Moscou 3: 94 (1857) – Typus: Taur. merid., 1803, *herb. Steven* (holo- H).
= *J. pseudacutus* Pau, Not. Bót. Fl. Españ. 6: 100 (1895) – Typus: Monreal del Campo, 8. 1894, *Juan Benedicto* (not traced).
= *J. paui* Sennen, Plantes d'Espagne *no. 5432* (descr. on labels) (1925) – Typus: Barcelone, Castelldefels, praire maritimes, *Sennen 5432* (BM!, G!, LD!).

Perennial, with a creeping, woody, up to 8 mm thick rhizome of varying internode length, in some localities laxly caespitose by frequent forkings of the short-noded rhizome, intravaginal shoots usually lacking. Culms 50–100 cm, usually 1.5–2 mm thick, rigid, usually with 2–4 light to dark reddish brown basal sheaths and 2–4 basal leaves. Leaves (10–)25–80 cm long, 1–3 mm thick, terete, pungent, auricles lacking. Inflorescence (4–)10–20 cm long, (2–)3–5(–8) cm broad, usually lax, rarely contracted to one or a few large clusters, with 20–100(–200) heads. Lowest two bracts leaf-like, pungent with wide sheaths, the first (7–)10–25(–40) cm long, including the 2.5–4 cm long sheath, usually exceeding the inflorescence, forming an apparent prolongation of the culm, the second usually inconspicuous, 1.5–3(–5) cm, including the 1–2 cm long sheath, erecto-patent; upper bracts small, the lamina a small mucro only, those of the heads shorter than flowers, ovate to narrowly ovate, amplexicaul, apiculate, non-herbaceous, straw-coloured. Heads (1–)2–6-flowered. Tepals 3–4 mm long, the outer slightly longer, with broad hyaline margins, non-scarious part centrally and basally herbaceous or later straw-coloured to light brown, marginally and apically from the start non-herbaceous and sometimes darker, outer tepals ovate, cymbiform, acute, with an 0–0.3 mm long mucro, inner tepals narrowly elliptic, with somewhat wider margins apically, obtuse. Stamens

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Fig. 12. *J. maritimus*. – A: End of rhizome with row of culms. – B, C: Inflorescences. – D: Head. – E: Flower. – G: One-flowered head (right) and flower in fruit. – H: Capsule. – J: Opened capsule. – K: Seeds. Material: A: Greece, Xanthis/Rodopis, Porto Lago, *Strid et al. 24277* (LD). – B, D, E, F, G, H, J, K: Sweden, Skåne, Ljunghusen, *Snogerup 1445* (LD). – C: Spain, Barcelone, Castelldefels, *Sennen 5432* (LD, isotype of *J. paui* Sennen).

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6 or rarely 3, c. 2/3 as long as tepals, anthers 0.8–1.2 mm long, 1.5–2(–2.5) times as long as filaments, yellow when young. Style 1–1.5 mm long, stigmas 1–2 mm long, soon contorted. Capsule 2.5–3.5 mm long, equalling or slightly exceeding tepals, trigono-ovoidal, obtuse or broadly attenuate, with an 0.3–0.6 mm long mucro, light brown to straw-coloured, trilocular, containing 60–100 seeds. Seeds 0.6–0.7 mm long, including the seed-coat 0.8–1.2 mm long, obliquely ovoidal, c. 25-striate; seed-coat forming two unequal white appendages.

Chromosome number: 2n = 48, chromosomes very small.

Distribution: Azores, NW and W Europe, Mediterranean area, E European inland near the lakes Balaton and Neusiedl, Black Sea area, Anatolia, W Iran and Buchara area. Introduced, probably casually, in E North America (Fig. 13).

Important specimens examined:
C e n t r a l A s i a : Dominum Buchara, p.p. Kaltaminor (inter Baissun et Siharsihaur), c. 1000 m, 23. 8. 1913, *Fedtschenko 1169 ed. Bornmüller* (B); ancien lit d'Amou Daria, Pie de Qizil Qala, 7. 1967, *Pelt* (W).
A z o r e s : Pico, seashore Lajes, 1929, *Tutin & Warburg H469* (K, O); Pico, Lajes, 1 m, 15. 6. 1965, *Goncalves 1936* (BM); prope Praya da Victoria insulae Terceiro, 5. 1838, *coll. ignot.*, Hb. Hookerianum (K); ibid., 9. 6. 1938, *Cedercreutz* (H); ibid., 3. 7. 1972, *Hansen* (C); Sao Jorge, Velas, 2 m, 6. 9. 1971, *Goncalves 3593* (BM).
U S A : Philadelphia, sea shore, 1845, *Watson* (E); New York, Kings Co., Coney Island, 4. 9. 1886, *Ruth* (RSA).

Ecology: In general *J. maritimus* is a plant of salt marshes but also occurs on maritime sand and rarely in freshwater on margins of rivers etc. at least up to 200 m in the S, in Anatolia in inland saline localities at least to 1000 m, and in Iran to 1200 m.

9. 6. ***J. rigidus*** Desf., Fl. Atlant. 1: 312 (1798) – Fig. 14.
Typus: Described from NW Africa (P-Desf., photo!).
= *J. procerus* Bianca in Atti Accad. Gioenia Sci. Nat. Catania ser. 2, 3: 65 (1846) nom. illeg., non E. Mey. (1828) ≡ *J. maritimus* Lam. var. *biancae* Lojac., Fl. Sicul. 3: 152 (1909) – Typus: [Sicily], in udis maritimis ad littorale di Noto, *Bianca* (FI!).
= *J. maritimus* Lam. var. *arabicus* Asch. & Buchenau in Boissier, Fl. Orient. 5: 354 (1882) ≡ *J. arabicus* (Asch. & Buchenau) Adamson in J. Linn. Soc., Bot. 50: 10 (1935) – Typus: Lectotype (selected here): W Sinai, ad scaturigines Raphidim, 17. 7. 1835, *Schimper 495* (W!, iso- CAS!, E!, FI!, M!).
[= *J. deserti* Caruel, Pl. exs. arab. – nom. nud.].
= *J. nevskii* V. Krecz. & Gontsch. in Komarov, Fl. URSS 3: 629 (1935) – Typus: Turcomania, ad fonticulum Kara-su prope pag. Kughitang, 12. 7. 1931, *Nevski 763* (holo- LE!).

Note: For the synonym *J. nevskii* see also *J. maritimus*.

Perennial with a creeping, woody, up to 10 mm thick rhizome of variable internode length, often laxly caespitose by frequent rhizome forkings. Culms (50–)75–150 cm, rigid, usually

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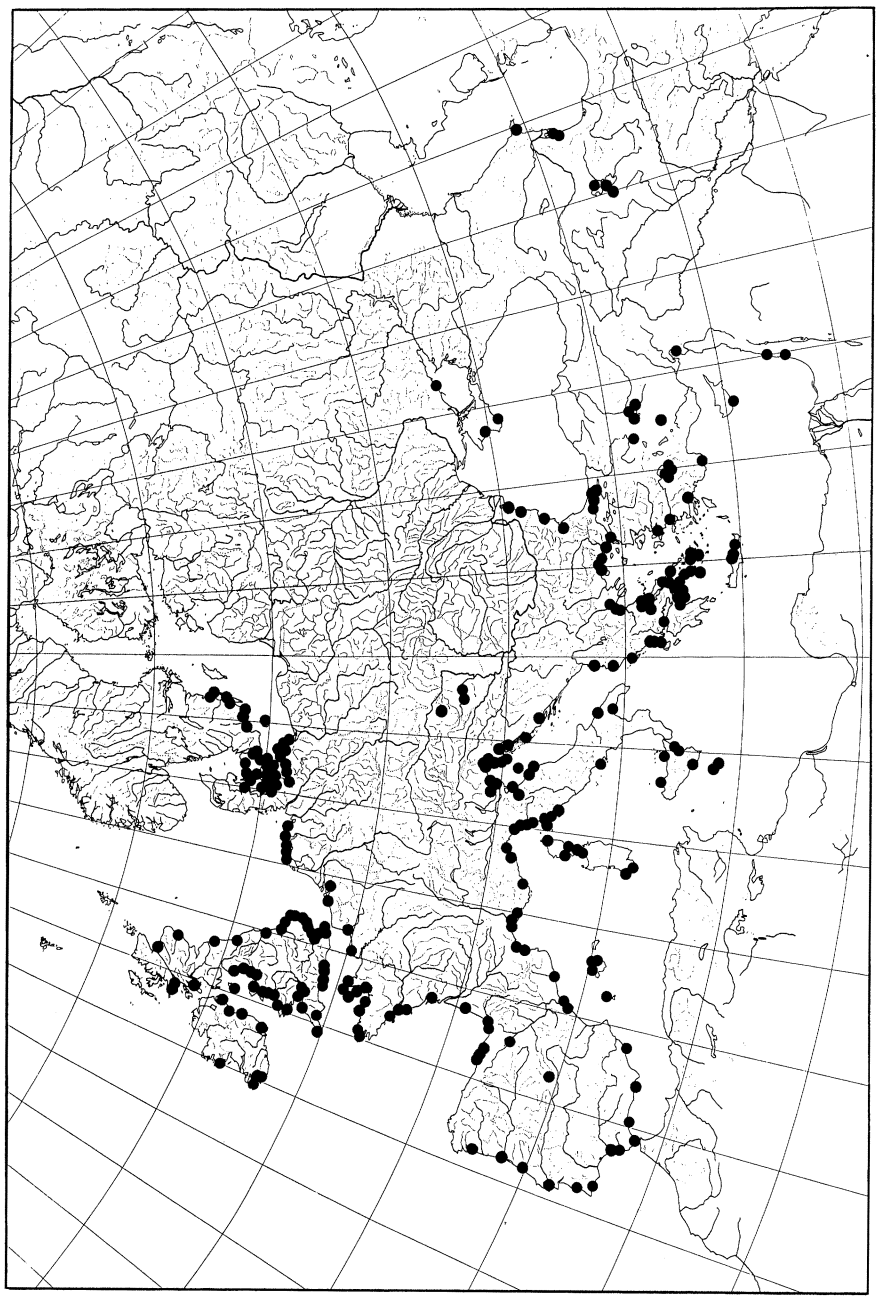

Fig. 13. *J. maritimus*, distribution according to revised material. Localities outside the map in the Azores, Turkestan and as introduced in North America, see under "Important specimens revised".

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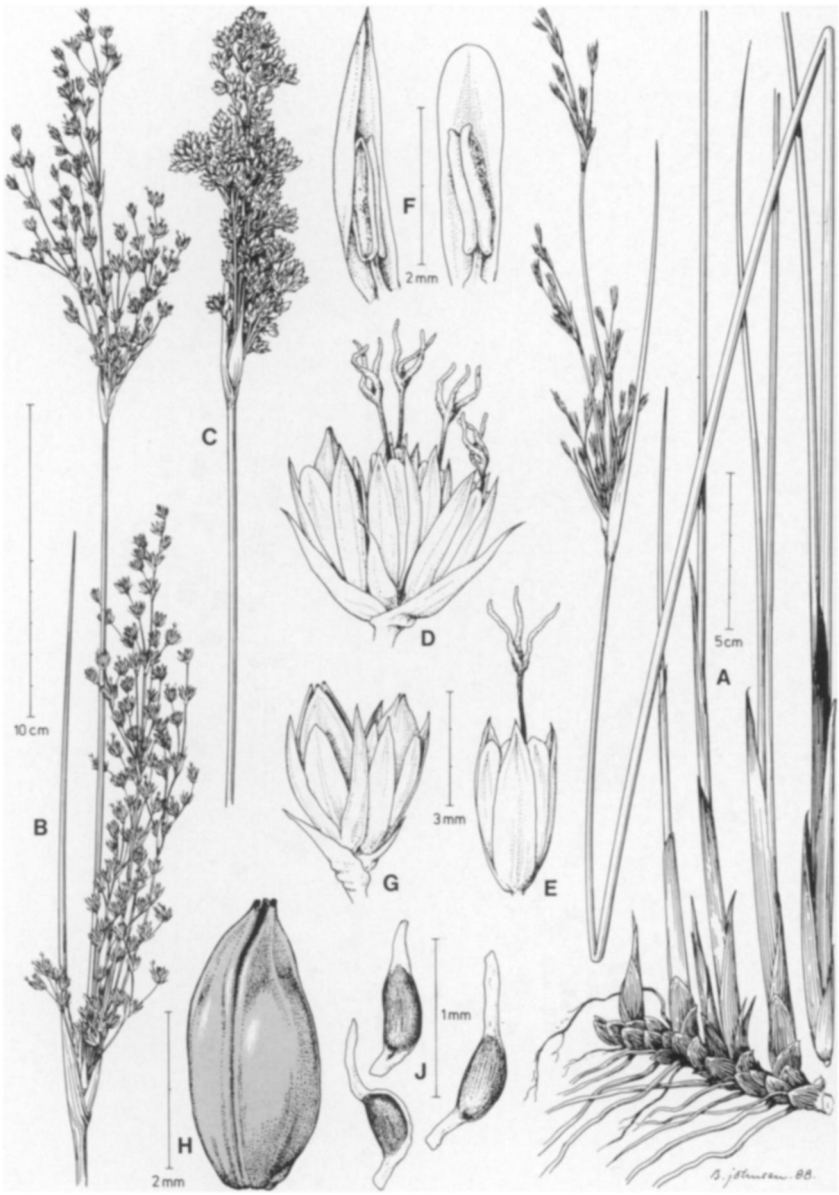

Fig. 14. *J. rigidus*. – A: Rhizome end and young inflorescence. – B, C: Inflorescences. – D: Head. – E: Flower. – F: Tepals with stamens. – G: Head with ripe fruits. – H: Capsule. – J: Seeds.
Material: A: NW Morocco, Jebel Kebir, *Dahlgren & Lassen 140-22* (LD). – B, D, E, F: Sinai, Wadi Talaa, *Snogerup et al. 2827* (LD). – C: Egypt, Wadi Kurkur, 16.12.1964, *Boulos s. n.* (CAI, LD). – G, H, J: Israel, Dead Sea, *Fl. Terr. Isr. Exs. 721* (LD).

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2–5 mm thick, with usually 4–5 basal sheaths and 2– 5 basal leaves. Leaves 25–110 cm long, 1.5–3 mm thick, terete, pungent, auricles lacking. Inflorescence 5–40 cm long, 2–5 cm broad, lax, usually elongated, rarely as broad as long, usually without any secondary branches in the axils of bracteoles, many-flowered, with (20–)50–150(–300) heads. Lowest two bracts leaf-like, pungent, with wide sheaths, the first 5–25 cm, including the 2–5 cm long sheath, shorter than to much exceeding the inflorescence, forming an apparent prolongation of the culm, the second 2–5 cm, including the 1.5–3 cm long sheath, erecto-patent; upper bracts small, those of the heads much shorter than flowers, ovate, amplexicaul, cuspidate, straw-coloured. Heads (1–)2–4(–6)-flowered; upper part of pedicel incrassate. Tepals 3.5–5 mm, equal or outer slightly longer, usually light brown to straw-coloured or when young herbaceous in central part, with broad scarious margins, rarely with a darker margin of the non-scarious part, outer tepals narrowly ovate, cymbiform, acute to obtuse, often with slightly wider scarious margins apically, sometimes with a small mucro, inner tepals oblong, obtuse, with the margin somewhat expanded apically. Stamens 6, 2/3–3/4 as long as tepals, anthers (1.0–)1.5–2.0(–2.5) mm long, 3–6 times as long as filaments, yellow when young. Style 0.7–1.2 mm long, stigmas 1–1.5 mm long. Capsule 3.5–5 mm, conspicuously exceeding or rarely equalling tepals, narrowly trigono-ovoidal with a tapering, trigonous top, sometimes abruptly contracted at apex (esp. in South African material), with an up to 0.5 mm long mucro, pale, usually light brown to straw-coloured (in South African material rarely darker brown apically), trilocular, usually containing 70–90 seeds. Seeds 0.6–0.7 mm, including the seed-coat 0.9–1.8 mm long, 0.2–0.3 mm broad, narrowly obliquely ovoidal, 20–25-striate; seed-coat forming two equal or subequal appendages.

Chromosome number: 2n = 46, 48, chromosomes very small.

Distribution: N Africa, scattered in W and E Africa, inland localities in S Africa, Cyprus, SE Turkey, Syria, Israel, Jordan, Iraq, the Arabian Peninsula, S and E Iran, S Afghanistan, S Pakistan and Turkestan (Fig. 15). In Europe there is only one well identified locality: Sicily, Avola, littorale di Noto, before 1859. I vainly searched for it in and around this place in 1973.

Important specimens examined:
Italy: Sicily, in uliginosis maritimis (Avola), 6. 7.[before 1859], *Bianca 283* (FI); in uliginosis maritimis (ad littorale di Noto), *Bianca* (FI); saline di S. Pietro, *Hb. Martelli* (FI); in arenosis maritimis Campaniae, Scavli, 6. 1824, *Terracino* (FI).
Unidentified localities in Central Asia: Amudaria-Gebiet von Ostbuchara, zwischen Kulab und Gullag, 1000′, 12.–24. 10. 1881, *Regel It. Turkest.* (LE); [?Kunu Kycumaur. Uemornuk Karnoy], 12. 7. 1883, *Regel* (K, LE, G).

Ecology: Maritime and inland, usually sandy, saline localities. Wadis, wells, depressions and other permanently or seasonally wet places in desert and steppe areas. *J. rigidus* is, in most of its area, a desert plant; it occurs in maritime localities in the Mediterranean part of its distribution only.

9. 7. ***J. kraussii*** Hochst. in Flora 28: 342 (1845).
Typus: Lectotype (selected here): Ad ripas Notsinakama R. distr. George, 1. 1839, *Krauss* (G-BOIS!, iso- M!).

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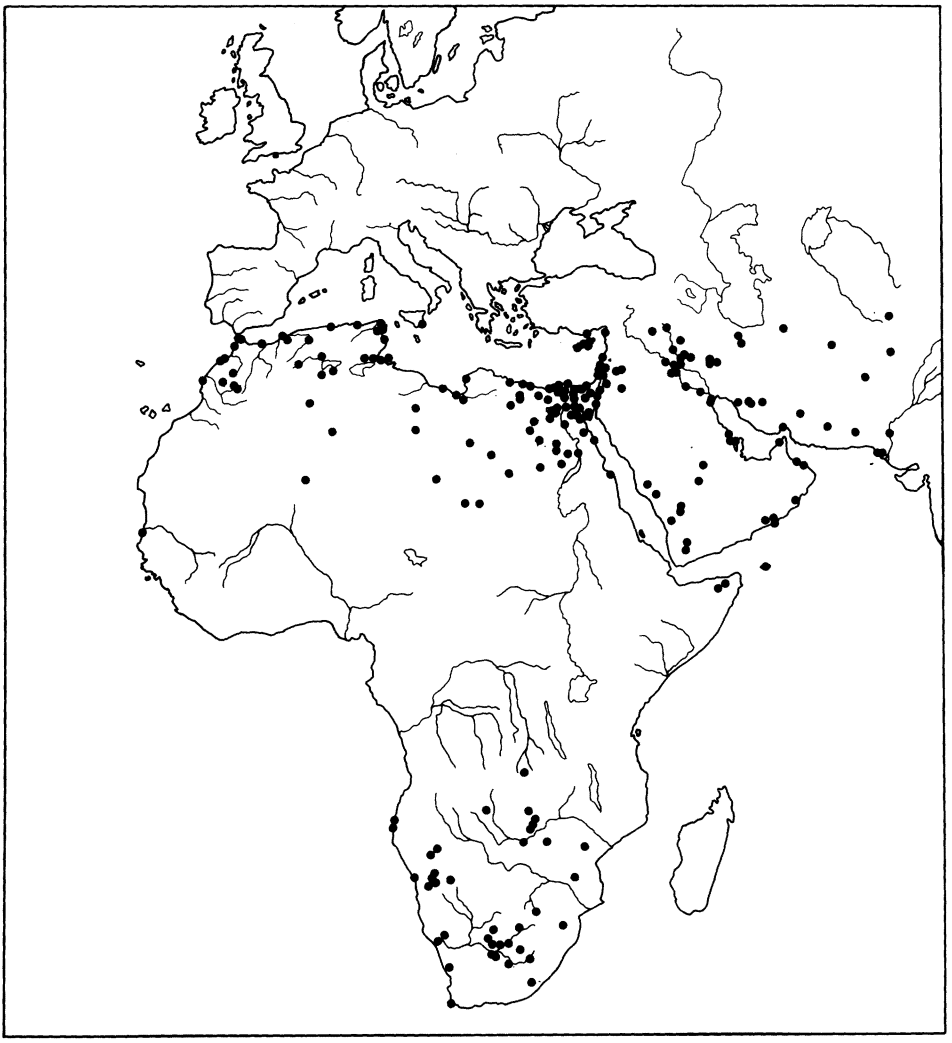

Fig. 15. *J. rigidus*, distribution according to revised material.

Perennial with a creeping, usually short-noded and densely branched rhizome, usually densely matforming to laxly caespitose, sometimes producing intravaginal shoots after resting periods. Leaves terete, pungent, auricles lacking. Inflorescence usually lax, rarely consisting of a few clusters. First two bracts leaf-like with wide sheaths, the first forming an apparent prolongation of the culm. Upper bracts narrowly ovate, amplexicaul, acuminate, often with a small, distinct lamina. Flowers dark. Anthers yellow when young. Capsule 2–2.5(–3) mm long, trigono-obovoidal to trigono-ellipsoidal, usually blunt, dark brown to chestnut-coloured at least in apical part. Seeds with very short, unequal appendages.

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9. 7a. ***J. kraussii*** subsp. ***kraussii*** – Fig. 16.
= *J. caffer* Bertol. in Mem. Reale Accad. Sci. Ist. Bologna 3: 253, t. 19, fig. 3 (1851) – Typus: Inhambane Mocambici, 6. 12. 1848, *Fornasinio* (holo- BOLO!).
= *J. fasciculiflora* Adamson in J. Linn. Soc., Bot. 50: 8 (1935) – Typus: Ceres, Zwartruggens, on rocks by waterfall, *Adamson 123* (BOL!).
= *J. kraussii* Hochst. var. *parviflorus* Adamson in J. Linn. Soc., Bot. 50: 8 (1935) – Typus: Lectotype (selected here): Buffalo Riv., 15 miles fr. E. London, 18. 1. 1930, *Adamson 179* (BOL!).
= *J. kraussii* Hochst. var. *effusus* Adamson in J. Linn. Soc., Bot. 50: 8 (1935) – Typus: Lectotype (selected here): Port Alfred in damp hollows near sea coast, alt. 50′, 24. 12. 1898, *Galpin 2946* (K!).
[= *J. spretus* Schult. & G. Schult. in Roemer & Schultes, Syst. Veg., ed. 7, 2: 1655 (1830), nom. inval. (not accepted by author)].

No intravaginal shoots observed. Culms 40–130 cm high, 2–4 mm thick, rigid, with 1–2 basal sheaths and 1–8 basal leaves. Leaves 20–65 cm long, 1.5–5 mm thick. Inflorescence 5–20 cm long, 3–7(–10) cm broad, lax, usually broad but sometimes elongated by subdivision in two parts, rarely congested to a few clusters, with 50–1000 heads. First bract 5–20(–40) cm long, including the 1.5–4 cm long sheath, the second 2–5 cm, including the 1–2 cm long sheath; bracts of the heads ovate, usually 2/3 as long as to equalling flowers. Heads 2–6-flowered. Most flowers functionally unisexual, in some specimens female with only rudimentary filaments, in others functionally male with degenerating ovary and reduced stigmata. Tepals 2.5–3(–4) mm, outer slightly longer, with a scarious margin, non-scarious part when young herbaceous, later straw-coloured to light brown, with darker, usually reddish brown to chestnut-coloured outer and apical zone, inside of a similar dark colour except for the scarious margin, outer tepals ovate, cymbiform, usually with a small mucro, with a conspicuously keeled basal part, when young with wide, fragile scarious margin apically, later and in dried state the scarious parts often collapsed, the tepals thus appearing acute and more long-mucronate, inner tepals oblong, with apical scarious wings but not notched. Stamens 6, c. 2/3 as long as tepals, anthers 1.3–1.6 mm long, 3.5–6.5 times as long as filaments, yellow as young, filaments 0.25–0.45 mm long. Style 0.4–0.75 mm long, stigmas 1.0–1.3(–1.8) mm long. Capsule 2–2.5(–3) mm long, equalling or up to 0.5 mm exceeding tepals, mucro 0–0.3 mm long, trilocular with obvious placental wings centrally, usually containing 25–35 seeds. Seeds 0.7–0.8 mm, including the seed-coat 0.8–0.9 mm long, 0.35–0.4 mm broad, 20–25-striate, transverse striae inconspicuous, c. 20 per longitudinal field; seed-coat forming two small, unequal appendages.

Comments: Adamson (1935) states that the plant described by him as *J. fasciculiflorus* has long-tailed seeds. The type at BOL has, however, only short-tailed seeds typical of *J. kraussii* and the plant as a whole is a usual *J. kraussii* subsp. *kraussii.*

Small-flowered specimens with a wide inflorescence were named *J. kraussii* var. *parviflorus* Adamson, but I find it impossible to delimit such a taxon which would mainly include male individuals.

Some of the Mozambique specimens have large flowers and a large, unusually light capsule with a large mucro. There is, however, a great variation in that area, including some specimens with the normal flower dimensions.

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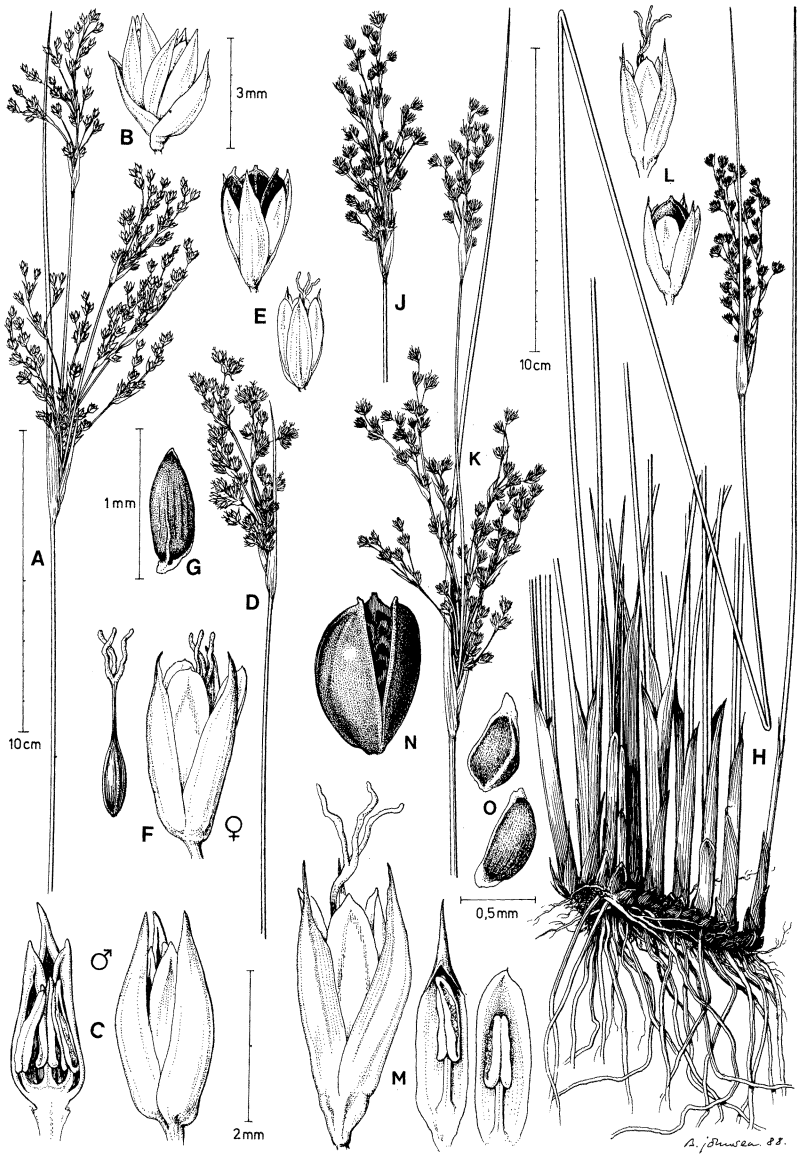

Fig. 16. *J. kraussii.* – A–G: subsp. *kraussii.* – A: Inflorescence of male individual. – B: Head of male individual. – C: Male flower. – D: Inflorescence of female individual. – E, F: Female flowers at different stages. – G: Seed. – H–O: subsp. *australiensis.* – H: End of rhizome. – J, K: Inflorescences. – L: Flowers in early flower and fruit. – M: Hermaphrodite flower and tepals with stamens. – N: Capsule: – O: Seeds. Material: A, B, C: S Africa, Uitenhage, *Ecklon & Zeyher Junc. 3* (LD). – D, F: S Africa, Uitenhage, *Ecklon & Zeyher Junc. 4* (LD). – E, G: Mocambique, Inharrime, *Schelpe 4516* (BM). – H, J, K, L, M: New Zealand, *Snogerup cult. nos. 3519, 3521* (LD). – N, O: Australia, Torrens river, *Müller s. n.* (LD).

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Distribution: South Africa, along the S and E coasts to S Mozambique (Fig. 17).

Ecology: In both salt and fresh-water marshes, on river margins, rarely in maritime sand, from sea level to 1700 m.

9. 7b. ***J. kraussii*** subsp. ***australiensis*** (Buchenau) Snogerup, **comb. nova** – Fig. 16.
≡ *J. maritimus* Lam. var. *australiensis* Buchenau in Bot. Jahrb. Syst. 12: 257 (1890) – Typus: Lectotype (selected here): Swan River, 1839, *J. Drummond, First Coll.*, det. Buchenau (BM!).

New shoots sometimes formed intravaginally at the base of strong culms in the lowest culm sheath or from a rhizome scale close to it. Culms 60–130 cm long, 1.5–2.5 mm thick, with 3–5 usually light glossy, basal sheaths, the uppermost of them up to 10(–15) cm long and often with a tiny lamina, and 2–5 basal leaves. Leaves 40–80 cm long, 1–4 mm thick. Inflorescence 6–25 cm long, 2.5–6 cm broad, variable in form but usually elongated and sometimes conspicuously bipartite, with 50–400 heads. First bract 4–40 cm long, including the 1.5–2.5(–4) cm long sheath, the second 1.5–5(–20) cm, including the 1–2 cm long sheath; bracts of the heads ovate, 1/2 as long as to almost equalling the flowers, usually light brown with darker base. Heads 3–6(–10)-flowered. Tepals 2.2–2.8(–3.3) mm, outer ones slightly or up to 0.5 mm longer, in central and basal part herbaceous when young, later straw-coloured to

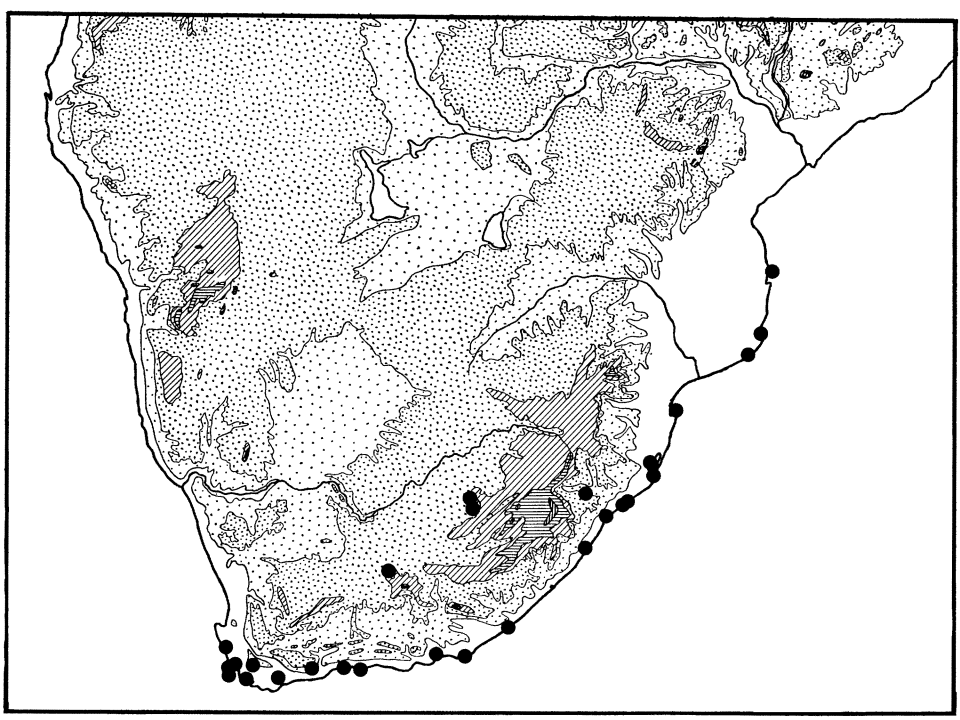

Fig. 17. *J. kraussii* subsp. *kraussii*, distribution according to revised material.

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light brown, with a darker brown to chestnut-coloured outer and apical zone, with a scarious margin, inside ± uniformly dark coloured except for the scarious margin, outer tepals ovate, cymbiform, with a conspicuously keeled basal part, scarious margin slightly broader in apical part, very fragile, with an arista up to 0.3 mm long, in dried state often apparently acute by collapse of the scarious parts, inner tepals oblong, obtuse, with a broader scarious part apically, sometimes with a mucro up to 0.2 mm long. Stamens 6 or by reduction of the inner ones 3, rarely in some flowers all rudimentary, 2/3–3/4 as long as tepals, anthers 0.7–1.2 mm long, 1.3–2.5 times as long as filaments, yellow when young, filaments (0.25–)0.45–0.6 mm long. Style 0.25–0.5 mm long, stigmas c. 1.5 mm long. Capsule 2–2.5 mm long, equalling or up to 0.5 mm exceeding tepals, trigono-ellipsoidal, acute to blunt with a mucro up to 0.3 mm long, glossy chestnut-coloured, trilocular with obvious placental wings centrally, usually containing 15–20(–25) seeds. Seeds 0.6–0.8(–0.9) mm, including the seed-coat 0.7–1.0 mm long, 0.3–0.4 mm broad, ellipsoidal to obliquely ovoidal, dark brown with one blackish, blunter end, (20–)25–30-striate, transverse striae inconspicuous; seed-coat forming one small appendage and sometimes an inconspicuous second one.

Distribution: Coastal areas of SW and S Australia, locally in saline localities of C Australia, Tasmania and the N and S Islands of New Zealand (Fig. 18).

Ecology: Salt marshes, mangrove swamps, in coastal sand fields, on the margins of rivers and rarely of lakes.

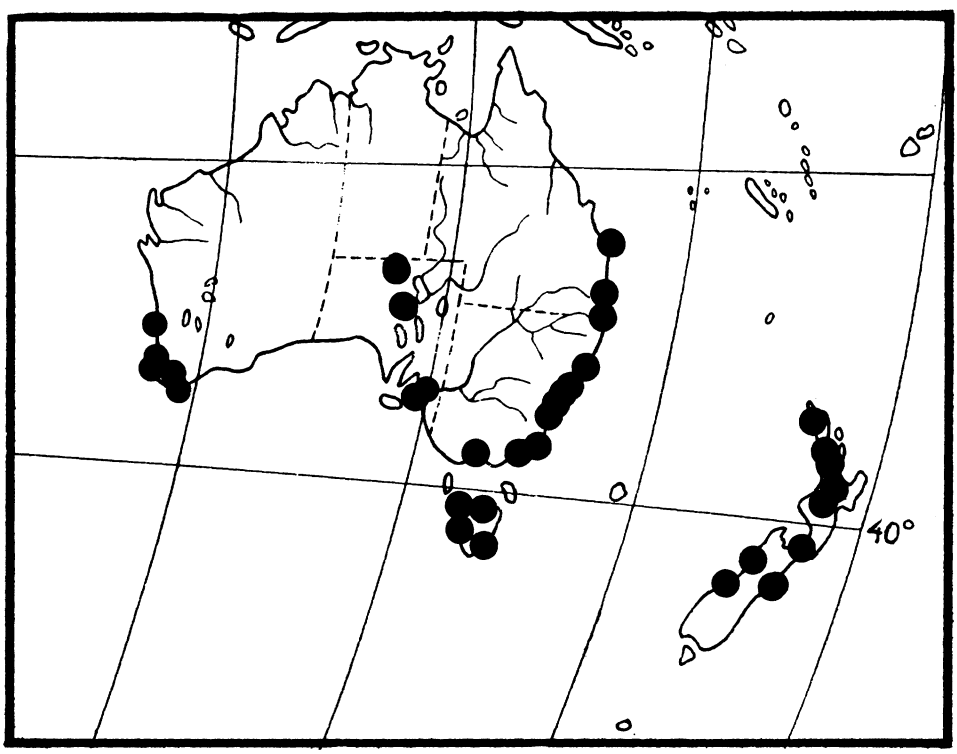

Fig. 18. *J. kraussii* subsp. *australiensis*, distribution according to revised material.

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9. 7c. ***J. kraussii*** subsp. ***austerus*** (Buchenau) Snogerup, **comb. nova** – Fig. 19.
≡ *J. austerus* Buchenau in Abh. Naturwiss. Vereine Bremen 6: 389 (1879) – Typus: Lectotype (selected here): Chile, San Carlo, *Lechler 3089* (K!).

No intravaginal shoots observed. Rhizome thick, with 5–20 mm long internodes. Culms (35–)80–120(– c. 200) cm high, 2–6 mm thick, with 3–5 light brown basal sheaths, the uppermost 2–10 cm long, sometimes with a short lamina, and 3–6 basal leaves. Leaves 30–100 cm long, or probably sometimes longer, 1.5–4 mm thick. Inflorescence (3–)8–12 cm long, (1.5–)3.5–5 cm broad, usually rather dense, flowers in (15–)75–200(– c. 1000) heads. First bract (3–)9–20(–60) cm long including the 2–6 cm long sheath, the second erecto-patent, 2–5 cm long including the 1–2 cm long sheath; bracts of the heads light brown, with a darker base, scariously margined, obtuse to often cuspidate, shorter than flowers. Heads (1–)3–8(–10)-flowered; pedicels up to 0.5 mm. Tepals 2.5–3.5 mm, the outer slightly longer, herbaceous in central and basal part, later light brown to straw-coloured, darker brown in a marginal-apical zone, with a scarious margin, outer tepals ovate, cymbiform, with a conspicuously keeled basal part, with an 0.1–0.3 mm long mucro, inner tepals oblong, obtuse, with a broad scarious part apically. Stamens 6, or by reduction of the outer ones 3, c. 2/3 as long as tepals, anthers rarely well preserved in fruiting flowers, 0.8–1.7 mm long, 1.5–3 times as long as filaments, yellow when young, filaments 0.3–0.7 mm long. Style 0.2–0.5 mm long, stigmas 1–1.5 mm long, soon contorted. Capsule 2.5–3 mm long, about equalling tepals, trigono-ellipsoidal to trigono-obovoidal, obtuse to acute, with a mucro up to 0.3 mm long, light brown to glossy chestnut-coloured, trilocular, usually containing 20–25 seeds. Seeds 0.7–0.9 mm, including the seed-coat 0.8–1.2 mm long, 0.3–0.4 mm broad, ellipsoidal to obliquely ovoidal, dark brown, c. 25-striate; seed-coat forming two small, unequal appendages.
Distribution: Locally in Chile, Argentina, Uruguay, S Brazil; only old collections seen (Fig. 20). As *J. acutus*, occurring in similar localities, has been repeatedly collected recently, *J. kraussii* subsp. *austerus* is certainly rare, even if sometimes overlooked because of similarity to the more common *J. acutus*.

Specimens examined:
C h i l e : St. Carlos prope Corall ad littora Oceani pacific Chile, 1. 1855, *Lechler 3089* (K).
A r g e n t i n a : Coast of Patagonia, early in Oct. 1832, *Darwin* (K).
U r u g u a y : Dep. Montevideo, Carasco, sandig-sumpfiges Terrain, salzhaltig, 24. 1. 1930, *Osten 21788b* (S).
B r a z i l : St. Catherine, *coll. ignot.*, Hb. Hookerianum (K); Prov. S. Paulo, Santos, 10. 1. 1875, *Mosén 3502* p.p. (LD, O, S); Prov. S. Paulo, Santos, S. Vicente in litore arenoso aprico muris, 10. 2. 1875, *Mosén 3502* p.p. (S).

Ecology: Seashores, at least two localities in maritime sand.

9. 8. ***J. roemerianus*** Scheele in Linnaea 22: 348 (1849) – Fig. 21.
Typus: Galveston island auf feuchtem Muschelsand, 4. 4.[1845-47], *Römer* (not traced, probably destroyed).

Perennial with a creeping rhizome, no intravaginal shoots observed, rhizome up to 7 mm thick, stout with nodes short or rarely up to 4 cm long. Some shoots often non-flowering, with

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Fig. 19. *J. kraussii* subsp. *austerus*. – A: Rhizome with several culms. – B: Inflorescence. – C: Head in late bud stage. – D: Flower and pistil. – E: Inner tepal with stamen. – F: Flower with ripe fruit. – G: Opened capsule. – H: Seeds.
Material: A, C, D, E: Uruguay, Montevideo, Carrasco, *Osten 21788b* (S). – B, F, G, H: Brasilia, Sao Paulo, Santos, *Mosén 3502* (S).

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Fig. 20: *J. kraussii* subsp. *austerus*, distribution according to revised material. The Darwin locality of "coast of Patagonia" not marked.

1–3 leaves only. Culms (15–)50–150(–230) cm high, 3–4 mm thick, rigid, with 2–5 basal sheaths, the uppermost up to 10 cm long with a tiny lamina, and 1–5(–8) basal leaves. Leaves 40–125 cm long, 1.5–4 mm thick, terete, pungent, auricles lacking. Inflorescence (2–)5–20(–45) cm long, 3–6(–12) cm broad, variable in form, usually lax and rather broad, with (15–)30–100(–200) heads, heads often aggregated in conspicuous clusters. Lowest two bracts leaf-like, pungent, the first (2–)5–20(–90) cm including the 1.5–3(–5) cm long sheath, forming an apparent prolongation of the culm, the second 2–5 cm including the 1–1.5 cm long sheath, erecto-patent; upper bracts small, amplexicaul, with no or very small lamina, those of the heads considerably shorter than flowers, ovate, straw-coloured to light brown, acuminate.

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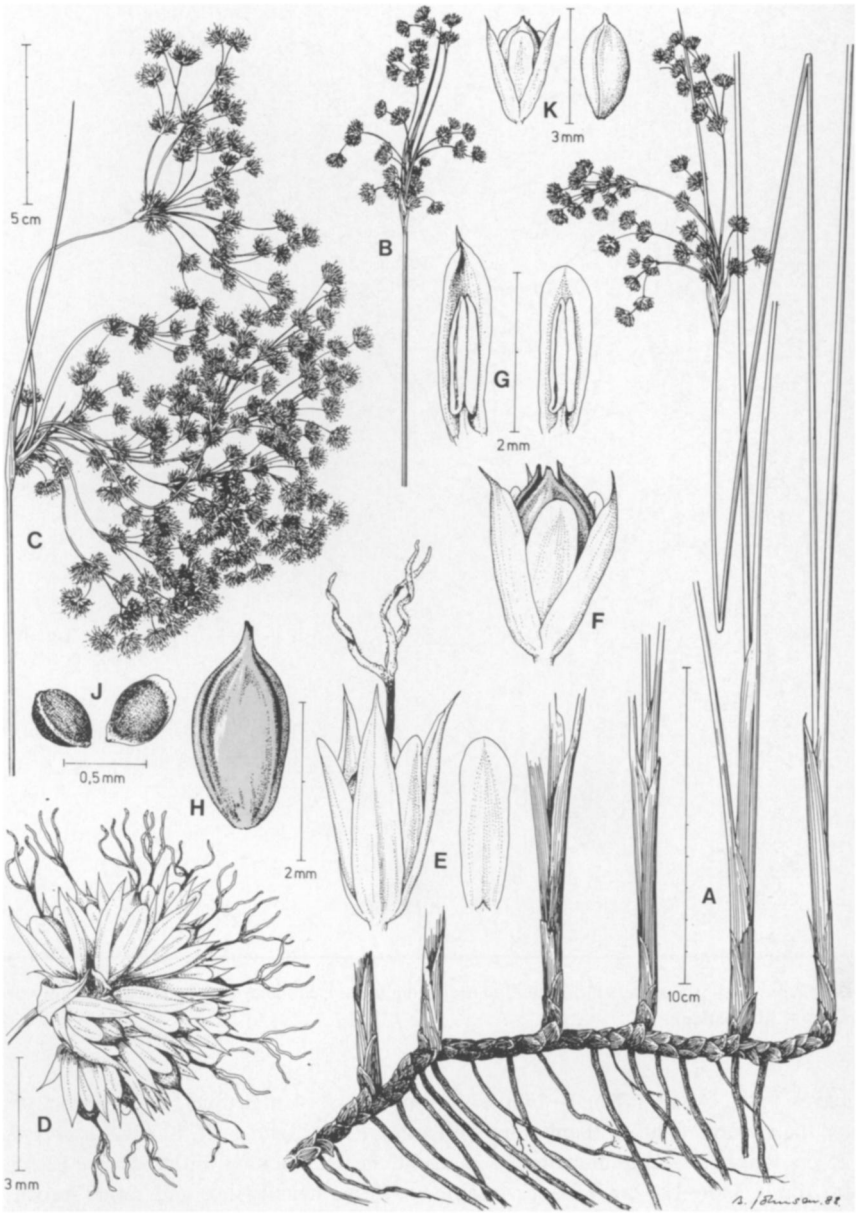

Fig. 21. *J. roemerianus*. – A: Base and inflorescence. – B, C: Inflorescences. – D: Female head. – E: Flower and tepal of female individual. – F: Hermaphrodite flower in fruit. – G: Tepals of hermaphrodite flower with stamens. – H: Capsule of female flower. – J: Seeds. – K: Hermaphrodite flower in fruit and capsule. Material: A, C, D, E, F, G, H, J: USA, Florida, Gulf Co., 25. 7. 1978, *D. Persson* (LD). – B: USA, Texas,

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Heads 2–8, or in material from Texas up to 25-flowered, if many-flowered few in number. Plant gynodioecious, with female and hermaphrodite clones, the latter with hermaphrodite flowers only or rarely mixed hermaphrodite and female. Tepals 2.2–3.5 mm long, usually smaller in pistillate than in hermaphrodite flowers, the outer slightly longer, when young herbaceous with a scarious margin, later in central part straw-coloured to light brown, sometimes darker in marginal and apical part, rarely light brown to dark reddish brown, inside uniformly dark brown to chestnut-coloured except for the scarious margin, outer tepals ovate or narrowly ovate, cymbiform with a conspicuously keeled basal part, with slightly wider scarious margins apically, with an arista up to 0.3 mm long, inner tepals oblong, obtuse, sometimes with a very small mucro, scarious part wide apically. Stamens 6 in hermaphrodite flowers, as long as tepals or slightly shorter, in pistillate flowers only rudimentary staminodes, anthers 1.4–1.7(–2.0) mm long, 5–7 times as long as filaments, yellow when young, filaments c. 0.25 mm long. Style 0.5–0.7 mm long, stigmas 1.5–2.5 mm long, yellow to light brown or in pistillate flowers dark to reddish brown and longer than in the hermaphrodite. Capsule in hermaphrodite flowers 2.5–3 mm, in pistillate flowers 3–5 mm long, usually slightly exceeding tepals, broadly trigono-ellipsoidal to trigono-obovoidal, blunt with a mucro 0.1– 0.3 mm long, light to dark brown glossy, trilocular with radiant, thick placentas. Seeds 0.5–0.7 mm long, 0.3–0.4 mm broad, including the seed-coat 0.6–0.8 mm long, ellipsoidal to obliquely ovoidal, usually pointed at both ends and one end darker, pale yellow to brown, c. 25-striate, striae inconspicuous; seed-coat appendages usually very small or one of them up to 0.1 mm long.

Distribution: Atlantic coasts of North America from Virginia to Texas (Fig. 22). According to Eleuterius (1976) also occurring in Delaware.

Ecology: Salt marshes, stabilized maritime sands. Often forming large, ± pure stands in tidal pools mainly in the upper part of the tidal zone. Dominating this zone in large parts of tidal marshes from N Carolina to Louisiana, less abundant in the more northern and western parts of its area.

9. 9. ***J. cooperi*** Engelm. in Trans. Acad. Sci. St. Louis 2: 590 (1868) – Fig. 23.
Typus: Camp Cady in the southern part of the State of California, *Cooper* (MO?).

Perennial, usually densely caespitose, rhizome 3–5 mm thick, very short-noded, branching. New shoots produced from the rhizome as well as intravaginally from the base of earlier shoots. Culms (40–)50–80(–100) cm high, (1.5–)2–4 mm thick, with 2–4(–5) basal sheaths, the longest up to 10 cm, and 3–5 basal leaves. Leaves 15–60 cm, including up to 10(– 25) cm long sheaths, (1.5–)2–3 mm thick. Culms and leaves rather pronouncedly striate. Inflorescence (3–)4–15 cm long, (1–)1.5–3(–5) cm broad, with 3–2(–25) heads, some heads often clustered into dense groups. First bract leaf-like, pungent, often very thin, (2.5–)6–22 cm long, including the 1.8–4 cm long sheath, forming an apparent prolongation of the culm, the second very small, similar to the upper bracts or up to 5 cm, with large sheath and small lamina; those of the heads usually much shorter than flowers but sometimes equalling or slightly longer, narrowly ovate, amplexicaul, with a small pungent lamina, scarious except for the midrib. Heads (1–)4–8(–12)-flowered; pedicels short, apically ± incrassate. Tepals 5–6.5 mm, the inner shorter, herbaceous with a scarious margin when young, later straw-coloured,

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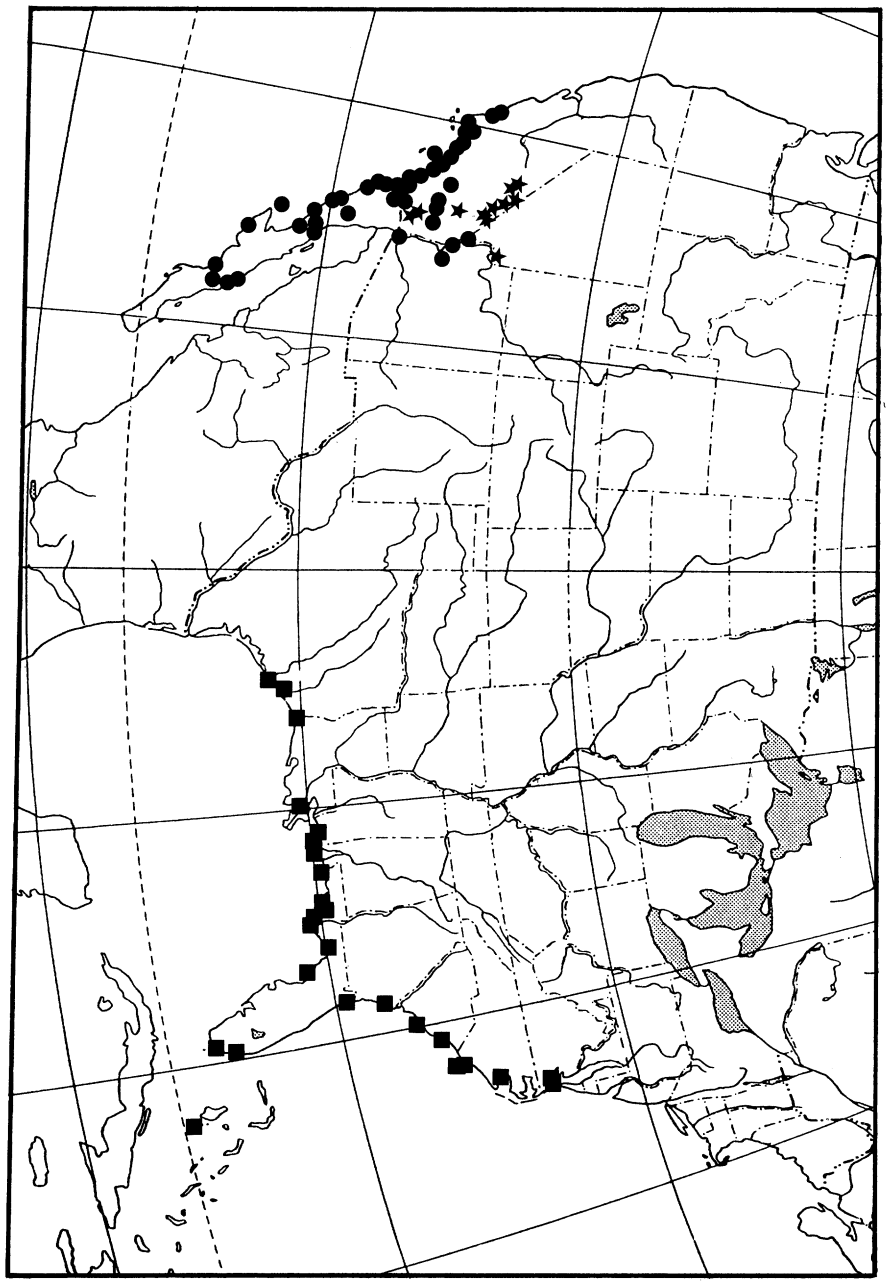

Fig. 22. Distribution in North America according to revised material. – Dots: *J. acutus* subsp. *leopoldii*. – Stars: *J. cooperi*. – Squares: *J. roemerianus*.

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in fruit with thick spongy bases below the insertion of other floral parts, outer tepals cymbiform, aristate with an arista up to 1 mm long, apically with a scarious margin up to 0.5 mm wide, inner tepals oblong, flatter, apically with wide scarious wings and usually ± emarginate, the wings very thin and usually early deformated. Stamens 6, 2/3–3/4 as long as tepals, anthers (2.2–)2.5–3.5 mm long, (2.5–)5–7 times as long as filaments, yellow when young, filaments 0.5–1.2 mm long. Style 1.5–2 mm long, stigmas 2.5–3.5 mm long. Capsule 4–5.5 mm long, slightly exceeding tepals, ovoidal and ± trigonous, attenuate, acute to blunt with a very small mucro, straw-coloured to light brown with darker mucro, trilocular with narrow placental wings, thick-walled, probably containing 60–70 seeds. Seeds 0.9–1.1 mm, including the seed-coat 1.5–1.9 mm long, 0.4–0.6 mm broad, ellipsoidal to ovoidal, c. 25-striate; seed-coat wide, forming two short, ± unequal, light appendages.

Distribution: In California from Inyo to Imperial Counties; in S Nevada only known from Saline Valley, Death Valley and Mohave desert.

Ecology: Saline or brackish marshes and periodically wet flats. The large populations of *J. cooperi* form a belt around the vegetation-less saline flats in the centres of the desert valleys. In this zone the salinity in the soil is considerable. Surface water collects in the central, flat depressions after each rain but dissolves salts from the soil and then evaporates. The *J. cooperi* vegetation comprises as most frequent associate species *Allenrolfea occidentalis* (Wats.) Kuntze and *Distichlis spicata* (L.) Greene. Some smaller populations are found along more or less saline streams associated with other halophytes. Flowering April to early May.

10. Distribution and probable phylogeny

In the E Mediterranean and SW Asia *Juncus* subgen. *Juncus* is represented with 6 species, in South Africa with 3, in other areas with 1 or 2 species only. The two endemic North American species are certainly no close relatives and have probably migrated there independently. *J. cooperi* is found in deserts of W North America and *J. roemerianus* on the SE coasts of the USA.

There are three comparatively wide-spread complexes in the subgenus: the *J. acutus* group comprising *J. acutus, J. littoralis, J. heldreichianus* and *J. socotranus*, the *J. maritimus* group with *J. maritimus* and *J. rigidus*, and the *J. kraussii* group with the subspecies of *J. kraussii* and *J. roemerianus*.

J. acutus has a natural distribution area including SW Asia, Europe, the whole of Africa, S and W South America, W North America and several islands in the Atlantic. This might suggest a South American-African origin from times when these areas were in better contact. On the other hand all closer relatives of *J. acutus*, i.e. *J. littoralis, J. heldreichianus* and *J. socotranus*, are distributed in the SW Asia-Mediterranean area. Consequently I believe that the *J. acutus* group differentiated within the Near East area and that *J. acutus* subsp. *leopoldii* later spread into its present large distribution area.

In the *J. maritimus* group one species, *J. rigidus*, occurs in the deserts throughout Africa and SW Asia, the other, *J. maritimus*, occurs in Europe and the more northern parts of SW Asia. Again, this points to a common origin in SW Asia. In this area thus both the *J. maritimus* and the *J. acutus* groups may have originated. How and when *J. cooperi*, closely allied to the *J. maritimus* group, reached the deserts of W North America remains unknown.

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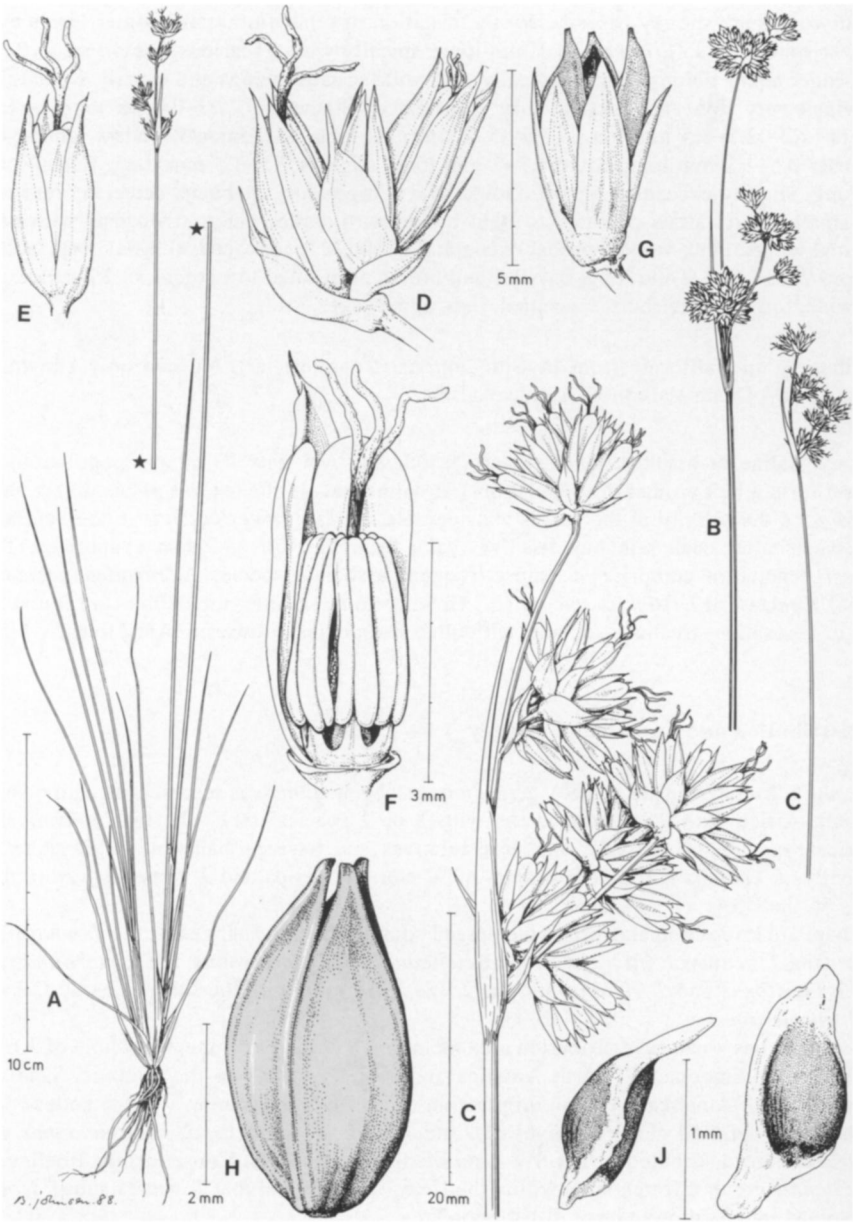

Fig. 23. *J. cooperi.* – A: 6 months old plant in first flower. – B, C: Inflorescences. – D: Head in onset of flowering. – E. Flower. – F: Dissected flower. – G: Flower with opened fruit. Apices of inner tepals collapsed. – H: Capsule: – J: Seeds.
Material: A, C, D, E, F, H, J: USA, California, Inyo Co., Death Valley, N Furnace Creek, coll. *S. Riebe*, *Snogerup cult. nos. 4166, 4165* (LD). – G: Death Valley, N Harmony Borax Works, *Snogerup 3440* (LD).

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J. kraussii with its three subspecies has a disjunct circum-Antarctic distribution occurring in S Africa, Australia, New Zealand and South America. The species probably reached these regions sometime in the Tertiary when a circum-Antarctic vegetation was better developed. *J. roemerianus* is probably closely related to *J. kraussii*, as they share the occurrence of functionally unisexual flowers as well as the small, dark and blunt capsule. How and when *J. roemerianus* reached North America is not known.

The probable phylogeny of *J.* subgen. *Juncus* is shown in Fig. 24. Fossile evidence is lacking. My conclusions are founded on the combinations of derived characters and on the distribution of the groups and species as outlined above. Further investigations are needed to make the picture more definite.

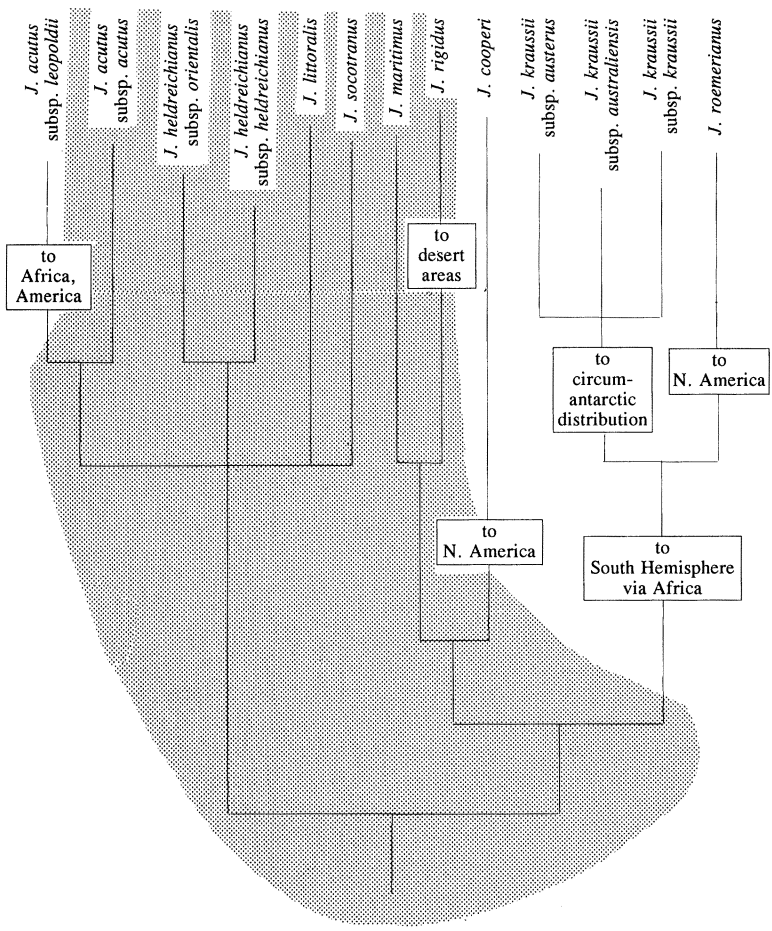

Fig. 24. *Juncus* subgen. *Juncus*, probable history and phylogeny. Continued differentiation within the SW Asia-Mediterranean centre is indicated by the shadowed area. *J. acutus* – *J. socotranus* share caespitose habit and auriculate inner tepals, *J. kraussii* – *J. roemerianus* share occurrence of unisexual flowers, short-tailed seeds, small few-seeded capsules and a change of area.

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Acknowledgement

This investigation was supported by grants from the Royal Physiographic Society, Lund, The Lars Hiertas Minne Foundation and the Swedish Natural Science Research Council. The drawings were made by Bent Johnsen, Copenhagen, and linguistic advice was given by Barbara Giles. B. Snogerup has assisted in the preparation of the manuscript.

References

Adamson, M. A. 1935: A revision of the South African species of *Juncus*. – J. Linn. Soc., Bot. **50:** 1–38.

Borgen, L. 1969: Chromosome numbers of vascular plants from the Canary Islands, with special reference to the occurrence of polyploidy. – Nytt Mag. Bot. **16**: 81–121.

Buchenau, F. 1875: Monographie der Juncaceen vom Cap. – Abh. Naturwiss. Vereine Bremen **4:** 393–512.

— 1890: Monografia Juncacearum. – Bot. Jahrb. Syst. **12:** 1–495.

— 1906: *Juncaceae*. – In: Engler, A. (ed.), Das Pflanzenreich **25**. – Leipzig.

Coville, F. V. 1913: *Juncaceae*, p. 465–485. – In: Britton, N. L. & Brown, H. A., An illustrated flora of the northern United States, Canada and the British possessions, ed. 2, **1.** – New York.

Dalgaard, V. 1986: Chromosome studies in flowering plants from Macaronesia. – Anales Jard. Bot. Madrid **43:** 83–111.

Eleuterius, L. N. 1976: The distribution of *Juncus roemerianus* in the salt marshes of North America. – Chesapeake Sci. **17:** 289–292.

— 1979: Amino acids of the salt marsh rush, *Juncus roemerianus*. – Arch. Hydrobiol. **87:** 112–117.

— 1984: Sex distribution in the progeny of salt marsh rush, *Juncus roemerianus*, in Mississippi. – Castanea **49:** 35–38.

Engelmann, G. 1866, 1868: A revision of the North American species of the genus *Juncus*, with a description of new and imperfectly known species. – Trans. Acad. Sci. St. Louis **2:** 424–458, 459–499.

Jarvis, C. E. et al. 1993: A list of Linnaean generic names and their types. – Regnum Veg. **127.**

Kreczetowicz, V. J. & Gontscharov, N. 1935: *Juncaceae*, p. 504–576. – In: Komarov, V. L. (ed.), Flora URSS **3**. – Leningrad.

Nilsson, Ö. & Snogerup, S. 1971: Drawings of Scandinavian plants 55–59. *Juncus* L. – Bot. Not. **124:** 311–316.

— & — 1972: Drawings of Scandinavian plants 75–80. *Juncus* L. – Bot. Not. **125:** 203–211.

Novara, L. J. 1976: Contribucion al concimiento de las inflorescencias de *Juncus* y su significacion taxonomica. – Kurtziana **9:** 41–61.

Novikov, V. S. 1976: *Juncaceae*, p. 59–83. – In: Fedorov, A. A. (ed.), Flora Evropejskoj Časti SSSR **2.** – Leningrad.

— 1990: Konspect sistemy roda *Juncus* L. (*Juncaceae*). – Bjull. Moskovsk Obšč. Isp. Prir., Otd. Biol. **95(5):** 111–125.

Riebe, S. 1978: Meiotic configurations and fertility in *Juncus alpinus* subsp. *nodulosus* x *articulatus*. – Bot. Not. **131:** 269–272.

Snogerup, B. 1985: Reports, p. 727–728. – In: Löve, Á. (ed.), Chromosome number reports LXXXIX. – Taxon **34:** 727–730.

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Snogerup, S. 1958: Studies in the genus *Juncus*. Some cytological observations. – Bot. Not. **111:** 249–250.
— 1963: Studies in the genus *Juncus* III. Observations on the diversity of chromosome numbers. – Bot. Not. **116:** 142–156.
— 1969: Studies in the genus *Juncus* II. Observation on *Juncus articulatus* L. × *bulbosus* L. – Bot. Not. **122:** 246–256.
— 1971: *Juncaceae*. – In: Rechinger, K. H. (ed.), Flora Iranica **75**. – Graz.
Stace, C. A. 1975: Hybridization and the flora of the British Isles. – London.
Zahran, M. A. 1975: On the germination of seeds of *Juncus rigidus* C. A. Mey. and *J. acutus* L. – Bull. Fac. Sci. Mansoura Univ. **3:** 75–84.
— , Kamal El-Din, H. & Boulus, S. 1972: Potentialities of fiber plants of Egyptian Flora in national economy. 1. *Juncus rigidus* C. A. Mey. and paper industry. – Bull. Inst. Désert Égypte **22:** 193–203.

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