

Life cycle, ecology and distribution of *Schoenoplectus triquetus* (L.) Palla (Cyperaceae), Triangular Club-rush, in Britain and Ireland

T. C. G. RICH

Dept. of Biodiversity and Systematic Biology, National Museum and Gallery, Cardiff CF10 3NP

and

R. FITZGERALD

Beggars Roost, Lilstock, Bridgwater, Somerset TA5 1SU

ABSTRACT

Schoenoplectus triquetus, Triangular Club-rush, is a rare plant which is declining in England. It is a rhizomatous perennial which rarely produces seed in the wild in Britain and Ireland but does so readily in cultivation and in Europe (and probably elsewhere). In Britain and Ireland it is restricted to the upper parts of tidal rivers where there are weakly brackish to fresh water conditions and large fluctuations in water level, but it occurs in a variety of wetlands and fresh water ecosystems elsewhere in the world. It has been recorded from four rivers in England (it was once locally abundant in at least three of these), but by 1995 was reduced to one or two plants on the Tamar. In Ireland it has been recorded in three rivers and, although gone from one river, still has a large and apparently stable population on the Shannon. The decline in England is probably due to destruction of habitats, spread of *Phragmites* and failure to recolonise after disturbance. It is probably not under threat world-wide.

KEYWORDS: biodiversity, conservation, reproduction, *Scirpus triquetus*.

INTRODUCTION

Schoenoplectus triquetus (L.) Palla (*Scirpus triquetus* L.), Triangular Club-rush, is a rare plant which is declining in Britain. It has been recorded from the rivers Arun, Medway, Tamar and Thames in England (and was once locally abundant in at least the latter three), but has recently become reduced to one or two plants on the Tamar. In Ireland it occurs along about 10 km of the River Shannon near Limerick and on the nearby River Maigue, where it is probably stable in both, and it was also recorded once on the River Cashen, North Kerry. In this paper, we draw together information about the life cycle, ecology and distribution of *S. triquetus* in Britain and Ireland which may help with the conservation of this critically endangered species which is on the priority biodiversity species list (UK Biodiversity Group 1998; Wigginton 1999).

Schoenoplectus triquetus is a distinct species, unlikely to be confused with any other species in Britain and Ireland except *S. pungens* (Vahl) Palla (*S. americanus* auct.) which has glumes with acute (not obtuse) lateral lobes (Lousley 1931). It is, however, more readily confused with its hybrids with *S. lacustris* (L.) Palla (= *S. × carinatus* (Sm.) Palla) and *S. tabernaemontani* (C. Gmelin) Palla (= *S. × kuekenhalianus* (Junge) D. H. Kent) which can have a markedly trigonous stem but differ in having at least some parts terete. Some inexperienced botanists have mis-named *Bolboschoenus maritimus* (L.) Palla as *S. triquetus*.

The hybrids are also declining, but are not dealt with in this paper. The genetics of the few remaining plants are currently being studied at the Royal Botanic Garden, Kew (M. Fay, pers. comm., 1999). Hybrids with *S. tabernaemontani* have been reported from all of the British sites and hybrids with *S. lacustris* from the River Tamar (one unconfirmed record) and the River Thames. No hybrids have been reported from Ireland. Hybrids have been reported widely elsewhere in the world (e.g. Lightcap & Schuyler 1984; Lousley 1931; Vanhecke 1986), and may form hybrid swarms (Bakker 1968).

LIFE CYCLE

Schoenoplectus triqueter is a long-lived, perennial helophyte. The plant spreads by rhizomes under the mud surface and often forms large clonal stands (e.g. Praeger 1900, 1934; Lousley 1931). Plants may fragment when rhizomes decay, separating parts of the clone. It is also possible that small, vegetative fragments may be able to establish themselves if eroded away from parent clumps and washed up in suitable places (e.g. Lousley 1931).

Aerial stems begin growth in late spring and die back in late autumn. Flowering may begin in early July and continues until the autumn (into October in cultivation in mild autumns). The inflorescences are composed of many heads, each of which is protogynous (the stigmas being exerted before the anthers dehisce). Although it usually flowers profusely, it very rarely sets seed in the wild in Britain and Ireland; in contrast, it produces abundant seed in Europe and the tropics, and in cultivation.

About 140 British and 20 Irish herbarium sheets from Britain and Ireland have been examined for seeds. The specimens were collected in various months and over many years, and most sheets have more than one specimen. It is remarkable that only three sheets (2%) have specimens with seeds: one collected from near Kew by R. Meinertzhagen (1878–1967), undated (**BM**), another from the same locality by W. McIvor in August 1846 (**DBN**) and the third from the River Cashen, Kerry, 1905, R. W. Scully (**DBN**). There is also one sheet with seedlings grown from seed by B. T. Lowne in **K** (no. 91–462) but there is no indication of the origin of the seed. Syme (1870) noted “Nut (which I have never seen to ripen in the British plant) about $\frac{1}{10}$ inch long, less rounded ...”. Jackson & Domin (1909) noted, when discussing identification of hybrids, “the character of the nuts we do not mention as nearly all the spikelets of *S. triqueter* and *S. carinatus* were found to be barren”. R. A. Stevens failed to find seed in 1994 and 1995 from the plant on the Tamar (pers. comm., 1996).

In contrast, abundant seed has been set in material from both the Tamar and Shannon in cultivation in fresh water/mud. Cuttings transplanted from the Tamar to the Royal Botanic Gardens, Wakehurst Place, West Sussex in 1994 have set seed, and self-sown seedlings have been observed (J. Terry, pers. comm. 1996). Cultivated material from the Shannon (ex D. A. Webb and University of Reading) set seed in North London in 1999 (J. Alder, pers. comm., 1999). Material of both clones set seed in 1999 in Cardiff, on both the hot sunny south-facing side of the house and also the shaded north side (material in **NMW**).

Similarly, most herbarium sheets examined from Europe have seed (52 fertile, 34 not fertile, = 60% fertile). Figure 1 shows the location of herbarium sheets with and without seed. A significant proportion of the European specimens which lack seed are immature plants collected early in the season.

Experiments are required to ascertain the causes of the lack of seed set in wild plants in Britain and Ireland. Clones apparently sterile in the wild are fertile in cultivation, and are also self-compatible (cf. seed produced in isolated clones at Wakehurst and North London above). Many wild plants occur in situations where they are regularly submerged by tides which might affect stigma or pollen function, but although numerous herbarium specimens are covered in fine mud, many are not. Initial thoughts by the first author were that the failure to set seed was due to climatic limitations (cf. Preston & Croft 1997; Stewart 1999) but the observations in cultivation noted above now also suggest other possibilities including physiological effects due to brackish growth conditions or fluctuating water levels.

Seeds are likely to be dispersed by water and by waterfowl (many of the sites are rivers or large wetlands of importance for birds). There is no information on seed dormancy in Britain. Watanaba & Miyahara (1989) studied seed dormancy of some lowland *Scirpus* weeds buried in paddy soil in Asia, including *S. triqueter*. They found that dormancy of seeds incubated at 5 or 15°C in the dark was broken after 2–3 months, with a maximum percentage germination of 91%.

S. triqueter is variable across its world-wide range in size, development of the uppermost stem leaf, number and size of inflorescences, development of peduncles and shape of glumes. Within Britain and Ireland, cultivation experiments have shown that a clone from the Shannon is about two-thirds the height of a clone from the Tamar (ex Wakehurst Place) when grown in the same conditions, indicating that there is some genetic variation in Britain and Ireland (specimens in **NMW**). Similarly, plants from several places in Europe and Asia (e.g. Japan) look different to plants from Britain, but are recognisable as this species.

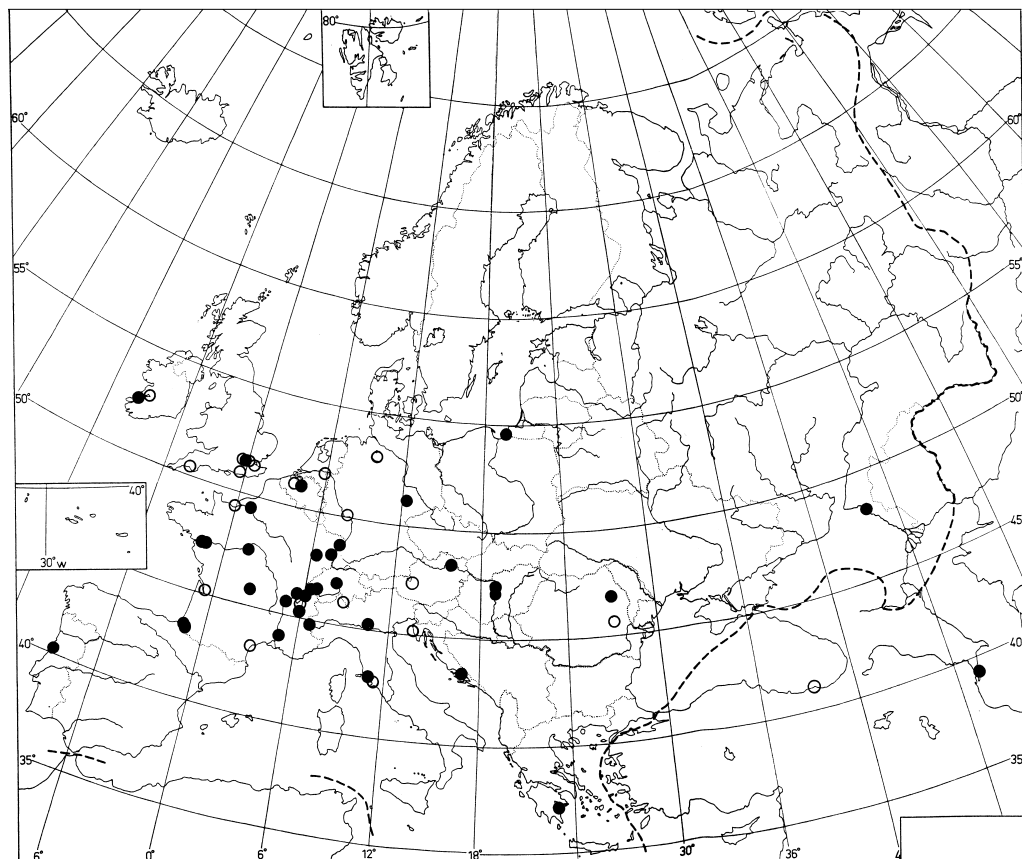


FIGURE 1. Location of herbarium specimens of *Scirpus triqueter* with seed (●) and without seed (○), compiled from specimens in BM, BRISTM, BTN, CGE, DBN, K, L, NMW, OXF, P, RNG and TCD. Only two of the 90 specimens examined from the River Thames had seed.

There are no published chromosome counts for material from Britain and Ireland. Clapham *et al.* (1987) give a chromosome number of $2n=40$ but do not indicate the origin. Otzen (1962) reported a chromosome number of $2n=42$ from Holland. Bir *et al.* (1993) reported a chromosome number of $n=21$ for material from Punjab State, India, and noted that the chromosomes were diffuse. Hoshino *et al.* (1993) reported $2n=42$ and $2n=41$ from material from China.

HABITATS

In Britain and Ireland, *S. triqueter* is usually regarded as a species of brackish mud in estuaries and tidal rivers, and rarely in “marshes”. It also occurs in these habitats elsewhere around the world, but overall is probably more common in freshwater lakes, rivers, ox-bows, ponds, ditches, muddy depressions, rice fields and other wetlands.

WATER AND SEDIMENT

In Britain and Ireland it grows in places where it may become partly or completely submerged due to tides. Along the Thames it used to grow at least partly submerged for the greater part of the day (Lousley 1931). Many herbarium specimens have fine mud, and sometimes flotsam debris, on the stems and inflorescences. Observations at its historic and extant sites suggest the water fluctuation is likely to have been in the order of 3–6 m, but it is difficult to be certain due to canalisation and embankment of the rivers. Similarly, in the Netherlands it is a pioneer plant of sand and mud flats

in the freshwater tidal area (Mennema *et al.* 1985); elsewhere in the world it grows in the tidal parts of estuaries. An important effect of the fluctuating water levels may be to reduce competition from other species.

Outside Britain and Ireland it may also grow in places where the water levels fluctuate little or only seasonally, and it is usually not completely submerged. For instance, in Germany it may grow in ditches, lakes, ponds and rivers (Hegi 1980), and in China it is a weed of rice fields (Yuan *et al.* 1991).

In Britain and Ireland, the associated species and hydrology suggest that it occurs in water which is weakly saline to fresh. Although there is no doubt that it does tolerate at least weakly saline conditions it is not found in any strongly saline situations. Stewart (1999) noted that it may be favoured by freshwater seepage around the roots, and recent surveys along the Shannon have confirmed that populations were most likely to be found where fresh water seeped onto brackish mud. Praeger (1934) also recorded it as growing "small and starved in running fresh water" above the head of the tide above Limerick, away from brackish influences. In Korea, the long-term salinity gradients appear to be primarily responsible for controlling its distribution in the Nagdong River, South Korea (Chung & Choi 1983). In the River Donets at Kharkov, Ukraine, its seasonal development in the hydroflora was connected with disturbance and pollution (Dogadina *et al.* 1979).

The upper parts of estuaries typically have fine, deep, soft mud which is likely to be nutrient-rich and weakly saline. Hegi (1980) and Ellenberg (1988) also regard it as a species of nutrient-rich mud in central Europe.

On the Tamar, plants occur where there are slight irregularities in the banks which may provide some protection from river flow; detailed observations are required. A bank on which it grew became subject to erosion in the 1990s, and by 1995 the one remaining *S. triquetra* clump had become under-cut and slumped down the bank into the river (FitzGerald *et al.* 1997). Similarly, observations on the hybrid clumps in the Medway in 1996 suggested that the river was changing course and under-cutting the plants, and that these were unable to grow quickly enough to re-establish on the newly exposed mud or the stony river bed.

VEGETATION

In Britain and Ireland, it is typically found on the outer edge of the swamp communities as a pioneer species forming relatively pure, single species stands. There are few records of associated species (there is no information on it in *British Plant Communities*; Rodwell 1991–2000). On the Tamar in 1989 it had no immediate associates, but *Agrostis stolonifera* L., *Oenanthe crocata* L. and *Phragmites australis* (Cav.) Trin. ex Steud. occurred within 1 m. W. B. Turrill noted that it grew in the Thames at Kew with *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* (K), as also did the hybrids observed on the Medway in 1996 (T. C. G. Rich & E. G. Philp, pers. obs.). Praeger (1934) noted that it was associated with *Typha angustifolia* L., *Phragmites communis*, *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus*, *Cochlearia anglica* L., *Rorippa sylvestris* (L.) Besser and *Eleocharis uniglumis* (Link.) Schult. along the Shannon, and the legend of the photograph of it at Limerick notes it with *Schoenoplectus tabernaemontani*, *Alisma plantago-aquatica* L., *Apium nodiflorum* (L.) Lag., *Persicaria maculosa* Gray, *Groenlandia densa* (L.) Fourr., *Chara* sp. and green algae. At Tervoe, Co. Limerick in 1988 it was growing with *Alisma plantago-aquatica* on otherwise bare mud (pers. obs.). Mrs S. C. P. Reynolds has recorded it with *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus*, *Persicaria amphibia* (L.) Gray, *Apium nodiflorum* and *Callitriche* sp. at Ballinacurra Creek, Co. Limerick and with *Aster tripolium* L. and *Rumex crispus* L. subsp. *uliginosus* (Le Gall) Akeroyd at Ferry Bridge, River Maigue, Co. Limerick (pers. comm., 2000; Reynolds 1997a, b). White & Doyle (1982) placed it in the *Scirpetum triquetri et maritimi* in Ireland. The associated species are all typical of wetlands with fluctuating water tables. It does not appear to tolerate competition from robust swamp species such as *Phragmites* or *Typha*.

In central Europe it is regarded as a member of the *Bolboschoenion maritimi* (Brackish-water reedbeds and related communities) of the *Phragmitetea* (Reed and Tall Sedge swamps), characterised by species such as *Bolboschoenus maritimus*, *Schoenoplectus* × *carinatus*, *S. pungens*, *S. tabernaemontani* and *S. triquetra* (Ellenberg 1988). It also occurs in *Phragmites* beds (Hegi 1980).

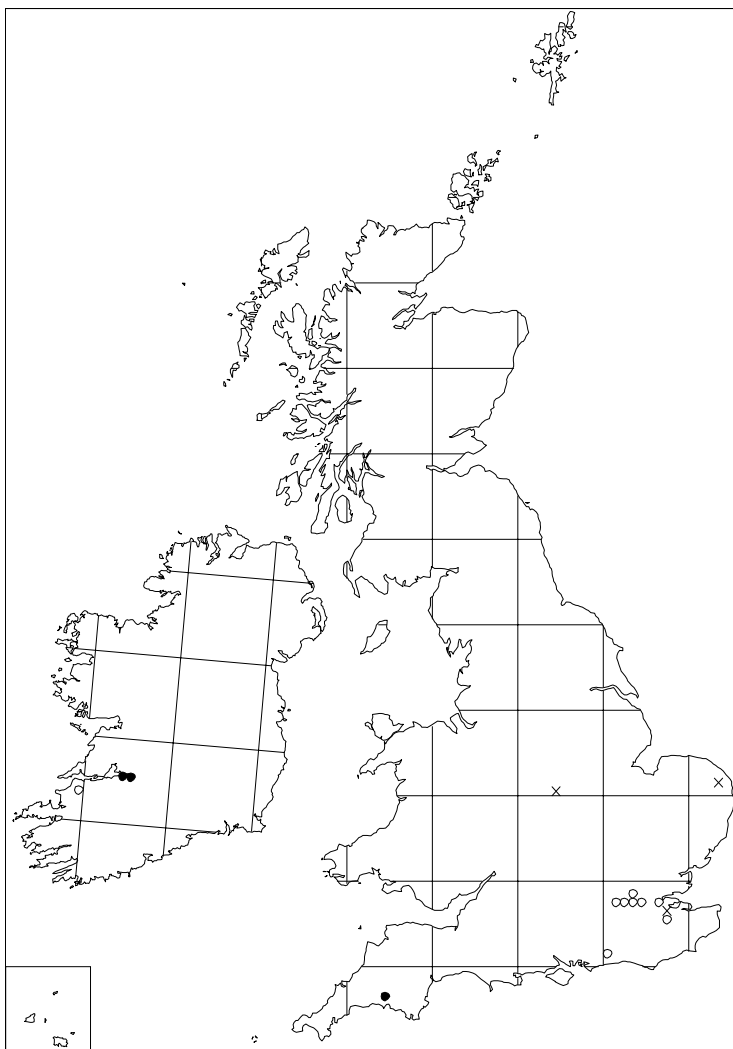


FIGURE 2. Distribution of *Scirpus triqueter* in Britain and Ireland. (●)1990 onwards. (○) pre-1990. (×) error.

HERBIVORY

There have been no detailed investigations of herbivory in Britain, but it may be eaten by swans and other wildfowl as it is elsewhere in the world. Observations suggest that ducks and geese graze heads at high tide on the Shannon (E. Meskall, pers. comm., 1994). Doornbos *et al.* (1986) report that the roots and rhizomes are the most important food source for wildfowl (mainly for swans) in the Nakdong Estuary, Korea, with approximately a quarter of its total production being eaten.

DISTRIBUTION

Data have been compiled from herbaria (**BM, BRISTM, BTN, CGE, DBN, K, L, LANC, NMW, OXF, RNG and TCD**), the literature (especially county floras), the Biological Records Centre, Monks Wood (BRC), and from correspondence with botanists and conservation officers. Details of all the records traced have been deposited at the BRC, and with the B.S.B.I. Threatened Plants Database. The records are mapped in Figure 2, and the history of each site is set out below.

RIVER TAMAR (V.C. 2 EAST CORNWALL AND V.C. 3 SOUTH DEVON)

This site was first discovered in July 1857 by C. Prentice, "most copiously on a mud bank for about a mile, or rather less, on the Calstock side of the Tamar [Cornwall] beyond Calstock, just opposite the rocks of Morwellham, on the opposite side of the river" (Prentice 1872). Prentice was surprised it had not been seen before as it was freely visible from boats on the river and the area had been visited by many notable botanists. He wondered if the plants had been washed away since he first saw it, but Briggs (1875) noted it was still present "in considerable quantity in two spots near Calstock, the higher being about ¼ mile above the village".

Botanists have sporadically visited the site since, but less so than the Devon side (see below). It was last recorded on the Cornish side of the river opposite Gawton Mine in August 1958 by Mrs I. G. Nicholson at SX451689 when four small clumps were seen on the river mud submerged at high tide (BRC record card; this is the origin of the record in Margetts & David 1980 and of three of the four records in French *et al.* 1999).

It seems to have been much rarer on the Devon side of the river when first found by T. R. A. Briggs in 1875 in three localities, Gawton, Tuckermarsh Quay and between Gawton and the Beer-Calstock Ferry (Briggs 1875, 1880). Again it has been irregularly recorded since then to the present day, but has declined. In 1985, surveys by M. E. Bradshaw revealed six patches covering 6 m², but in 1989 and 1994 only four patches remained covering a total of c. 2 m² (unpublished survey data by R. FitzGerald, R. Sparshott and R. Walton). In 1995 only one clump was known to survive, which was beginning to slump into the river (R. A. Stevens, pers. comm.). Stevens took cuttings in 1994 and 1995 which now form the basis of a conservation programme, including reintroductions. A full survey by boat in 1997, however, found two clumps about 20 m apart in the site where there had been four in 1994; there was no obvious reason for the loss (FitzGerald *et al.* 1997). Another site at Tuckermarsh Quay where two plants had been observed by T. Lording in 1994 (photographs in *NMW*) and one by D. Holyoak in 1995 was also found to have gone due to the bank slumping into the river (FitzGerald *et al.* 1997). Its survival is clearly very precarious.

The majority of the decline may be due to spread of *Phragmites* into its habitat (FitzGerald *et al.* 1997). Historic photographs from the period when it was abundant show that the river banks were open with low marshy vegetation, and no over-hanging trees or fringing *Phragmites* as they have today. The open banks were probably maintained for the river towpath and by grazing (Paige 1984 makes the tantalising but unsupported observation that "industry and river traffic destroyed the reed beds"). The cessation of towing, restriction of grazing animals and the water eutrophication caused by agriculture may have all contributed to the spread of *Phragmites*, which now forms a tall dense zone along much of both sides of the river. Unlike the other sites (see below) river engineering has not caused decline at this site.

RIVER ARUN (V.C. 13 WEST SUSSEX)

It was first recorded on the banks of the Arun near Amberley on 28 July 1832 by J. A. Power (**BM**, **K**), and by G. C. Druce in July 1918 "near Arundel", which we take to be the same locality (**OXF**). It was also reported at Stoke by G. J. Davies, in what was probably a separate locality to the south (Wolley-Dod 1937). Wolley-Dod (1937) reported that it was "still there, but much rarer than the hybrid", although, as in many cases in his flora, it is difficult to be certain that he had seen it recently. It was last collected in June 1967 by S. Hooper from Houghton Bridge (**K**). No plants have been seen by the Sussex Botanical Recording Society on several more recent visits, but a search by boat would be worthwhile.

The populations are reputed to have disappeared following canalisation and "improvements" to the banks of the river, but the river has not been investigated in sufficient detail to be certain.

RIVER MEDWAY (V.C. 15 EAST KENT AND V.C. 16 WEST KENT)

It was first found "in plenty" on the right bank of the Medway between Aylesford and Forstal in July 1894 by A. H. Wolley-Dod (**BM**; Hanbury & Marshall 1899). Marshall immediately visited the site and also saw it on the left bank both above and below Aylesford Bridge, and remarked that it was strange that it had been so long over-looked as there was a great deal of it at intervals for about a mile (**BM**, **BRISTM**, Hanbury & Marshall 1899).

It appears to have been only irregularly recorded afterwards. Lousley (1931) reported it had gone from the Medway by 1930, though hybrids were still present at Aylesford Bridge, but he subsequently re-found it at Forstal in 1934 (**RNG**). The most recent record traced is September

1938, N. D. Simpson (BRC record card). It is thought to have disappeared after the river walls were constructed and a new cut straightened the river. The late C. West told E. G. Philp that as a young man in the 1930s he remembered seeing *S. triqueter* by the Medway at Aylesford before the works were carried out, but afterwards only found it along by the Friary (pers. comm., 2000).

In 1987 a search by boat from Rochester to Aylesford was initiated by E. G. Philp with J. Bevan and R. FitzGerald. It was initially thought to have been refound at Burham Marsh (Philp 1988), but some doubts were expressed at the time and re-examination of the clumps in 1996 by E. G. Philp and T. C. G. Rich showed them to be *S. × kuekenthalianus* (Rich 1996) (material taken into cultivation at Royal Botanic Gardens, Wakehurst Place). Further searches on foot upstream to Allington Lock by E. G. Philp have been unsuccessful (pers. comm. 2000).

RIVER THAMES (V.C. 16 WEST KENT, V.C. 17 SURREY AND V.C. 21 MIDDLESEX)

The earliest record traced for Britain and Ireland is a manuscript annotation by William How for near the Horse Ferry at Westminster, c. 1650–1656 (Kent 1975). It was subsequently recorded from over 17 km of the River Thames between Richmond and Greenwich, and the London records are too numerous to present in detail. There are records in v.c. 16 West Kent between Greenwich and Woolwich (Cooper 1836; reported as extinct by Hanbury & Marshall 1899), in v.c. 17 Surrey from Lambeth (E. Forster, undated), Battersea (1832–1857), Wandsworth (1842–1856), Putney (1832–1932), Barnes (1891–1931), Mortlake (1836–1941), Kew–Mortlake (1880–1930), Kew (1832–1946) and Richmond (c. 1930–1931), and from v.c. 21 Middlesex from the Isle of Dogs (c. 1700), Limehouse (c. 1700), Chelsea (pre-1771), London (1670–1836), Westminster (c. 1650–1700), Fulham–Hammersmith (pre-1869) and Brentford (pre-1887).

The London records show a generally progressive loss upstream, and from the Middlesex side before the Surrey side, presumably related to the intensity of development along the Thames. Lousley (1931) noted “at one time the plant occurred on both banks of the Thames between Limehouse and Kew ... the embankments of the Thames have now destroyed it in all localities except around Mortlake and Kew where it still occurs in fair quantity”. Later he recorded “The one near Kew Bridge survived until about 1946 when a major reconstruction of the river-wall destroyed the last remaining patch of estuarine mud on which the plant grew” (Lousley 1976).

There is a specimen from a marsh at Gravesend, August 1840 in CGE (rejected as possibly misidentified by Preston & Croft 1997; the identification has now been confirmed); it has not been reported again from this site.

RIVER CASHEN (V.C. H2, NORTH KERRY)

The history of this site is documented in detail in the correspondence and maps held with the specimen in DBN, and in Praeger (1935, 1946).

In July 1905, R. W. Scully was investigating the distribution of *Eleocharis parvula* (Roem. and Schult.) Link ex Bluff, Nees & Schau. along the west bank of the tidal portion of the River Cashen and, being aware of the recent discovery of *S. triqueter* in the Shannon (see below), but not knowing what it looked like, collected *Schoenoplectus* inflorescences. Most were *S. tabernaemontani*, but the identity of one head was not ascertained until suggested to be *S. triqueter* by Miss M. C. Knowles in 1929 and subsequently confirmed by J. E. Lousley. Lousley also remarked that it was “off” the type and that he had not seen anything quite like it (similarly, T.C.G.R. agrees it is unlike other material seen from Britain and Ireland, and is exceptional in being fully fertile). Scully was sure the inflorescence had been collected between Dysert Church and the River Brick (c. Q9033). Despite being crippled by arthritis, he joined R. L. Praeger in an unsuccessful attempt to refind it on 16 July 1931. Praeger searched unsuccessfully again for three days in 1932, concentrating on both sides of the tidal part of the river.

This record has not been accepted by a number of authors (e.g. Perring & Walters 1962; Scannell & Synnott 1987; Preston & Croft 1997) and some doubts about it remain (Praeger 1935, 1946). However, its occurrence in the nearby Shannon estuary where the main population occurs (see below), its distinct morphology, and Scully’s certainty about the origin of the specimen suggest that it is acceptable. Searches on the river by boat in 1994 by R. FitzGerald with Wildlife Service staff were unsuccessful; the river had recently been embanked and there was no suitable habitat for either the *Eleocharis* or *Schoenoplectus*. In light of what is now known about fruiting, another search of fresh water rather than brackish habitats in the areas indicated by Scully might be rewarding.

RIVER SHANNON (V.C. H8 LIMERICK AND V.C. 9 CLARE)

It was first found new to Ireland by R. D. O'Brien in August 1900, and boat surveys showed it to occur in abundance on foreshores on both sides of the Shannon from Limerick city downstream to Tervoe Lower Light on the Limerick shore and to Coonagh Light on the Clare shore (Praeger 1900). One clump was also present in Cratloe Creek (later reported as "sparingly" by Praeger 1909). It also occurred sparingly above the town as far as the old canal entrance 1 mile ENE of the city, growing "small and staved in running fresh water" (Praeger 1934). Many botanists have seen it at the site in Limerick pictured in Praeger (1934).

Surveys by boat by R. FitzGerald and Wildlife Service staff in 1994 showed that the plant was found more or less in the same areas as when it was discovered. It was found in about 14 locations, most only accessible by boat, and some with substantial populations. On the Clare bank it was found downstream to, and in, Cratloe Creek. Several large patches were seen at the end of a small side creek at Tervoe in 1988 by N. Taylor and T. C. G. Rich, and in 1989 by G. M. Kay and T. C. G. Rich, but by 1992 the road had been blocked off, the area appeared to have building development, and we were unable to gain access. A number of the creeks and riverside sections of the Shannon both upstream and downstream of Limerick have been searched with a number of botanists including Mrs S. Reynolds and Miss C. Brady (v.c. Recorders for H8 Limerick and H9 Clare respectively) but without finding any new sites.

RIVER MAIGUE (V.C. H8 LIMERICK)

Several patches on estuarine mud were first found on the River Maigue at Ferry Bridge on 6 September 1996 by Mrs S. Reynolds (Reynolds 1997a, b) and are still present. Although this river drains into the Shannon Estuary, this is probably sufficiently distinct (c. 7 km) to be a separate site.

ERRONEOUS RECORDS

No evidence supporting Druce's (1932) record for v.c. 14 East Sussex has been traced. A record for Ballerden, Surrey (CGE), which cannot be traced (J. E. Smith, pers. comm.) is assumed to be a mistranscription of Battersea. There are (probably) erroneous records for v.c. 27 East Norfolk from Acle Dam (Trimmer 1866, rejected by Nicholson 1914) and v.c. 55 Leicestershire from Market Bosworth Park (Kirby 1850, rejected by Horward & Noel 1933).

WORLD DISTRIBUTION

It is a very widespread species which is locally abundant in the tropics and becomes rarer further north (map in Hultén 1958). It is recorded from west, central and southern Europe through western, central and eastern Asia to Japan and the Philippines, and in north Africa (recorded once on the Suez canal only) and South Africa. It is so prolific in some areas that control with herbicides is required (Yuan *et al.* 1991). It occurs from sea level in many parts of the world to an altitude of at least 2400 m in Kashmir (cf. Sharma 1979).

It was introduced to the Columbia River system, North America where it hybridised with *S. tabernaemontani* (Lightcap & Schuyler 1984).

DISCUSSION

Our current interpretation of the occurrence of *S. triqueter* in Britain and Ireland is that it is a relict species which is slowly declining due to the rate of loss of habitat being higher than the rate of recolonization. It presumably became established in Britain and Ireland earlier in the interglacial when the climate was warmer and other conditions were more suitable. A tantalising, tentative record of seeds of *S. × carinatus* from late-glacial beds at Waltham Cross (Godwin 1975) hints that *S. triqueter* could have occurred more widely in freshwater habitats. It may be less able to compete in freshwater habitats in northern areas due to the cooler climate, and be thereby restricted to the upper parts of tidal rivers, a sub-optimal habitat, where competition with other clonal swamp species is reduced by the severity of the habitat (e.g. brackish water with fluctuating levels and strong currents). It does not reproduce by seed or does so only rarely and now maintains itself vegetatively. Consequently, slow random events associated with natural changes in river dynamics, and more recently rapid changes brought about by river engineering, have resulted in

destruction of its habitats and fragmentation of the populations at a pace at which vegetative growth and recolonization cannot compensate for the losses. Hence it is now on the verge of extinction in England.

The three main causes of the decline in Britain appear to be direct loss of habitat due to construction of embankments (cf. Lousley 1976, etc.), growth of *Phragmites*, and failure to recolonise after indirect changes in the river flow patterns resulting from river engineering, canalisation, etc., which cause erosion of the river banks and the subsequent loss of colonies. Increased flow rates resulting from extensive drainage of the catchments may also contribute to changing water flows. Increased sedimentation rates due to high sediment runoff from ploughed fields may also have changed deposition and erosion patterns. There is no direct evidence that water pollution, wash from boat traffic, collection by botanists or hybridisation has caused decline.

The dangerous and inaccessible habitat, and it being a dull-flowered, unspectacular species have probably contributed to the lack of conservation. Surveys by boat are essential to assess the populations fully since sites may be inaccessible from the land, as found during the Shannon surveys in 1994. Significant action on the species in Britain began only in 1994 when R. A. Stevens of Plymouth City Council became concerned about the few remaining Tamar plants, which seemed to be declining further, and sent a cutting to Royal Botanic Gardens, Wakehurst Place for safe keeping. Independently, in June 1995 Eric Philp became concerned about the "second" British site on the Medway, but when he and T. C. G. Rich tried to bring material into cultivation it was found that the plants previously reported as *S. triqueter* were hybrid (cf. Philp 1988), and that *S. triqueter* was extinct in the Medway. In 1996, there was also concern for the safety of the plants at Limerick which were threatened by some of the early proposals for the Limerick Main Drainage Scheme.

The decline in the species in Britain had been noted by the conservation agencies (cf. Perring & Farrell 1977) but little was done to prevent it. Although it is protected under Schedule 8 of the Wildlife and Countryside Act 1981 in England and the River Tamar is a Site of Special Scientific Interest/Special Area for Conservation, the legislation provides no protection against the physical changes in its habitats which are now the biggest threats. In Ireland it is protected under the Flora (Protection) Order, 1999.

The longer term future for the species in Britain may now be brighter. A species action plan prepared by R. A. Stevens in 1996 has now been updated by a full national action plan (UK Biodiversity Group 1998). As part of a collaborative project between English Nature, Plymouth City Council and the Environment Agency cuttings have now been planted out in five places on the Tamar to reinforce the last population, some of which are growing well (FitzGerald *et al.* 1997); full details will be published elsewhere. Seed from the Tamar plants is held in the Millennium Seedbank, and live material from the Tamar and Shannon are being cultivated at Wakehurst Place, at Reading University and by a number of botanists.

World-wide, the species does not seem to be under any special threat, though it may be so in individual countries where it is rare. Estuarine barrage and land reclamation projects (e.g. Mennema *et al.* 1985; Doornbos *et al.* 1986) undoubtedly threaten local populations.

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