

Genetic distinctiveness supports
the resurrection of the South African *Juncus acutissimus*
(Buchenau) Adamson as a subspecies of *J. inflexus* L.

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Genetic distinctiveness supports the resurrection of the South African *Juncus acutissimus* (Buchenau) Adamson as a subspecies of *J. inflexus* L.

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ABSTRACT

Juncus acutissimus (Buchenau) Adamson was originally described by Buchenau in 1875 as a variety of *J. glaucus* Sibth. (now *J. inflexus* L.) from South Africa and elevated to species rank by Adamson in 1935. Contemporary taxonomic treatments, including Kirschner's global monograph, currently consider it a synonym of *J. inflexus*. However, recent findings along the Meuse River in Limburg, the Netherlands – originating from the soil seed bank – have revealed populations of *J. acutissimus* with a likely historical link to the wool-processing industry upstream along the Vesdre River in Belgium. This industry imported large quantities of raw wool primarily from Australia, South Africa, and South America. Genetic analysis (ITS and *trnL-F* markers) confirms that these populations are closely related to *J. inflexus* but exhibit consistent genetic divergence. Based on morphological, genetic, and biogeographical evidence, we propose to recognize *Juncus acutissimus* as a subspecies of *J. inflexus*.

RÉSUMÉ

La caractérisation génétique justifie la résurrection de Juncus acutissimus (Buchenau) Adamson d'Afrique du Sud en sous-espèce de J. inflexus L.

Juncus acutissimus (Buchenau) Adamson a été initialement décrit par Buchenau en 1875 comme une variété de *J. glaucus* Sibth. (aujourd'hui *J. inflexus* L.) d'Afrique du Sud, puis élevé au rang d'espèce par Adamson en 1935. Les traitements taxonomiques contemporains, y compris la monographie mondiale de Kirschner, le considèrent actuellement comme un synonyme de *J. inflexus*. Cependant, des observations récentes le long de la Meuse, au Limbourg (Pays-Bas) – à partir de la banque de graines du sol – ont révélé des populations de *J. acutissimus* probablement liées historiquement à l'industrie lainière, en amont le long de la Vesdre, en Belgique. Cette industrie importait d'importantes quantités de laine brute, principalement d'Australie, d'Afrique du Sud et d'Amérique du Sud. L'analyse génétique (marqueurs ITS et *trnL-F*) confirme que ces populations sont étroitement apparentées à *J. inflexus*, mais présentent une divergence génétique constante. Sur la base de preuves morphologiques, génétiques et biogéographiques, nous proposons de reconnaître *Juncus acutissimus* comme une sous-espèce de *J. inflexus*.

KEY WORDS

Juncaceae subspecies,
genetic divergence,
ITS,
trnL-F,
biogeography,
wool industry,
introduced populations,
new combination,
new status.

MOTS CLÉS

Juncaceae,
sous-espèce,
divergence génétique,
ITS,
trnL-F,
biogéographie,
industrie lainière,
populations introduites,
combinaison nouvelle,
statut nouveau.

INTRODUCTION

Juncus inflexus L. (syn.: *J. glaucus* Sibth., nom. superfl.) is a widespread species native to temperate Eurasia, with more scattered occurrences in North Africa and the Arabian Peninsula. It belongs to section *Juncotypus* Dumort. [the genus *Agathryon* (Raf.) Závěská Drábková & Pročkův, according to some recent authors; Pročkův & Drábková 2023] and is readily distinguished within this section by its glaucous, coarsely grooved stems with interrupted pith and glossy, dark basal cataphylls. Historically, numerous infraspecific taxa – mostly varieties or forms – have been described within the species. In addition, several species once considered distinct are now treated as heterotypic synonyms of *J. inflexus* (POWO 2025). Current treatments, however, including Kirschner's global monograph of the genus (Species Plantarum: Flora of the World 2002), recognize only two infraspecific taxa: *Juncus inflexus* subsp. *brachytepalus* (Trautv. ex V.I.Krecz. & Gontsch.) Novikov, from Central and Eastern Asia, and the autonymic subspecies. The *Juncus inflexus* subsp. *brachytepalus* is distinguished by thicker stems, paler basal sheaths, and larger capsules that are much longer than the tepals (Krechetovich & Goncharov 1964).

In the summers of 2024 and 2025, populations resembling *Juncus inflexus* were discovered at several locations along the Meuse River in the Netherlands. At the same sites, numerous plants of typical *J. inflexus* were also present, a widespread native species along the river. This provided the opportunity to compare the aberrant individuals directly in the field with unequivocal representatives of the species. Interestingly, upon reviewing our photographic archives, we found that similar plants had already been documented near Geulle-aan-de-Maas, approximately five km upstream from Grevenbicht, in August 2017. At that time, their unusually finely ribbed stems and very acute, elongate tepals were noted as atypical for *J. inflexus*, although their identity remained unresolved. This early observation indicates that the same morphologically distinctive taxon has been present along the Meuse for at least several years prior to its recent rediscovery.

Since 2016, numerous exotic rushes have been recorded on these riverbanks, following extensive restoration works in the Meuse valley. These activities exposed long-lived seed banks, many of which contained diaspores historically introduced via the wool-processing industry located further upstream in the Vesdre valley in Belgium. Since the onset of these developments, around 30 exotic *Juncus* taxa have been identified along the Meuse, most of which are native to Australia or New Zealand, with a few originating from South America (Gonggrijp & Verloove, unpublished data). Following the 2021 floods that reshaped the Vesdre valley, a South African rush species (*J. capensis* Thunb.) was also recorded there (Verloove *et al.* 2026). Australia, South Africa, and South America were the principal suppliers of raw wool to the region during the 19th and 20th centuries.

Initially, the enigmatic Meuse populations were suspected to represent hybrids of *J. inflexus*, as mixed populations of

numerous native and exotic *Juncus* species – often several thousand individuals strong – frequently give rise to natural hybrids. Notably, in recent years, putative hybrids between *J. inflexus* and at least four or five Australian *Juncus* species have been observed along the Meuse, further supporting the potential for natural hybridization in this genus under sympatric conditions. However, the plants in question consistently produced viable seeds, and their pollen appeared to be fully fertile.

A thorough review of all historical synonyms and infraspecific taxa of *J. inflexus* revealed a perfect morphological match with *Juncus glaucus* var. *acutissimus* Buchenau (1875), a taxon described from South Africa. Buchenau distinguished *Juncus glaucus* var. *acutissimus* from typical *J. glaucus* (now *J. inflexus*) by its paler basal sheaths, finely (not coarsely) grooved culms, and lanceolate-subulate, very acute tepals exceeding the trigonous-ovoid, mucronate capsule. He noted some uncertainty regarding the exact coloration of the basal sheaths due to incomplete type material, initially describing them as pale but later suggesting “chestnut” as a more accurate characterization. Tepals were described as long and pointed. At the time, Buchenau did not assign species rank, but highlighted these morphological distinctions as potentially significant. Adamson (1935) later examined South African material and, based on similar morphological features and its distinct geographical distribution, raised the taxon to species rank as *J. acutissimus*. However, in *Flora of Southern Africa* (Obermeyer 1985), the taxon was treated as a synonym of *J. inflexus* without further explanation. It remains unclear whether Obermeyer was the first to formally make this change or if it had already been reduced to synonymy earlier by another authority, which we could not trace in the literature. Nonetheless, this treatment of the taxon as a synonym has been maintained in subsequent works, including Kirschner (2002) and the current Plants of the World Online (POWO 2025).

Due to the distinct morphological appearance of the Meuse populations in the field – and in light of the biogeographically disjunct native range of *J. inflexus* in South Africa – it was decided to subject these plants to molecular phylogenetic analysis. The results of this investigation form the basis of the present study.

MATERIAL AND METHODS

Systematic fieldwork in the Meuse valley has been conducted since 2016, with numerous localities surveyed during dozens of visits. Herbarium specimens of the aberrant plants, representing the taxon under study, were collected in four locations (Grevenbicht, Meers, Nattenhoven, and Schipperskerk) and are currently preserved in the herbaria of Naturalis, the Netherlands (L) and Meise Botanic Garden, Belgium (BR). These collections provided the basis for morphological comparisons. For molecular and pollen analyses, a single voucher specimen was selected: *F. Verloove 15443* (BR0000027059944V) (see Taxonomic treatment).

HERBARIUM ABBREVIATIONS

BR	Meise Botanic Garden, Meise;
E	Royal Botanic Garden, Edinburgh;
K	Royal Botanic Gardens, Kew;
L	Naturalis Biodiversity Center, Leiden;
LD	Herbarium – Lund University Biological Museum, Lund;
LE	Herbarium – Komarov Botanical Institute of RAS;
P	Muséum national d'Histoire naturelle, Paris;
S	Department of Botany – Swedish Museum of Natural History, Stockholm;
W	Herbarium – Naturhistorisches Museum Wien/Natural History Museum Vienna, Vienna;
WRSL	Wrocław University, Wrocław.

REMARKS ON OBSERVATIONS

All observations were recorded on the online platform <https://waarneming.nl/> and, after validation, subsequently uploaded to the Global Biodiversity Information Facility (GBIF; www.gbif.org). To better evaluate species-specific morphological traits and assess their consistency, several individuals were uprooted for cultivation ex situ.

In addition to the specimens collected in the Meuse valley, we examined numerous images of *Juncus inflexus* from southern Africa on iNaturalist, as well as digitized herbarium specimens from online repositories, in particular the Kew Herbarium (K). This allowed us to assess the morphological variation of the South African populations in their native range and to evaluate the consistency of the traits observed in the secondary (European) range.

Molecular phylogenetic analyses were based on the nuclear rDNA internal transcribed spacer (ITS) region, and the plastid marker spanning the *trnL* intron and *trnL-trnF* intergenic spacer (*trnL-F*). The selection of these markers was based on the availability of sequences of *J. inflexus* and related taxa in public sequence databases. Total genomic DNA was extracted from silica-dried leaf material using a modified CTAB protocol. The ITS region was amplified using primers ITS1 and ITS4 (White *et al.* 1990) and *trnL-F* region was amplified using primers *trnLe* and *trnL-F* (Taberlet *et al.* 1991). PCR conditions followed Verloove *et al.* (2024). PCR products were sequenced by Macrogen (Seoul, South Korea). Forward and reverse sequences were assembled using Geneious Prime v2023.2.1. (Biomatters, Auckland, New Zealand). Sequences have been deposited in EMBL/GenBank under project number PRJEB101738 and accession numbers OZ352870 (*trnL-F*) and OZ352871 (ITS). Two datasets of 24 ITS (576 positions), and 26 *trnL-F* (828 positions) were constructed, including the sequences generated in this study and publicly available sequences obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Sequences were aligned using MUSCLE (Edgar 2004). Phylogenetic relationships were reconstructed using maximum likelihood and 1000 ultrafast bootstrap replicates in IQ-TREE 2.4.0 (Minh *et al.* 2020) on the IQ-TREE server (<http://iqtree.cibiv.univie.ac.at/>) (Trifinopoulos *et al.* 2016).

Pollen viability was assessed using lactophenol-cotton blue staining, following standard protocols. Pollen samples were taken from anthers of flowering individuals. Slides were examined under a compound microscope, and viability was inferred from uniform staining and absence of morphological abnormalities.

RESULTS

MORPHOLOGY

Juncus glaucus var. *acutissimus* was described by Buchenau (1875) as differing from typical *J. glaucus* (now *J. inflexus*) by the colour of its basal sheaths, culm striation, and tepal morphology. Examination of our own and South African material (e.g., K003055549, K00345818) confirmed the following.

Basal sheaths

Chestnut-coloured to dark at the base. South African material showed no consistent difference from *J. inflexus*.

Tepals

Lanceolate-subulate, sharply acute, and consistently exceeding the capsule. While overall morphology is similar to *J. inflexus*, our observations – including archival photographs from 2017 – indicate that the tepals of these populations often appear somewhat narrower, more acutely pointed, and consistently longer than the capsule.

Culms

Finely striate with up to *c.* 40 ribs, compared with the 10–22 coarse ribs typical of *J. inflexus* (Figs 1, 2). Ribs in South African material were less raised, more evenly integrated into the culm surface, and more closely spaced, resulting in a smoother appearance. Depth and spacing of ribs also differed consistently from *J. inflexus*.

Inflorescence coloration after flowering

Reddish to ferruginous (Fig. 3), contrasting with the darker brown inflorescences of *J. inflexus* (Fig. 4). The difference in coloration is subtle and varies over the season; nevertheless, the reddish inflorescences notably drew our attention during the summer of 2024 when populations were first observed at Koeweide-Trierveld.

POLLEN VIABILITY

All pollen grains examined were well developed, uniformly stained, and showed no signs of abortion.

MOLECULAR CHARACTERIZATION (Fig. 5)

The phylogenetic analysis based on *trnL-F* sequences resolved the analyzed *Juncus acutissimus* sample as sister to *J. inflexus* (AY850167; sequence available at NCBI) (Fig. 5), differing by four nucleotide substitutions and one indel. The ITS-based phylogeny provided weaker resolution: *J. acutissimus* (FV15443) clustered within a broader clade comprising *J. inflexus* and allied taxa, but the interspecific relationships within this clade were poorly supported. The ITS sequences of *J. acutissimus* and *J. inflexus* differed by three nucleotide positions.

DISCUSSION

Buchenau (1875) described var. *acutissimus* in detail, remarking on its finely striate culms (“subtiliter valleculati”) and distinct

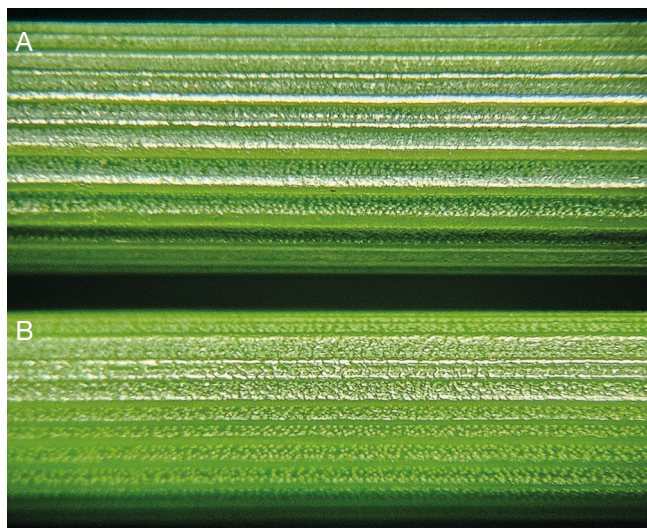


FIG. 1. — Close-up of stems of *Juncus inflexus* L. subsp. *inflexus* (A) and *Juncus inflexus* L. subsp. *acutissimus* Verloove & Gonggrijp, comb. nov., stat. nov. (B). In the latter taxon, the ribs are more numerous but less pronounced. Photo taken in Koeweide-Trierveld on 29 June 2024 by S. Gonggrijp.

inflorescence coloration, but withheld species rank due to incomplete type material. He also noted its disjunct distribution and the absence of closely related taxa in South Africa. Adamson (1935) emphasized similar features and elevated it to species rank, citing both morphological distinctness and geographical isolation. Later treatments (Obermeyer 1985; Kirschner 2002) subsumed the taxon under *J. inflexus* without comment. However, as shown in this study, the South African populations previously referred to as *J. inflexus* differ consistently from Eurasian populations in both morphology and genetics.

The most striking difference lies in culm ornamentation: *J. acutissimus* has finer and more numerous ribs (up to *c.* 40), less protruding, and more closely spaced than the coarser 10–22 ribs of *J. inflexus*. Inflorescences appear reddish to ferruginous after anthesis and are paler than the darker brown typical of *J. inflexus* at fruiting; this variation makes color a subtle rather than definitive diagnostic feature, although the reddish inflorescences notably drew our attention during the summer of 2024 at Koeweide-Trierveld. Tepals also show minor, consistent differences: tepals tend to be somewhat narrower, more acutely pointed, and consistently longer than the capsule. Basal sheaths show negligible differentiation. Within section *Juncotypus*, to which *J. inflexus* belongs, the number, spacing, and prominence of culm ribs are recognized as key diagnostic features (Johnson 1991; Johnson 1993; Kirschner 2002). The consistent differences observed in the South African material therefore carry significant taxonomic weight and cannot be dismissed as minor variation, while tepal and inflorescence traits provide additional supporting evidence.

The plastid and nuclear DNA markers support the morphological differentiation, revealing a close phylogenetic affinity between *J. acutissimus* and *J. inflexus*, while only showing minor genetic divergence. The limited number of nucleotide

differences and the restricted sampling suggest that the genetic data are insufficient to justify recognition at the species level.

Taken together, the morphological and molecular evidence, along with historical observations by Buchenau (1875) and Adamson (1935), support recognition of the South African taxon. Although it exhibits consistent, albeit subtle, differences in stem rib number and shape, inflorescence color, and DNA sequences, its close phylogenetic relationship with *J. inflexus*, coupled with limited genetic divergence, suggests that subspecific rank may be most appropriate. This aligns with the rationale of Sosef *et al.* (2020), who define a subspecies as a population within a species that is morphologically or genetically distinct and generally occurs in a geographically separate region. The apparent endemism of the South African taxon, combined with its disjunction from the primarily Eurasian distribution of *J. inflexus*, highlights its evolutionary and biogeographical distinctness, while still reflecting its close relationship to the parent species.

TAXONOMIC TREATMENT

Family JUNCACEAE Juss.

Genus *Juncus* L.

Juncus inflexus L. subsp. *acutissimus* (Buchenau)

Verloove & Gonggrijp, comb. nov., stat. nov.

(Figs 1–5)

Juncus glaucus var. *acutissimus* Buchenau in Monographie der Juncaceen vom Cap. (*Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen* 4): 417 (1875). — *Juncus acutissimus* (Buchenau) Adamson, *Juncus*. *Linnean Society of London. Botany* 50: 6 (1935).

TYPE MATERIAL. — **South Africa** • Cape Province, Wodehouse, Klein Buffels Vallei near Gaatjie; leg. J.F. Drège 8796c; (holotype: WRSB [Herb. Henschelianum]; isotype: E, LE, LD, P [P01731874, P01731876], S, W – *fide* Pročków *et al.* (2020).

ADDITIONAL SPECIMENS EXAMINED. — **Netherlands** • Grevenbicht, Koeweide-Trierveld, gravelly border of the Maas River, scattered; 23.VI.2024; F. Verloove 15443 (BR0000027059944V); with corresponding observation: <https://waarneming.nl/observation/316528151/>. An additional specimen from the same clone was collected by the second author for the Naturalis herbarium in Leiden (L), the Netherlands, under number S. Gonggrijp 753.

DESCRIPTION

Perennial herb forming dense tufts, with short creeping rhizomes. Culms erect, wiry, terete, 40–90 cm tall, 1.5–3 mm wide above the cataphylls, glaucous to straw-colored when dry, with up to *c.* 40 fine longitudinal striations and interrupted central pith. Stem ribs fine, irregularly spaced – some positioned more closely together, others more distantly –, and weakly raised above the culm surface, in contrast to the coarser, more prominent ribs in *J. inflexus* L. subsp. *inflexus*. Basal leaf sheaths tight, usually castaneous to dark (almost blackish) brown, not differing from *J. inflexus* L. subsp. *inflexus* in this respect. Leaves reduced to bladeless sheaths. Inflorescence lateral, paniculate, much-branched, straggly in appearance, composed of repeatedly dichotomous



FIG. 2. — Stems and lower basal sheaths of *Juncus inflexus* L. subsp. *acutissimus* Verloove & Gonggrijp, comb. nov., stat. nov. in Koeweide-Trierveld, the Netherlands. The numerous, closely spaced ribs are characteristic. Photographed on 23 June 2024 by S. Gonggrijp.



FIG. 3. — Inflorescence of *Juncus inflexus* L. subsp. *acutissimus* Verloove & Gonggrijp, comb. nov., stat. nov. in Koeweide-Trierveld, the Netherlands. The inflorescence is reddish to ferruginous after flowering, contrasting with the blackish inflorescences of *Juncus inflexus* L. subsp. *inflexus* (see Fig. 4). Photographed on 23 June 2024 by S. Gonggrijp.



FIG. 4. — Inflorescences of *Juncus inflexus* L. subsp. *inflexus* in Zemst, Belgium. After flowering, the inflorescence turns blackish due to the darkening capsules. Photographed on 25 July 2025 by M. Pauwels.

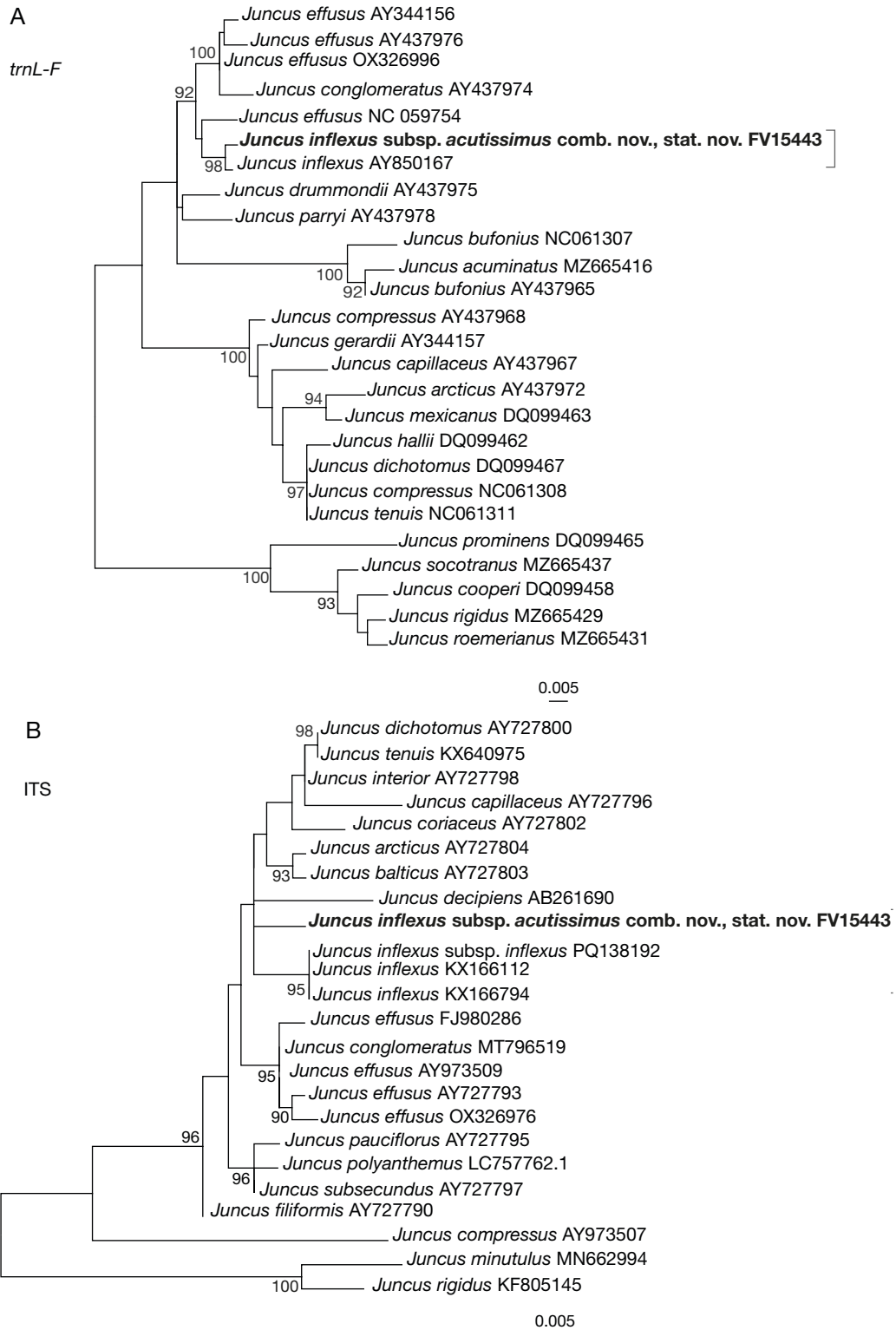


FIG. 5. — Maximum-likelihood trees (IQ-TREE) based on the nuclear rDNA internal transcribed spacer (ITS, **B**) region and the plastid trnL intron and trnL-F spacer (**A**), illustrating the phylogenetic position of *Juncus inflexus* subsp. *acutissimus* comb. nov., stat. nov. and *Juncus inflexus* L. subsp. *inflexus*. Solid square brackets indicate the monophyly of *Juncus inflexus* and *J. inflexus* subsp. *acutissimus*, whereas dotted brackets indicate unsupported relationships between these taxa.

branches. Overall coloration reddish-brown to ferruginous, clearly distinct from the typically darker inflorescences of *J. inflexus* L. subsp. *inflexus*. Bracts ovate, green, much shorter than the perianth. Tepals rigid, lanceolate to subulate, sharply acute,

greenish with whitish translucent margins; inner tepals longer than outer, all exceeding the capsule. Stamens 6. Capsule oblong to trigonous-ovoid, attenuate, pale chestnut-brown, shorter than the tepals. Seeds minute, finely reticulate, without appendages.

CONCLUSION

This study demonstrates that South African populations previously treated as *Juncus inflexus* represent a distinct evolutionary lineage. They are consistently distinguished from Eurasian *J. inflexus* by their finer and more numerous culm striations, less prominent rib structure, reddish inflorescence coloration, and tepals that are consistently narrower, more acutely pointed, and longer than the capsule. They further show clear genetic differentiation in both nuclear and plastid markers. Historical observations by Buchenau (1875) and Adamson (1935) already emphasized these differences, but subsequent treatments failed to recognize their significance. Integrating morphological, molecular, and historical evidence, we conclude that the South African taxon warrants formal recognition as *J. inflexus* subsp. *acutissimus* comb. nov., stat. nov.

The recognition of this taxon also has important biogeographical implications: it represents an isolated lineage within *Juncus* section *Juncotypus*, disjunct from its primarily Eurasian relatives and apparently endemic to South Africa. This reassessment not only corrects a long-standing taxonomic oversight but also underscores the importance of integrating morphology and molecular data to resolve overlooked diversity in widely distributed genera.

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