

## The *Juncus bufonius* L. aggregate in western Europe

T. A. COPE

Royal Botanic Gardens, Kew, Richmond, Surrey

and

C. A. STACE

Botanical Laboratories, University of Leicester

### ABSTRACT

The history of the taxonomic treatment of the *Juncus bufonius* L. aggregate is surveyed. Five species within it are recognized in Europe: *J. foliosus* Desf., *J. bufonius* L., *J. ambiguus* Guss., *J. hybridus* Brot. and *J. sorrentinii* Parl. Each of these is described, and a list of synonyms and details of distribution and habitat preferences are provided for each. The first three of these five species occur in the British Isles.

### INTRODUCTION

The genus *Juncus* L. comprises about 300 species varying from dwarf, ephemeral annuals to large tufted or rhizomatous perennials. Buchenau (1890, 1906) divided *Juncus* into eight subgenera, and his classification is still largely followed today. The only notable modifications are the three accepted by Krechetovich & Goncharov (1935) and Snogerup (1971a, 1971b, 1972) involving the division of subgenus *Poiophylli* Buchenau into subgenera *Poiophylli* (annuals) and *Pseudotenageia* Krech. & Gonch. (perennials); the division of subgenus *Graminifolii* Buchenau into *Graminifolii* (perennials) and *Juncinella* (Fourr.) Krech. & Gonch. (annuals); and the amalgamation of subgenus *Singulares* Buchenau with *Graminifolii sensu stricto*. Apart from *Poiophylli sensu stricto* and *Juncinella*, annual species are found only in subgenus *Septati* Buchenau (in this subgenus with perennials also). It should be mentioned that, if these nine subgenera are recognized instead as sections, the correct names are mostly different, largely dating from those of Kuntze (1903).

The *Juncus bufonius* L. aggregate belongs to subgenus *Poiophylli sensu stricto*, which consists of annual species with grass-like leaves and rather diffuse, leafy, terminal inflorescences. Apart from *J. bufonius* agg., the subgenus contains only two other species, both European: *J. tenageia* Ehrh. and *J. sphaerocarpus* Nees. These both differ from *J. bufonius* agg. in their possession of more or less spherical (not oblong) capsules.

*J. bufonius* agg. is morphologically extremely variable. It is a small, green, tufted annual up to 40 cm high, with flattish, convolute or subterete leaves up to 15 cm  $\times$  0.5–5 mm. The flowers are in a compound, bracteate, dichasial cyme (often termed an anthela) and may be distantly spaced or partly or densely clustered. The outer tepals vary from acute to long-acuminate or cuspidate at the apex and are 4–9 (–11) mm long. The inner tepals are acute or subacute to rounded or truncate at the apex and sometimes also emarginate and mucronate, and are shorter than the outer. The capsule is 3.5–5  $\times$  1.2–2 mm, oblong, acute to truncate at base and apex, and trilocular. The seeds are 0.3–0.5  $\times$  0.2–0.3 mm, frequently obliquely obovoid or sometimes ovoid to barrel-shaped, and without appendages.

*J. bufonius* agg. is distributed throughout the world, but is less frequent in tropical and polar regions. Being a weed of cultivation it is undoubtedly adventive in some localities (Good 1953). It is ubiquitous in Europe except for parts of the extreme north. It is also almost ubiquitous in Asia, occurring eastwards to temperate China, Japan and northern India. In Africa it is generally confined to the north and it is believed by Adamson (1950) to have been introduced to South Africa. It is found in Greenland,

much of Canada and large parts of the United States and Central and South America. Although found throughout Australia and New Zealand, Cheeseman (1925) considered it to have been introduced to New Zealand with grass seed during the early days of colonization. It is found throughout the British Isles, being recorded from every vice-county (Perring & Walters 1962). It is clearly not possible to determine the native distribution of such a common and successful weed species; it is probably not native outside Eurasia, North Africa and perhaps eastern North America.

According to Laurent (1904), *J. bufonius* is cleistogamous or rarely chasmogamous, although Buchenau (1906) said that the converse was the case. Cleistogamy is unusual in *Juncus*, a genus believed by Cronquist (1968) to be a reduced anemophilous derivative of the entomophilous Commelinales. Only rarely in Britain have the flowers of *J. bufonius* agg. been seen to open before anthesis, but in the Mediterranean region, for which no data are at present available, the situation may be different. In Britain the flowering period ranges from about mid-June through to mid- or late-September, and the capsules are ripe about a month after flowering.

There is no normal dormancy in the seeds of *J. bufonius* agg., so that in mild, wet weather germination often takes place inside the dehiscent capsules. Normally, however, soil temperatures are too low in autumn and winter for germination, which is therefore delayed until the following spring. Germination usually occurs in damp, exposed places and the species is a colonizer of bare ground. *J. bufonius* agg. cannot tolerate much shade or competition either from other species or from individuals of its own species. It prefers a high water-table and grows best when its roots are waterlogged. It is, however, generally intolerant of total submergence by salt-water and therefore is restricted in coastal habitats to those areas above the mean high-water mark. It is also intolerant of drought and seldom recovers after a prolonged dry spell. According to Good (1953), *J. bufonius* is the only species in the genus that is a weed of cultivated ground. However, *J. effusus* L. can also be so.

Proliferation, in which flowers are replaced by clusters of leaves and eventually new inflorescences, can easily be induced in some strains in cultivation by overcrowding, but proliferating specimens have not been seen in the wild or in herbarium material.

Dispersal of *J. bufonius* agg. may be brought about in several ways. On arable land it is most probably spread when the seeds adhere to mud that is transported on the wheels of vehicles and on the feet of man, cattle, horses or birds. The seeds become viscid when wet, an adaptation to dispersal by animals' feet common to many other species of *Juncus*. In waterside situations seeds and seedlings may be dispersed when stuck to the feet of waterfowl or by floating on moving water. As most seeds of *Juncus* are reported to sink in water almost at once (Ridley 1930), dispersal by floating seedlings seems to be more likely than by floating seeds, although flooding may deposit seeds, carried in silt, on to previously uncolonized ground. The seeds of *J. bufonius* agg., which weigh about 0.015 mg (Porsild 1920), may possibly also be dispersed by wind (Löve 1963).

Historically, the taxonomy of *J. bufonius* agg. has been very confused. The present investigation was undertaken in an attempt to clarify the classification of the aggregate as represented in western Europe and the western Mediterranean region, and it involved anatomical, cytological, breeding behavioural, ecological, and experimental cultivation and hybridization studies in addition to orthodox taxonomic procedures. In this paper we describe the taxonomic history of the aggregate and set out the results of our investigation in the form of a brief, illustrated, systematic account. In it we recognize five species: *J. bufonius* L. *sensu stricto*, *J. foliosus* Desf., *J. ambiguus* Guss., *J. hybridus* Brot. and *J. sorrentinii* Parl. It should be emphasised that in western Asia there are further taxa not covered by us, although we believe there are no additional species in Europe. We intend to present more detailed reasons for adopting the above classification, and the results of cytological studies and hybridization experiments, in later papers.

#### THE HISTORY OF THE TAXONOMY OF THE *JUNCUS BUFONIUS* AGGREGATE

Linnaeus (1753) described *J. bufonius* as '*Juncus culmo dichotomo, foliis angulatis, floribus solitariis sessilibus*', and he described five varieties of it, none of which, as far as can be ascertained, is synonymous with any subsequently published taxon. Since 1753 about 60 names applicable to *J. bufonius* agg. have been published, and clearly there are far more available than are necessary to account for the variation of the aggregate. There is inevitably some overlap in the limits and interpretations of the various taxa, as well as some nomenclatural synonymy. While it is not possible to

review all of the relevant literature, most of the important Floras and monographs have been consulted, and the noteworthy ones are discussed below.

The first significant classification to appear after 1753 was that of Buchenau (1890, 1906). The single species *J. bufonius* was divided into seven varieties, of which only three, vars. *genuinus* Cout., *foliosus* (Desf.) Buch. (based on *J. foliosus* Desf.) and *halophilus* Fern. & Buch., are retained in any form today. The remainder, vars. *kochii* Buch., *leucanthus* Asch. & Graeb., *pumilio* Griseb. and *subauriculatus* Buch., are now generally disregarded, although the last was revived by Post (1933).

Husnot (1908) concerned himself with only European varieties, and to the three retained from Buchenau he added vars. *hybridus* (Brot.) Husnot (based on *J. hybridus* Brot.) and *sorrentinii* (Parl.) Husnot (based on *J. sorrentinii* Parl.). Var. *halophilus* he renamed var. *ambiguus* (Guss.) Husnot (based on *J. ambiguus* Guss.), listing *J. ranarius* Song. & Perr. as a synonym. Although Buchenau had reported that plants intermediate between var. *genuinus* and var. *halophilus* (which he said occurred in Canada, Germany and Sicily) were common in saline places and he mentioned *J. ranarius* as one of these, he mistakenly regarded *J. ambiguus* as a synonym of *J. tenageia*. Husnot, however, indicated in his synonymy a link between var. *halophilus*, *J. ambiguus* and *J. ranarius* that was to persist in many subsequent accounts. Buchenau did not think that *J. hybridus* was anything more than an unimportant form of var. *genuinus* with congested flowers, and var. *sorrentinii* did not appear in his account except in a note to the effect that var. *condensatus* Cout. (now an accepted synonym of it) was probably a good variety; the name *J. sorrentinii* appeared as a synonym of *J. pygmaeus* Rich., a synonymy that Husnot showed to be erroneous.

Shortly after the appearance of Husnot's paper, Briquet (1910) divided the aggregate into five varieties. These were taxonomically, although not nomenclaturally, the same as those of Husnot except that var. *ambiguus* was cited only as a variety of doubtful status.

Rouy's (1912) account in *Flore de France* included the same five taxa as Husnot, but each was treated as a species. The only significant nomenclatural change was to call *J. hybridus* by the later name *J. insulanus* Viv.; Rouy did not adopt the earlier name because he thought Brotero's type material of *J. hybridus* included two species, the second being *J. pygmaeus* Rich. Husnot, however, did not think that this was so and that, in any case, Brotero's description could not possibly have applied to *J. pygmaeus*, a member of subgenus *Septati*. Briquet (1910), too, was in some doubt about the status of *J. hybridus*, for he called his equivalent variety *congestus* Wahlb., and only included *J. hybridus* in the synonymy preceded by a question mark.

Fiori's (1923) account in *Nuova Flora analitica d'Italia* once more relegated all of the taxa to varieties of *J. bufonius*, but to the exclusion of *J. sorrentinii*, which did not appear anywhere in his *Flora*.

Krechetovich & Goncharov (1935) produced a very complex treatment for *Flora U.R.S.S.*, although this is not strictly concerned with our area of study. The subgenus *Tenageia* (Dumort.) O. Kuntze (= subgenus *Poiophylli*) was divided into three series and six species. The western and Mediterranean species *J. foliosus*, *J. hybridus* and *J. sorrentinii* were of course absent, while *J. bufonius* and *J. ambiguus* were joined by *J. minutulus* Krech. & Gonch. and three other new species. Each principal species was placed in its own series as follows: *J. bufonius* (along with the new species *J. nastanthus* Krech. & Gonch.) in series *Bufonii* Krech. & Gonch.; *J. ambiguus* (along with two further new species, *J. turkestanicus* Krech. & Gonch. and *J. juzepczukii* Krech. & Gonch.) in series *Ranarii* Krech. & Gonch.; and *J. minutulus* in series *Minutuli* Krech. & Gonch. The separation of species within each series was based on extremely critical characters, and the account in *Flora U.R.S.S.*, although potentially applicable to large parts of Europe and Asia, has not been generally adopted.

Another complex treatment of the aggregate is found in *Flore de l'Afrique du nord* (Maire 1957), in which *J. bufonius* has two subspecies, *eu-bufonius* Briq. and *foliosus* (Desf.) Maire & Weiller. Subsp. *eu-bufonius* contains five varieties: *laxus* Čelak. (= *J. bufonius sensu stricto*), *ambiguus*, *rhaphaenus* (Pau & Font-Quer) Maire & Weiller, *congestus* (= *J. hybridus*) and *mogadorensis* (H. Lindb.) Maire & Weiller. Two of these, vars. *mogadorensis* and *rhaphaenus*, are unknown from the European literature. The latter is remarkable, for among its synonyms is to be found *J. tenageia* subsp. *sphaerocarpus* (Nees) Trabut var. *rhaphaenus* (Pau & Font-Quer) Maire, a combination involving the names of two very different European species from outside the aggregate and a third, non-European, name from within it. To further confuse the situation, var. *rhaphaenus* is now known to be synonymous with *J. foliosus*, which Maire treated as his second subspecies.

Segal (1960) discussed the taxonomy of the aggregate and recognized seven species: *J. bufonius*, *J. foliosus*, *J. ambiguus*, *J. ranarius*, *J. mutabilis* Savi, *J. sorrentinii* and *J. sphaerocarpus*. He mentioned

that the last six were generally regarded as varieties of *J. bufonius* but that he treated them as species for convenience. One of these, *J. sphaerocarpus*, is not considered by us to be a part of the *J. bufonius* aggregate. Another species, usually called *J. hybridus*, he called *J. mutabilis* Savi. While this name may be correctly applied to this species, it is a later homonym of *J. mutabilis* Lam. (Subgenus *Septati*) and therefore illegitimate. Segal discussed the suggestion of Fernald & Buchenau (1904) that *J. ambiguus* and *J. ranarius* should be separated, stating that, while they are often considered to be synonymous, they are not identical. He considered that North American plants (previously known as var. *halophilus*) and northern European plants both correspond to *J. ambiguus* (whose type locality, however, is in Sicily), but pointed out that numerous authorities had considered European specimens to represent *J. ranarius*, said by Fernald & Buchenau to be intermediate between *J. bufonius* and *J. ambiguus*.

Duvigneaud (1967), in an ecological account of the halophytic flora of eastern Lorraine (Dép. Moselle, north-eastern France) recognized the two segregates (*J. bufonius* and *J. ambiguus*) occurring there as distinct species.

Snogerup (1971a), in *Flora Iranica* (only of partial relevance to our area), recognized five species; *J. ambiguus*, *J. foliosus* and *J. sorrentinii* are absent from the area covered. *J. minutulus* was recognized by Snogerup although he cited Albert & Jahandiez as authorities. These authors clearly intended their taxon to be a forma of *J. bufonius*, a point which escaped Snogerup and, later, Van Loenhoud & Sterk (1976), who all cited it as a species. *J. turkestanicus* Krech. & Gonch. was also accepted by Snogerup, although he confessed that he was unable to distinguish readily all populations of it from *J. hybridus*. *J. rechingeri* Snogerup (a new, very distinct species), *J. bufonius* and *J. hybridus* were the other three species recognized.

Van Loenhoud & Sterk (1976) made a detailed study of the aggregate in the Netherlands and concluded that it was represented by three species. Apart from *J. bufonius*, they recognized, for the first time in that part of Europe, *J. minutulus*, but incorrectly cited (see above). The third species, which was recognized by Reichgelt (1964) in *Flora Neerlandica* as *J. bufonius* subsp. *ambiguus* (Guss.) Schinz & Thell., they called *J. ranarius* Song. & Perr. A synonym for *J. ranarius* which they mentioned was *J. bufonius* var. *halophilus*, a commonly accepted synonym for *J. ambiguus*. They gave no reason for using the name *ranarius* instead of *ambiguus*; if, as they implied, they considered the two as taxonomic synonyms their choice was incorrect, as *ambiguus* is the older name.

In an interesting paper concerning the Czechoslovakian flora, Holub (1976) added *J. minutulus* to that country's list. He was aware of Albert & Jahandiez's intention that *J. minutulus* should be considered subordinate to *J. bufonius*, but was in some doubt about the correct form of citation. He suspected that Prain *et al.* (1921) in *Index Kewensis*, Suppl. 5, made a new combination at specific rank based on forma *minutulus* Alb. & Jah., but it is much more likely that they intended to copy the citation directly from Albert & Jahandiez without making any judgement on its rank. Holub mentioned a remarkable work by Čerepanov (1973), who drew a taxonomic distinction between '*J. minutulus* Alb. & Jah.' and *J. minutulus* Krech. & Gonch.

A further point of interest in Holub's paper is the expansion of an idea, first mentioned by Segal (1960), that *J. ranarius* and *J. ambiguus* may not be conspecific. Indeed, Holub spoke of '*J. ranarius* Song. & Perr. s.l.', accepting this name for the aggregate in preference to *J. ambiguus*. He cited the latter as *J. ambiguus* auct., suggesting that the name is misapplied in the commonly accepted sense, but in his key to species he gave the name of the taxon in question as '*J. ranarius* Song. & Perr. s.l. (an *J. ambiguus* Guss.?)'. Included in the *J. ranarius* aggregate were four taxa: *J. ranarius* Song. & Perr. s.s., *J. ambiguus* auct., *J. juzepczukii* and *J. nastanthus*. The inclusion of the last of these is a little surprising for Krechetovich & Goncharov placed it in their series *Bufonii*, rather than in series *Ranarii*.

As far as the British Isles are concerned, only one species has usually been accepted, although the name var. *fasciculatus* Koch is sometimes found in local and national Floras (e.g. Colgan & Scully 1898, White 1912, Wolley-Dod 1937, Richards 1962). Druce (1911, 1912) is the only author to have seriously considered the possibility that *J. ranarius* (= *J. ambiguus*) might occur in Britain. He said (Druce 1911, p. 327) that this species (which he called *J. ranarius* Nees emend. Song. & Perr.) 'has either been confused with or called var. *fasciculatus* of *Juncus bufonius*'. The presence of *J. foliosus* in Britain was first indicated by Simpson & Walters (1959) and later by Allen (1969) and Benoit (1973). It was recorded by these authors from W. Cork and S. Kerry, from the Isle of Man and from Wales respectively. While discussing *J. bufonius* in *The flowering plants of the Isle of Man*, Allen (1969) said that 'populations approaching the "Lusitanian" race ssp. *foliosus* (Desf.) Maire & Weiller have recently been detected'. Although many field botanists are aware of their existence, *J. ambiguus* and *J. foliosus* have not hitherto been formally accepted as taxa for the British Isles.

In the recognition of five western European species within *J. bufonius* agg. our treatment agrees with those of Husnot (1908) and Rouy (1912).

## MATERIALS

Material used in this study consisted of herbarium specimens and photographs from **BM**, **C**, **DBN/DUB**, **FI**, **K**, **L**, **LD**, **LISU**, **LTR**, **LIV**, **LY**, **MANCH** and **P**, and seed or living plants collected by us and numerous correspondents or obtained via seed exchange schemes. Altogether 85 samples were grown in cultivation, representing all five species recognized.

For the most part we have restricted our studies to material from western Europe and the western Mediterranean region (as far east as Germany, Italy and western Libya), with special emphasis on the British Isles. We feel this is a valid exercise, since the western Mediterranean is a centre of genetic diversity for the aggregate and it includes all the species we recognize in Europe.

The chromosome numbers given for each species refer to our own counts, of which details will be given in a later paper, but other counts (where different) are mentioned as well.

## KEY TO SPECIES

- 1 Leaves bright green, more than 1.5mm wide; tepals usually with dark line on either side of midrib; anthers 1.2–5 times as long as filaments; seeds with 20–30 conspicuous longitudinal ridges (use  $\times 20$  hand-lens) . . . . . 1. *J. foliosus*
- 1 Not with above combination of characters; leaves usually darker and seldom more than 1.5mm wide; seeds apparently smooth or with minutely reticulate surface
  - 2 Inflorescence partly (rarely wholly) contracted; inner tepals rounded, often emarginate and mucronate at tip; capsule truncate, as long as or longer than inner tepals . . . . . 3. *J. ambiguus*
  - 2 Inflorescence variable; inner tepals acute to subacute; capsule acute to subacute, rarely truncate but then clearly shorter than inner tepals and these not rounded or emarginate-mucronate
    - 3 Inflorescence with widely spaced flowers, or if contracted then inner tepals and capsule acute and seeds obliquely obovoid . . . . . 2. *J. bufonius*
    - 3 Inflorescence contracted; seeds barrel-shaped or ovoid
      - 4 Flowers fasciculate in open, fan-shaped clusters; outer tepals acute; inner tepals subacute, 3/4–4/5 as long as outer; capsule about 4/5 as long as inner tepals; lowest bract generally shorter than inflorescence . . . . . 4. *J. hybridus*
      - 4 Flowers fasciculate in dense, fan-shaped clusters; outer tepals long acuminate to cuspidate; inner tepals acute to acuminate, up to 2/3 as long as outer; capsule about 1/2 as long as inner tepals; lowest bract often greatly exceeding inflorescence . . . . . 5. *J. sorrentinii*

## SYSTEMATIC ACCOUNTS

In the following accounts the synonymy is given as fully as we are able, although in a number of cases (indicated by ?) the identification is doubtful. We have seen and vetted the type specimens indicated. We do not formally recognize any infraspecific taxa, although some are discussed under *J. bufonius*.

1. *J. FOLIOSUS* Desf., *Fl. Atlant.*, 1: 315, t. 92 (1798); (Fig. 1, Plates 1A and 2A)  
 Type: 'Algeria in paludibus', *Desfontaines* (**P**, holotype).  
*J. bufonius* L. var. *major* Boiss., *Voy. Bot. Esp.*, 2: 624 (1841), based on *J. foliosus* Desf.  
*J. bufonius* L. var. *foliosus* (Desf.) Buch. in Engl., *Pflanzenreich*, 25: 105 (1906)  
*J. rhiphaenus* Pau & Font-Quer in Font-Quer, *Iter Maroc*. (Sched. 1929), No. 64 (1930) (**BM**, isotype)

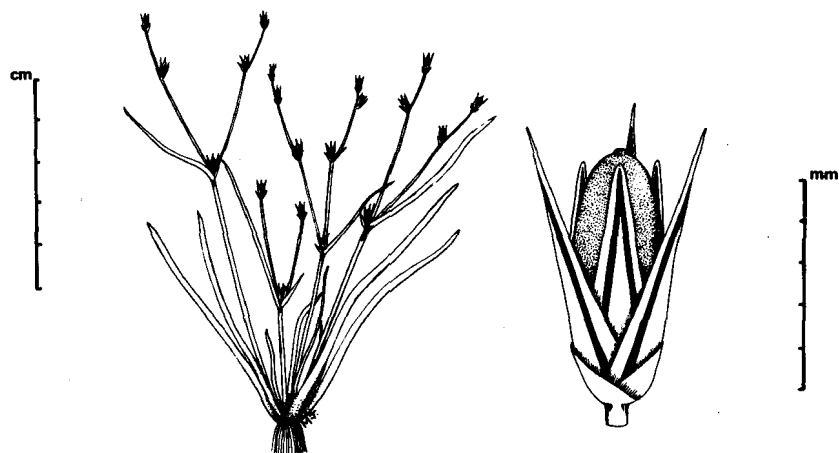


FIGURE 1. *Juncus foliosus* Desf. Whole plant and capsule.



FIGURE 2. *Juncus bufonius* L. Whole plant and capsule.

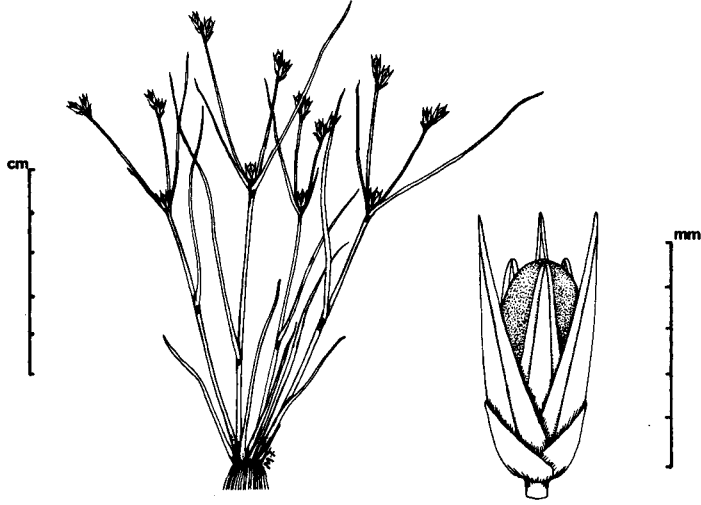


FIGURE 3. *Juncus ambiguus* Guss. Whole plant and capsule.



FIGURE 4. *Juncus hybridus* Brot. Whole plant and capsule.

FIGURE 5. *Juncus sorrentinii* Parl. Whole plant and capsule.

*J. sphaerocarpus* Nees var. *rhypaenus* (Pau & Font-Quer) Maire in *Cavanillesia*, 4: 97 (1931)

*J. bufonius* L. subsp. *eu-bufonius* Briq. ex Jah. & Maire var. *rhypaenus* (Pau & Font-Quer) Maire & Weiller in Maire, *Fl. Afr. nord*, 4: 264 (1957)

*J. bufonius* L. subsp. *foliosus* (Desf.) Maire & Weiller var. *major* ('Boiss') Maire, *Fl. Afr. nord*, 4: 266 (1957), based on *J. foliosus* Desf.

*J. bufonius* L. subsp. *foliosus* (Desf.) Maire & Weiller var. *flaccidus* Maire, *Fl. Afr. nord*, 4: 266 (1957)

*J. tenageia* Ehrh. subsp. *sphaerocarpus* (Nees) Trabut var. *rhypaenus* (Pau & Font-Quer) Maire, *Fl. Afr. nord*, 4: 264 (1957), in synonym.

Annual or short-lived perennial; culms densely tufted, erect or ascending from slightly procumbent base, up to 35cm. Leaf-blades light green, 2–5mm wide; stomata 31–45 $\mu$ m. Inflorescence open; branches  $\pm$  straight, often widely diverging or almost horizontal. Flowers 1–3(–5) per ultimate branch; tepals usually with pale brown to almost black line on either side of midrib; outer tepals acute, 4.6–6.8mm; inner tepals usually subacute, sometimes acute, 3.6–5.4mm; capsule usually subacute, sometimes obtuse, 3.7–5.3mm, about equalling inner tepals (0.8–1.25 times as long); anthers 1.2–5 times as long as filaments. Seeds obovoid, often truncate at one end and tapered at other, 430–600  $\times$  270–400 $\mu$ m; interstices of testa large, c 60  $\times$  20 $\mu$ m; longitudinal ridges pronounced, clearly visible through  $\times$  20 hand-lens as 20–30 ribs.  $2n=26$ .

*Habitat.* This species occurs exclusively in freshwater habitats such as on the muddy margins of pools, ponds, lakes, streams and rivers, in wet fields and marshes, in roadside ditches and on waste land, in oceanic parts of western Europe.

*Distribution* (Figs. 6 and 10). Western and south-western Europe (northern Sardinia, southern Spain, Portugal, western France and British Isles); North Africa (Algeria, Morocco and Tunisia); Madeira. Britain (mainly in the south and west in vice-counties 1, 6, 10, 11, 14, 15, 17, 27, 45, 47, 48, 49, 52, 70, 71, 97, 103, 104); Ireland (widespread in vice-counties H1, 3, 6, 12, 16, 20, 21, 29, 34, 35);



Channel Isles (Sark). Allen (1969) considered it to be a member of the so-called Hiberno-Lusitanian element of the British flora.

*J. foliosus* is the most easily distinguished of the segregates. Its broad, bright-green leaves and striped tepals are very striking and the conspicuously ribbed seeds are diagnostic.

2. *J. BUFONIUS* L., *Sp. pl.*, p. 328 (1753); (Fig. 2, Plates 1B and 2B)  
Type: Europe, *Van Royen* (L, sheet 904,145-433, lectotype; L, numerous paratypes).  
*J. divaricatus* Gilib., *Exerc. phyt.*, 2: 506 (1792)  
*J. prolifer* H., B. & K., *Nov. gen. sp.*, 1: 236 (1815)  
*J. bufonius* L. var. *congestus* Wahlenb. in Thunb., *Fl. Goth.*, p. 38 (1820)  
*J. bufonius* L. var. *gracilis* St Amans, *Fl. Agen.*, p. 149 (1821)  
*J. inaequalis* Willd. herb. in E. H. F. Meyer, *Syn. Luzul.*, p. 33 (1823)  
*J. bufonius* L. var. *grandiflorus* Schult. & Schult. f., *Syst. veg.*, 7(1): 227 (1829)  
*J. bufonius* L. var. *fasciculatus* Koch, *Syn. fl. Germ.*, p. 732 (1837)  
*J. dregeanus* C.B. Presl, *Bot. Bemerck.*, p. 117 (1844)  
? *J. ranarius* Nees in *Linnaea*, 20: 243 (1847), *nom. nud.*  
*J. bufonius* L. var. *parvulus* Hartm., *Handb. Skand. fl.*, 7th ed., p. 241 (1858)  
*J. bufonius* L. var. *longiflorus* Kit. in *Linnaea*, 32: 333 (1863)  
*J. bufonius* L. var. *alpinus* Schur, *Enum. pl. Transs.*, p. 688 (1866)  
? *J. bufonius* L. var. *longifolius* Genn., *Fl. Sarda*, p. 31 (1867)  
*J. bufonius* L. var. *compactus* Čelak., *Prodr. fl. Böhm.*, 1: 83 (1869)  
*J. bufonius* L. var. *laxus* Čelak., *Prodr. fl. Böhm.*, 1: 83 (1869)  
*Tenageia bufonia* (L.) Fourr. in *Annls Soc. linn. Lyon*, n.s., 17: 172 (1869)  
*J. bufonius* L. var. *jadarensis* Brym in *Bot. Notiser*, 1877: 87 (1877)  
*J. bufonius* L. var. *pumilio* Griseb. in *Abh. Ges. Wiss. Göttingen*, 24: 316 (1879)  
*J. bufonius* L. var. *genuinus* Cout. in *Bolm Soc. broteriana*, 8: 102 (1890)  
*J. bufonum* Bubani, *Fl. Pyren.*, 4: 187 (1901)  
*J. bufonius* L. var. *leucanthus* Asch. & Graeb., *Syn. mitteleur. Fl.*, 2(2): 422 (1904)  
*J. bufonius* L. var. *subauriculatus* Buch. in Engl., *Pflanzenreich*, 25: 107 (1906) (K, MANCH, isotypes)  
*J. bufonius* L. forma *minutulus* Alb. & Jah., *Cat. vasc. pl. Var.*, p. 501 (1908)  
*J. bufonius* L. subsp. *eu-bufonius* Briq. ex Jah. & Maire, *Cat. pl. Maroc.*, 1: 114 (1931)  
? *J. nasthanthus* Kreh. & Gonch. in Kom., *Fl. U.R.S.S.*, 3: 624 (1935)  
*J. minutulus* Kreh. & Gonch. in Kom., *Fl. U.R.S.S.*, 3: 625 (1935)

Annual; culms tufted or solitary, erect or ascending from procumbent base, up to 35(-50)cm. Leaf-blades dark green, 0.5-1(-1.5)mm wide; stomata 29-47µm. Inflorescence open, rarely partly or wholly contracted; branches usually straight, diverging at less than 90°. Flowers 1-5 per ultimate branch; tepals usually without dark lines; outer tepals acute or shortly acuminate, 4.1-7.3mm; inner tepals usually acute, sometimes subacute, 3.4-5.8mm; capsule acute, subacute or rarely truncate, 3.1-4.9mm, usually shorter than inner tepals (0.7-1.1 times as long); anthers usually shorter than filaments, though occasionally much longer (0.3-1.1(-5) times as long). Seeds obliquely obovoid, rarely barrel-shaped or ovoid, 340-520 × 210-350µm; interstices of testa small, *c* 15 × 5µm, or outer integument sometimes lost and seeds perfectly smooth. *2n* = 108 (*c* 54, *c* 60, 70, *c* 72, 80, 104-110 also reported).

*Habitat.* *J. bufonius* is found in all kinds of habitat where the water-table is high, at least seasonally, and where competition is slight or absent. It occurs on the muddy, sandy or gravelly margins of ponds, lakes, streams and rivers, on marshes and, much less frequently, on acid bogs. It is also frequent in brackish situations such as estuarine mud- and sand-flats, dune-slacks in coastal dune-systems, and on the margins of saline or brackish lakes. Other situations occupied by *J. bufonius* are those associated with cultivation and it will grow in bare patches among crops, on and by paths and tracks, in wheel-ruts and drainage ditches and on waste ground.

*Distribution.* Cosmopolitan, but probably native only in Eurasia, North Africa and North America. Recorded from every vice-county in the British Isles (Perring & Walters 1962).

The extreme variability of *J. bufonius* has led to the creation of numerous infraspecific taxa, of which the following should be mentioned:

Var. *fasciculatus* Koch is a small variety with subfasciculate flowers described from the Rhine Valley and is often considered to be the same as *J. ambiguus*. No authentic material has been seen, but it seems that this combination could be reserved for those variants of *J. bufonius* that have subfasciculate flowers. There is no suggestion in the description that it differs from the type in any other way.

Var. *congestus* Wahlb. is a little more extreme than the previous variety and is usually regarded as having wholly fasciculate flowers. It is often considered to be synonymous with *J. hybridus*, but this is unlikely since it was described from Göteborg in Sweden, whereas *J. hybridus* is restricted to the Mediterranean region.

Var. *subauriculatus* Buch. differs from the type only in having the leaf-sheaths subobtusate instead of tapered at the top.

Forma *minutulus* Alb. & Jah. is a diminutive variant of *J. bufonius* first published in 1908 at forma level but subsequently accepted by other authors as a species and often mis-cited as *J. minutulus* Alb. & Jah. instead of *J. minutulus* Krech. & Gonch. The morphological limitations set by various authors for this taxon differ considerably and are summarized in Table 1.

TABLE 1. COMPARATIVE CHARACTERS FOR *J. BUFONIUS* AND *J. MINUTULUS* GIVEN BY VARIOUS AUTHORS

	Krechetovich & Goncharov 1935	Snogerup 1971a	Van Loenhoud & Sterk 1976	Extremes of all authors combined
<i>J. bufonius</i>				
Height, cm	10-50	5-50	—	5-50
Outer tepal, mm	6.5-7.5	(4.5-)6.0-8.0	—	4.5-8.0
Inner tepal, mm	5.0-6.0	4.0-6.5	—	4.0-6.5
Capsule, mm	4.0-4.5	(3.0-)3.5-5.0	3.0-4.0	3.0-5.0
Anthers	$\pm 1.0 \times$ filaments	0.4-1.0 $\times$ filaments	0.35-0.67 $\times$ filaments	0.35-1.0 $\times$ filaments
Seed length, mm	0.30	0.40-0.55	0.41-0.49	0.30-0.55
Seed width, mm	—	—	0.24-0.30	0.24-0.30
<i>J. minutulus</i>				
Height, cm	0.8-5	0.5-5	—	0.5-5
Outer tepal, mm	2.5-3.5	4.0-6.5	—	2.5-6.5
Inner tepal, mm	2.0-3.0	3.0-4.5	—	2.0-4.5
Capsule, mm	1.5-2.5	2.5-3.0	2.7-3.7	1.5-3.7
Anthers	$\pm 0.67 \times$ filaments	0.25-0.33 $\times$ filaments	0.4-1.25 $\times$ filaments	0.25-1.25 $\times$ filaments
Seed length, mm	0.30	0.35-0.40(-0.50)	0.36-0.42	0.30-0.50
Seed width, mm	—	—	0.23-0.27	0.23-0.27

Clearly there is much disagreement about the upper size limits of *J. minutulus*. In considering the total range of measurements given by the various authors for each characteristic of *J. bufonius* and *J. minutulus*, we find considerable overlap in all except height. Our own results, to be presented in a later paper, fail to show any bimodality in any feature of *J. bufonius* that would indicate the presence of two taxa in our sample. Both Snogerup and Van Loenhoud & Sterk support their recognition of *J. minutulus* with cytological data, both reporting that it is tetraploid ( $2n = c\ 72$  and  $70$  respectively), rather than hexaploid. While this may be so, our own cultivation and cytological studies have shown that diminutive plants are not necessarily tetraploid and that tetraploids can be of the perfectly normal stature for *J. bufonius*. For these reasons we do not consider the recognition of *J. minutulus* at the species level to be practicable. Nor, since the two taxa are sympatric throughout the range of *J. minutulus*, do we think it worthy of the rank of subspecies.

3. *J. AMBIGUUS* Guss., *Fl. Sic. prodr.*, 1: 435 (1827); (Fig. 3, Plates 1C and 2C)  
 Type: Holotype not traced; the earliest known authentic specimen is from Sicily, Trapani, 1856, Gussone (FI, topotype).  
*J. ranarius* Song. & Perr. in Billot, *Annot.*, p. 192 (1859) (P, lectotype)  
*Tenageia ranaria* (Song. & Perr.) Fourr. in *Annls Soc. linn. Lyon*, n.s., 17: 172 (1869)  
 ? *J. bufonius* L. var. *major* Cand. in *Bull. Soc. bot. Fr.*, sér. 4, 3: 373 (1897), non Boiss. (1841)  
*J. bufonius* L. var. *halophilus* Fern. & Buch. in *Rhodora*, 6: 39 (1904) (K, isotype)  
 ? *J. bufonius* L. var. *kochii* Buch. in Engl., *Pflanzenreich*, 25: 107 (1906)  
*J. bufonius* L. var. *ambiguus* (Guss.) Husnot in *Bull. Soc. bot. Fr.*, 55: 49 (1908)  
*J. bufonius* L. subsp. *ambiguus* (Guss.) Schinz & Thell., *Fl. Schweiz*, 1: 126 (1923)  
*J. bufonius* L. subsp. *ranarius* (Song. & Perr.) Hiit., *Enum. pl. vasc. Fenn. or.*, p. 22 (1934)  
*J. juzepczukii* Krech. & Gonch. in Kom., *Fl. U.R.S.S.*, 3: 625 (1935)  
 ? *J. turkestanicus* Krech. & Gonch. in Kom., *Fl. U.R.S.S.*, 3: 625 (1935)

Annual; culms densely tufted or solitary, erect or ascending from procumbent base, up to 17 cm. Leaf-blades dark green, 0.5–1 mm wide; stomata 24–36  $\mu$ m. Inflorescence open; branches scorpioid with ultimate 2 or 3 flowers on each close together. Flowers 2–4(–5) per ultimate branch; tepals without dark lines; outer tepals acute, 4.0–6.8 mm; inner tepals obtuse or rounded, often emarginate and mucronate, 3.3–5.3 mm; capsule truncate, 3.3–5.3 mm, equalling or slightly shorter than inner tepals or sometimes longer and equalling outer tepals (0.9–1.1 times as long); anthers usually shorter than filaments (0.5–1.0 times as long). Seeds ovoid or barrel-shaped, 330–440  $\times$  250–350  $\mu$ m; interstices of testa small, c 15  $\times$  5  $\mu$ m, or outer integument sometimes lost.  $2n=34$  (30, 32, 60 also reported).

*Habitat.* *J. ambiguus* is typically a halophyte, occurring on the coast on mud- and sand-flats above the high-water mark and on the margins of saline and brackish lakes. It is also found on bare mud and waste-ground associated with inland salt-flashes and salt-workings and on the highly basic substrate provided by lime-waste tips.

*Distribution* (Figs 7 and 11). Europe (in suitable habitats over much of the continent, seen by us from Au, Bl, Br, Co, Da, Ga, Ge, Gr, Hb, He, Hs, Hu, Is, It, No, Po, Sa, Si, Su and reliably recorded also from Cz, Ho and Rs); parts of North Africa, Asia and North America (distribution incompletely known). Britain (around most of the coast and in inland saline areas, especially in Cheshire, Staffs. and Worcs., in vice-counties 1, 2, 4, 6, 9, 10, 11, 13, 14, 15, 21, 27, 28, 29, 37, 38, 39, 45, 48, 49, 51, 52, 54, 58, 59, 68, 69, 82, 85, 88, 94, 103, 104, 111); Ireland (around much of the coast, in vice-counties H1, 3, 5, 6, 12, 21, 23, 38, 40); Channel Isles (Guernsey).

This species is frequently known as *J. ranarius* Song. & Perr. and there has been much argument over the correct name for it. Segal (1960) thought that *J. ambiguus* and *J. ranarius* might not be conspecific (see above), and that North American material corresponds to *J. ambiguus* while European material is *J. ranarius*. Fernald & Buchenau (1904), in discussing their var. *halophilus*, cited not only North American material under this name, but German and Sicilian specimens as well. Furthermore, the type locality of *J. ambiguus* is in Sicily. Having seen type material of *J. ambiguus*, *J. ranarius* and *J. bufonius* var. *halophilus* we feel certain that they are conspecific.

4. *J. HYBRIDUS* Brot., *Fl. Lusit.*, 1: 513 (1804); (Fig. 4, Plates 1D and 2D)  
 Type: 'Circa Conimbricam et alibi in Beira'. Holotype not traced; according to Professor A. Fernandes (pers. comm. 1974) Brotero's herbarium was probably lost at the time of the Napoleonic Peninsular Wars.  
*J. mutabilis* Savi, *Fl. Pisana*, 1: 364 (1798), non Lam. (1789)  
*J. pygmaeus* Savi, *Bot. Etrusc.*, 2: 69 (1815), non Rich. (1799)  
*J. congestus* Schousb. in E. H. F. Meyer, *Syn. Junc.*, p. 40 (1822)  
*J. insulanus* Viv., *Fl. Cors.*, p. 5 (1824)  
*J. fasciculatus* Bertol., *Fl. Ital.*, 4: 190 (1839), non Schousb. (1865)  
*J. bufonius* L. var. *fasciculiflorus* Boiss., *Voy. bot. Esp.*, 2: 624 (1841)  
*J. querrioides* Pourr. herb. teste Willk. & Lange, *Prodr. fl. Hisp.*, 1: 181 (1861), nom. nud.  
*J. bufonius* L. var. *hybridus* (Brot.) Husnot in *Bull. Soc. bot. Fr.*, 55: 50 (1908)  
*J. bufonius* L. subsp. *insulanus* (Viv.) Briq. ex Jah. & Maire, *Cat. pl. Maroc.*, p. 114 (1931)  
 ? *J. bufonius* L. subsp. *mogadorensis* H. Lindb. in *Acta Soc. Sci. Fenn.*, n.s., B1(2): 31, t. 11 (1932)

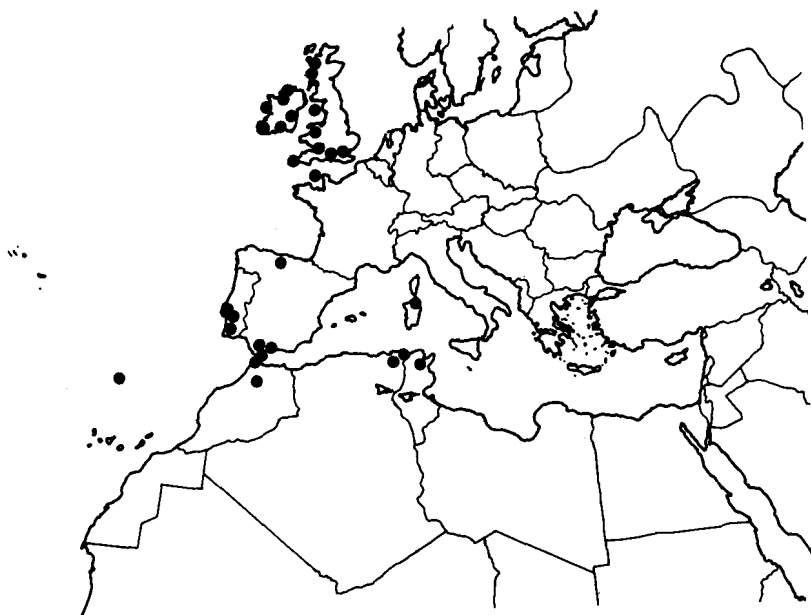


FIGURE 6. Distribution of *Juncus foliosus* Desf., compiled from herbarium material and certain published records.

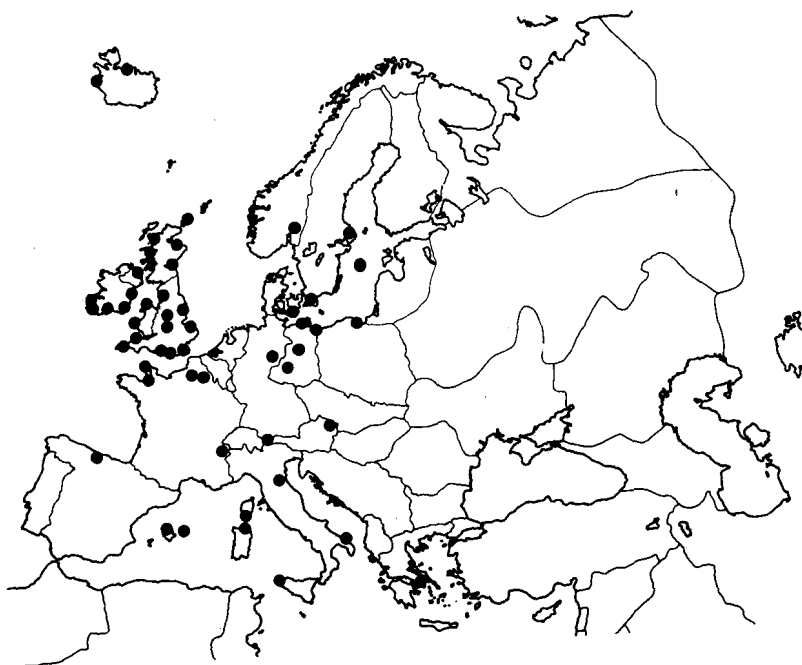


FIGURE 7. Distribution of *Juncus ambiguus* Guss. (excluding America and Greenland), compiled from herbarium material and certain published records.



FIGURE 8. Distribution of *Juncus hybridus* Brot., compiled from herbarium material and certain published records.



FIGURE 9. Distribution of *Juncus sorrentinii* Parl., compiled from herbarium material and certain published records.



- J. bufonius* L. subsp. *eu-bufonius* Briq. ex Jah. & Maire var. *congestus* Maire & Weiller in Maire, *Fl. Afr. nord*, 4: 265 (1957), non Wahlb.  
 ?*J. bufonius* L. subsp. *eu-bufonius* Briq. ex Jah. & Maire var. *mogadorensis* (H. Lindb.) Maire & Weiller in Maire, *Fl. Afr. nord*, 4: 265 (1957)  
*J. bicephalus* auct. non Viv. (1879)

Annual; culms fasciculate, rarely solitary, erect or ascending from slightly procumbent base, up to 31 cm. Leaf-blades dark green, 0.5–1 mm wide; stomata 25–39  $\mu$ m. Inflorescence contracted, with flowers disposed in open fan-shaped clusters. Flowers 3–6 per ultimate branch and 2–4 branches per cluster; tepals usually without dark lines; outer tepals acute to slightly acuminate, 4.9–7.3 mm; inner tepals subacute, very rarely acute or obtuse, 4.0–5.8 mm; capsule subacute, very rarely acute or truncate, 3.3–4.9 mm, somewhat shorter than inner tepals (0.7–0.9 times as long); anthers longer or shorter than filaments (0.25–2.0 times as long). Seeds ovoid, occasionally barrel-shaped, 280–410  $\times$  190–310  $\mu$ m; interstices of testa small,  $c$  15  $\times$  5  $\mu$ m, or outer integument sometimes lost.  $2n=34$ .

*Habitat.* *J. hybridus* is found in similar habitats to *J. bufonius* and *J. ambiguus*.

*Distribution* (Fig. 8). Circum-Mediterranean; Canary Islands; Azores; Atlantic coast of Europe north to Sables d'Olonne, Vendée, France, Recorded in the British Isles as a casual on two occasions towards the end of last century, once in S. Kerry, v.c. H1, and once in N. Devon, v.c. 4. Also introduced in parts of North America and Australia.

Trimen (*vide* Husnot 1908) suggested that Brotero had mixed two species in his type collection and was describing both *J. hybridus* and *J. pygmaeus* Rich., but his long description, following his diagnosis, does not support this suggestion. Husnot considered that the citation for *J. bicephalus* in the synonymy should read *J. bicephalus sensu* Gren., non Viv., as *J. bicephalus* Viv. is conspecific with *J. pygmaeus* Rich. (with which we agree judging from the description of *J. bicephalus* and a sheet at K collected and named as such by Viviani). Since we have not been able to trace this interpretation by Grenier, we have cited *J. bicephalus* auct., non Viv.

5. *J. SORRENTINII* Parl., *Fl. Ital.*, 2: 356 (1857); (Fig. 5, Plates 1E and 2E)  
 Type: Sicily, Alcamo, Aug. 1853, *Duca da Sorrento* (FI, lectotype); Corsica, Portovecchio, May 18-- (date illegible), *Requien* (FI, lectoparatype).  
*J. bufonius* L. var. *condensatus* Cout. in *Bolm Soc. broteriana*, 8: 102 (1890)  
*J. bufonius* L. var. *sorrentinii* (Parl.) Husnot in *Bull. Soc. bot. Fr.*, 55: 50 (1908)

Annual; culms fasciculate, rarely solitary, erect or ascending from slightly procumbent base, up to 20 cm. Leaf-blades dark green, 0.5–1 mm wide; stomata 29–42  $\mu$ m. Inflorescence strongly contracted, with flowers disposed in dense fan-shaped heads. Flowers 3–6 per ultimate branch and 4–6 branches per head; tepals without or rarely with weak dark lines; outer tepals acute to long-acuminate or cuspidate, 5.8–8.2 mm; inner tepals acute, sometimes subacute, 4.3–6.0 mm; capsule variable in shape, 2.9–4.6 mm, much shorter than inner tepals (0.65–0.8 times as long); anthers usually shorter than filaments, rarely longer (0.28–1.7 times as long). Seeds ovoid, 320–420  $\times$  220–480  $\mu$ m; interstices of testa small,  $c$  15  $\times$  5  $\mu$ m, or outer integument sometimes lost.  $2n=28$ .

*Habitat.* In similar situations to *J. hybridus*.

*Distribution* (Fig. 9). Southern Europe (Corsica, southern Spain, Portugal, Sardinia and Sicily eastward to Greece); North Africa (Morocco); Madeira.

*J. sorrentinii* is either rare or under-collected and relatively little is known about it. Of the wealth of names to be found in the literature, only Coutinho's var. *condensatus* can be ascribed to the synonymy with any certainty.

#### ACKNOWLEDGMENTS

We acknowledge with gratitude the help of many people in supplying information and specimens, especially Dr S. Snogerup for much correspondence and for allowing us to see his draft account of *Juncus* for *Flora Europaea*; Mrs J. Lions for making available valuable data on British material, particularly *J. ambiguus*; Miss M. J. P. Scannell for correspondence and help during a collecting trip in

Ireland; Miss Scannell, Dr A. Hansen, Dr G. Halliday, Mr P. M. Benoit and others for sending seeds or live plants; Mr R. D. Meikle and Dr W. T. Stearn for help with the typification of *J. bufonius*; Miss S. Duffey for preparing the European maps; and the curators of the herbaria cited for allowing us to consult or borrow their collections. Figures 1–5 were very kindly prepared and donated by Mrs M. Tebbs. This work was carried out while T.A.C. was in receipt of an S.R.C. Research Studentship.

## REFERENCES

- ADAMSON, R. S. (1950). *J. bufonius*, in ADAMSON, R. S. & SALTER, T. M. *Flora of the Cape Peninsula*, p. 163. Cape Town & Johannesburg.
- ALLEN, D. E. (1969). *The flowering plants of the Isle of Man*, p. 78. Douglas, I.O.M.
- BENOIT, P. M. (1973). *Juncus foliosus* Desf.—In Wales. *Watsonia*, 9: 373.
- BRIQUET, J. (1910). *Prodrome de la flore Corse*, 1: 249. Lyon, Geneva & Basle.
- BUCHENAU, F. (1890). Monographia Juncacearum. *Bot. Jb.*, 12: 1–495.
- BUCHENAU, F. (1906) in ENGLER, A., ed. *Das Pflanzenreich*, 25 (IV, 36): 102–109. Berlin.
- ČEREPANOV, S. K. (1973). Svod dopolnjenij i izmjenjenij K 'Flore SSSR' (tt. 1–XXX). Leningrad.
- CHEESMAN, T. F. (1925). *Manual of the New Zealand flora*, 2nd ed., p. 295. Wellington.
- COLGAN, N. & SCULLY, R. W. (1898). *Cybele hibernica*, p. 358. Dublin & London.
- CRONQUIST, A. (1968). *The evolution and classification of flowering plants*, pp. 331–361. London.
- DRUCE, G. C. (1911). The international phytogeographical excursion in the British Isles, 3. The floristic results. *New Phytol.*, 10: 321, 327.
- DRUCE, G. C. (1912). The international phytogeographical excursion in the British Isles, 11. Additional floristic results. *New Phytol.*, 11: 361.
- DUVIGNEAUD, J. (1967). Flore et végétation halophiles de la Lorraine Orientale. *Mem. Soc. roy. bot. Belg.*, 3: 49–52.
- FERNALD, M. L. & BUCHENAU, F. (1904). *Juncus bufonius* and its representatives in America, in FERNALD, M. L. Preliminary lists of New England plants, 13. Juncaceae. *Rhodora*, 6: 38–40.
- FIORI, A. (1923). *Nuova Flora analitica d'Italia*, 1: 234. Florence.
- GOOD, R. (1953). *The geography of flowering plants*, 2nd ed. London.
- HOLUB, J. (1976). *Juncus minutulus*—a neglected new species in the Czechoslovak flora. *Preslia, Praha*, 48: 329–339.
- HUSNOT, T. (1908). Notes sur quelques Joncées. *Bull. Soc. bot. Fr.*, 55: 48–55.
- KRECHETOVICH, V. I. & GONCHAROV, N. F. (1935). *Juncus*, in KOMAROV, V. L., ed. *Flora U.R.S.S.*, 3: 517–520, 624–626. Leningrad.
- KUNTZE, O. (1903). *Juncus*, in POST, T. VON & KUNTZE, O. *Lexicon generum phanerogamarum*, p. 303. Stuttgart.
- LAURENT, M. (1904). Recherches sur le développement des Joncées. *Annls Sci. nat., Bot.*, sér. 8, 19: 97–194.
- LINNAEUS, C. (1753). *Species plantarum*, p. 328. Stockholm.
- LOENHOUD, P. J. VAN & STERK, A. A. (1976). A study of the *Juncus bufonius* complex in the Netherlands. *Acta bot. neerl.*, 25: 193–204.
- LÖVE, D. (1963). Dispersal and survival of plants, in LÖVE, Á. & LÖVE, D., eds. *North Atlantic biota and their history*, pp. 189–205. London & New York.
- MAIRE, R. (1957). *Flora de l'Afrique du nord*, 4: 263–266. Paris.
- PERRING, F. H. & WALTERS, S. M., eds (1962). *Atlas of the British flora*, p. 318. London.
- PORSILD, A. E. (1920). Sur le poids et les dimensions des graines arctiques. *Revue gén. Bot.*, 32: 97–120.
- POST, G. E. (1933). *Flora of Syria, Palestine and Sinai*, 2nd ed., 2: 668–669. Beirut.
- PRAIN, D. et al. (1921). *Index Kewensis*, Suppl. 5, p. 143.
- REICHGELT, T. J. (1964). Juncaceae, in OOSTSTROOM, S. J. VAN et al., eds. *Flora neerlandica*, 1(6): 164–166.
- RICHARDS, P. W. (1962). *Juncus*, in CLAPHAM, A. R., TUTIN, T. G., & WARBURG, E. F. *Flora of the British Isles*, 2nd ed., p. 987. Cambridge.
- RIDLEY, H. N. (1930). *The dispersal of plants throughout the world*, pp. 52 & 189. Ashford, Kent.
- ROUY, G. (1912). *Flora de France*, 13: 251–254. Paris.
- SEGAL, S. (1960). Een Vooronderzoek naar de systematische positie van *Juncus ambiguus* Guss. *Correspondentiablad Rijksherbarium, Leiden*, 16: 169–172.
- SIMPSON, N. D. & WALTERS, S. M. (1959). *Juncus bufonius* ssp. *foliosus*. *Proc. bot. Soc. Br. Isl.*, 3: 335.
- SNOGERUP, S. (1971a). Juncaceae, in RECHINGER, K. H., ed. *Flora Iranica*, 75: 15–18. Graz.
- SNOGERUP, S. (1971b). *Juncus* L., in SNOGERUP, S. & NILSSON, Ö. Drawings of Scandinavian plants, 45–80. *Bot. Notiser*, 124: 1–8, 179–186, 312–316, 435–441.
- SNOGERUP, S. (1972). *Juncus* L., in SNOGERUP, S. & NILSSON, Ö. Drawings of Scandinavian plants, 45–80. *Bot. Notiser*, 125: 1–8, 131–138, 203–211.
- WHITE, J. W. (1912). *The Bristol flora*, p. 600. Bristol.
- WOLLEY-DOD, A. H. (1937). *The flora of Sussex*, p. 477. Hastings.



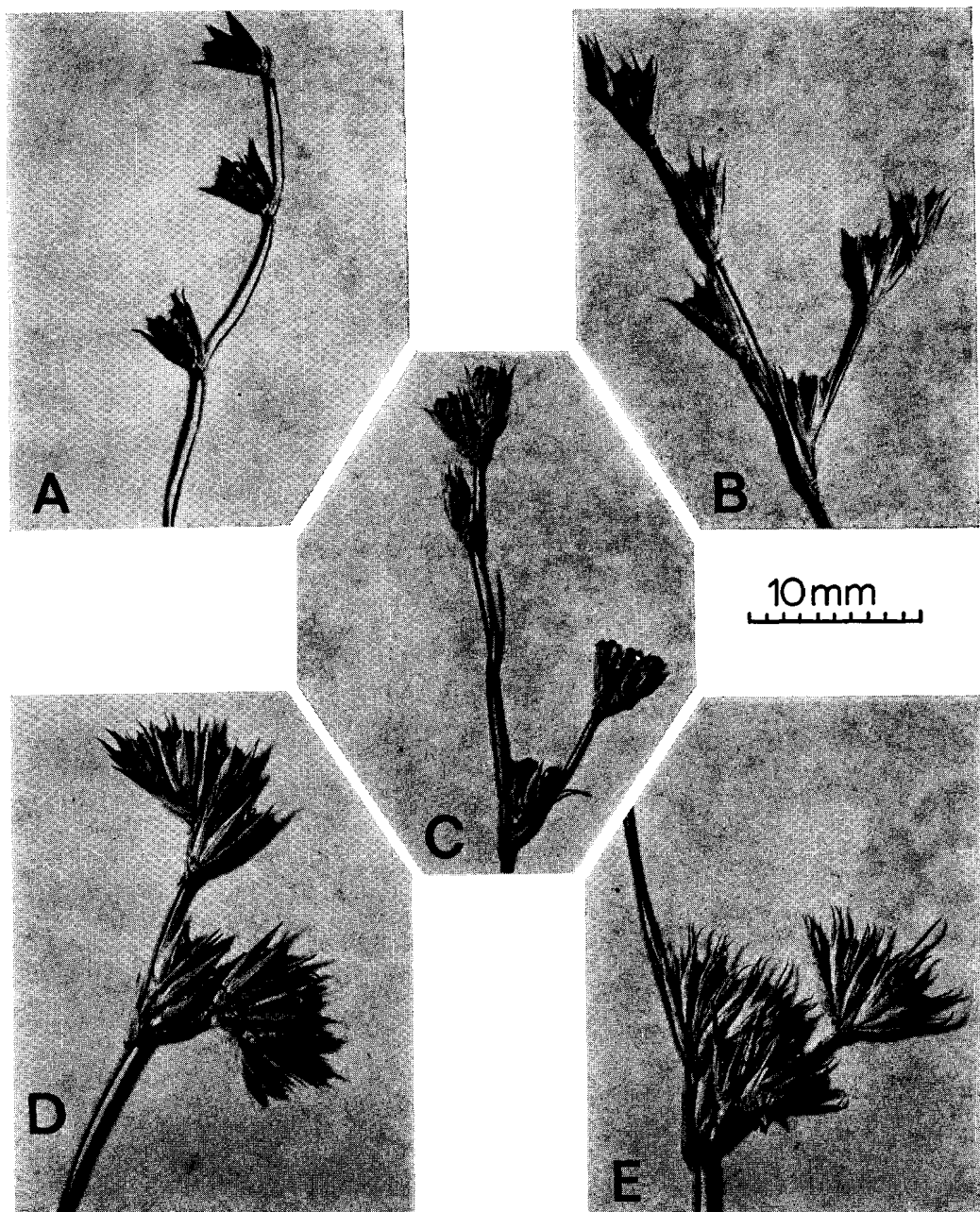


PLATE 1. Portions of inflorescences of A. *Juncus foliosus* Desf., B. *J. bufonius* L., C. *J. ambiguus* Guss., D. *J. hybridus* Brot., E. *J. sorrentinii* Parl.

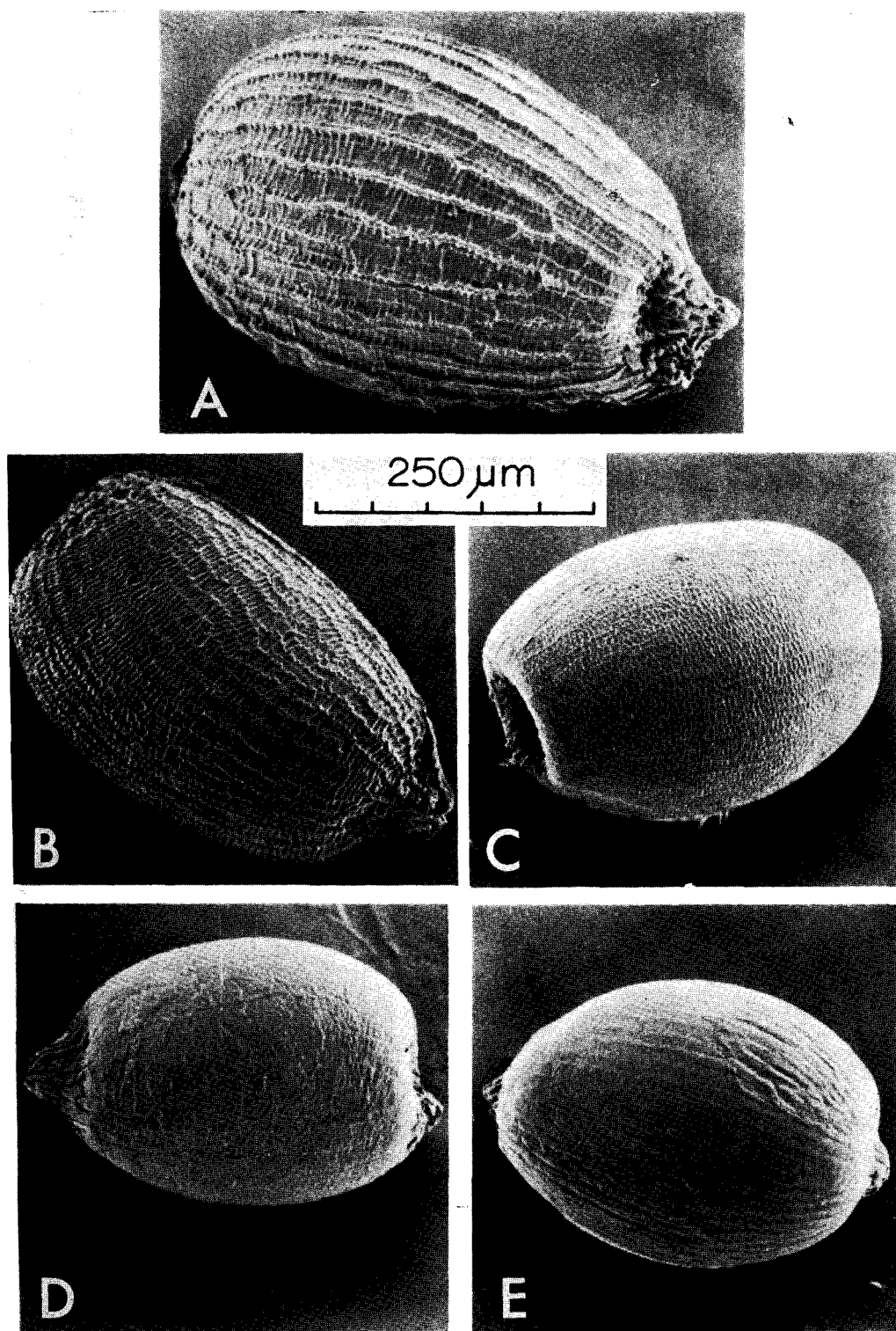


PLATE 2. Scanning electron micrographs of seeds of A. *Juncus foliosus* Desf., B. *J. bufonius* L.  
C. *J. ambiguus* Guss., D. *J. hybridus* Brot., E. *J. sorrentinii* Parl.