

***Schoenoplectus* × *flevensis* (*S. lacustris* × *S. tabernaemontani*, Cyperaceae) in Britain**

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Abstract

Intermediates between *Schoenoplectus lacustris* and *S. tabernaemontani* have been recognised at least since the late 19th century and for much of that time, there has been speculation that such intermediates may involve hybridisation. In 2017 the hybrid status of a population growing in the South-Forty-foot Drain in Lincolnshire was confirmed using molecular tools. This article presents information on the hybrid, both from the Lincolnshire population and from the literature, as well as providing an indication of how hybrid populations might be recognised. The binomial *Schoenoplectus* × *flevensis* (D.Bakker) Lansdown & Rumsey is proposed for the hybrid.

Keywords: hybridisation; molecular identification; Lincolnshire

Introduction

Many authors have recognised the occurrence of intermediates between *Schoenoplectus lacustris* (L.) Palla and *S. tabernaemontani* (C.C.Gmel.) Palla (e.g. Otzen, 1962; Davis, 1968; Kukkonen, 1996; Jermy *et al.*, 2007) and the frequent occurrence of such intermediates is likely to have contributed to uncertainty about the taxonomic status of these two taxa (e.g. Bakker, 1954). One element of these intermediates was described as *Scirpus lacustris* subspecies *flevensis* (Bakker, 1954). At least since the late 18th century some authors have considered these intermediates to represent hybrids (e.g. Buchenau, 1877; Focke, 1881; Brügger, 1882; Lousley, 1931; Davis, 1968; Easy, 1990), but to-date this has not been confirmed.

In 2010 parts of the South Forty-foot Drain, between Boston and Guthram Gowt, near Spalding, South Lincolnshire (v.c.53), were surveyed as a contribution to works to inform the proposed Fen Waterways Link project (Lansdown, 2010). The South Forty-foot Drain supports extensive populations of both *Schoenoplectus lacustris* and *S. tabernaemontani*, occasionally in mixed stands. During surveys, a number of stands of *Schoenoplectus* were encountered which were very tall, resembling *S. lacustris* but grey-green or glaucous, resembling *S. tabernaemontani* and which appeared likely to represent hybrids (Fig. 1). Inclusion of such plants in work funded by the Natural England Species Recovery Programme to investigate the identity of *Schoenoplectus* populations in the UK (Lansdown, 2017; Saubin *et al.*,

2018) provided molecular data that strongly supported their identification as hybrids between *S. lacustris* and *S. tabernaemontani*. This article presents a formal description of the hybrid and considers evidence for its occurrence elsewhere in the United Kingdom, as well as in other regions.



Figure 1. Extensive stands of *Schoenoplectus* × *flevensis* on the South Forty-Foot Drain, Lincolnshire

Taxonomic treatment

Schoenoplectus* × *flevensis (D.Bakker) Lansdown & Rumsey **comb. & stat. nov.**

Type: *Scirpus lacustris* subsp. *flevensis* D. Bakker (1954). Type: Ketelveld, bij de uitmonding van de Yssel (Flevoland), ondiep uoet water, Netherlands, 1 July 1953, Bakker, D. 1153 (L 0442940).

Voucher: South Forty-foot Drain, approximately 1.5 km north of Guthram Gowt Lincolnshire, TF1689424115, 13th August 2017, R.V. Lansdown s.n. (**BM**).

- *Scirpus* × *buchenau* Cif. & Giacom., *nom. nud.*
- *Schoenoplectus* × *buchenau* (Cif. & Giacom.) Rothm. *nom. nud.*

Description

Perennial, rhizomatous forming extensive stands. Stems (125-)142-194 cm high × (0.7-)0.6-1.2 cm diameter, terete, glaucous. Leaves of terrestrial plants reduced to sheaths, pale brown, free part of sheath 1.4-120 cm, leaves of plants growing in water not seen. Inflorescence branched, with 16-55 spikelets, on peduncles 0-47(-51) mm, secondary peduncles 0-21(-23) mm bearing 1-5 spikes, Inflorescence

lowest bract 3.2-4.9(-5) mm, brown and dry. Spikes 7.1-14.8mm, ovate to ovate-lanceolate, 13-28 flowered. Glumes (Fig. 2) 3.6-4.3 mm, ovate; smooth, with glabrous margins, denticulate to the apex, which is not emarginate; pale brown, scarious to the base, 1-nerved, usually with a green central band and narrow scarious margins, sometimes absent. Filaments 2.8-3.8 mm, anthers 1.2-1.8 mm, yellow. Styles 2.4-2.9 mm, 2-3-fid. Achenes 2.2-2.8 mm not including beak 0.1-0.3 mm, obovate, broadly trigonous, with small irregularly distributed wrinkles visible under magnification, yellowish when immature, dark brown to blackish when mature, shining; perianth bristles 5, 2.1-2.8 mm.

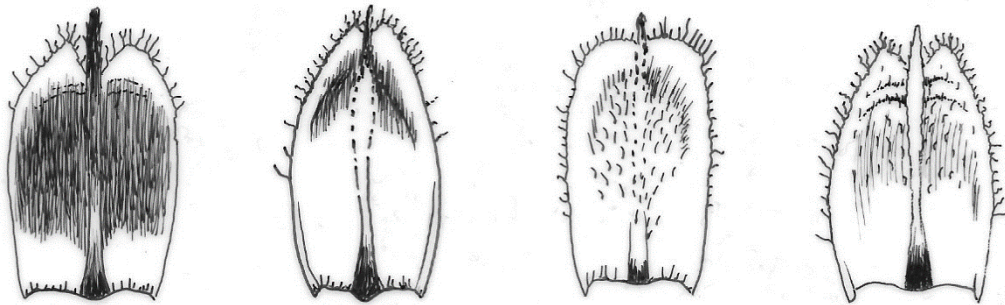


Figure 2. Illustrations of the glumes of (left to right) *Schoenoplectus lacustris*, *S. x flevensis*, *S. tabernaemontani* and *S. hippolyti*

S. lacustris, Little Avon River, Berkeley, West Gloucs. v.c. 34, ST67831.99049, 16th May 2020, R.V. Lansdown.

S. tabernaemontani, small pond off the Stroudwater Canal, Queen Elizabeth II Playing Field, West Gloucs., SO083220.04710, 16th May 2020, R.V. Lansdown.

S. hippolyti, swamp near Kurchenko Village, Astrakhan Oblast, 40° 12' 11" N, 47° 30' 17" E, 7th June 2012, A. Mesterhazy & D. Pitko s.n. (herb. A. Mesterhazy).

Identification

The populations of *S. x flevensis* on the South Forty-Foot Drain are most readily recognised by their stem size being more typical of *S. lacustris* but (usually) being glaucous in colour, combined with their lax and open panicles due to the length of the secondary branches (Fig. 3) (see also Table 1).

Data from the literature (Buchenau, 1877; Focke, 1881; Bakker, 1954; Lousley, 1931) suggest that hybrids may have stems green, ≤2.75 m high and < 6 cm diameter, glumes smooth (glabrous), reddish-brown and anthers not bearded. Bakker's (1954) circumscription of his subsp. *flevensis* (Table 2) provides a number of other characters which may be useful in recognition of the hybrid.

Distribution

S. x flevensis has only been confirmed from the margins of the southern end of the South Forty-foot Drain in Lincolnshire. Plants intermediate between the parents and likely to involve this hybrid have also been reported from Denmark (Lousley, 1931; Bakker, 1954); France (Grenier and Godron, 1855-56); Bremen (Focke, 1881;

Buchenau, 1877), Germany (Brügger, 1882; Lousley, 1931, Bakker, 1954); the River Medway near Newwhythe; Wytham ditches (Lousley, 1931), Whittlesford Gravel Pit (Easy, 1990), the old chalk pit at Barrington, Cambridge and the country park beside Addenbrooke's Hospital, Cambridge (A. Leslie pers. comm.), Great Britain (Jermy *et al.*, 2007); Lago di Chiusi, Italy (Pignotti, 2003); Zwarte Water and a pool along Overijsselse Vecht near Dalfsen, brackish tidal estuaries in the south-west, the IJsselmeer, Koelood, Oude Mass and Kamperisland (Bakker, 1954), Netherlands (Lousley, 1931, Otzen, 1962); and Kartal to Maltepe, Istanbul, Turkey (Davis, 1968).

Table 1. Identification characters of *Schoenoplectus × flevensis*

	<i>S. lacustris</i>	<i>S. × flevensis</i>	<i>S. tabernaemontani</i>
Stem	Robust, green, <350(-400) × 0.5-1.5 cm	Robust, glaucous 125-200 ¹ × (0-7)0.6-1.2 cm	Slender, glaucous <150(-270) × 3-9 cm
Secondary panicle branches	<1.5 cm	<2.3 cm	<1.3 cm
Spikelets	6-15 mm	7.1-14.8 mm	4-10 mm
Glumes	2.5-4 mm, without hooked barbs	3.6-4.3 mm, without hooked barbs	2.5-3.7 mm, with hooked barbs
Anthers	2-2.5 mm, apex rounded	1.2-1.3 mm, apex variable	2-2.5 mm, apex tapered
Stigmas	(2-)3	2-3	2(-3)
Achenes (excluding beak)	2.5-3 mm, trigonous	2.2-2.8 mm	2-2.5 mm, compressed

¹ *Scirpus lacustris* subsp. *glaucus* f. *maior* is described as reaching <2.75 m in height



Figure 3. A range of flowering heads of *Schoenoplectus × flevensis* on the South Forty-Foot Drain, Lincolnshire

Habitat and ecology

There is very little information in the literature on the habitat in which *S. × flevensis* occurs. As might be expected from the habitat preferences of the parents, most accounts are from coastal areas or the tidal reaches of large rivers, such as the former mouth of the R. IJssel which was a freshwater estuary, with occasional seawater inflow due to tide and storms, and the Oude Maas (Bakker, 1954), as well as the R. Medway (Lousley, 1931). The IJsselmeer is an interesting situation, where *S. × flevensis* occurred around the mouth of the River IJssel but after this was enclosed to form the IJsselmeer, *S. × flevensis* would have disappeared, as it could not compete with *S. lacustris*, were it not continually replanted, at least until the 1950s (Bakker, 1954). The plant was propagated and preserved as it was used for the manufacture of rush-bottomed chairs for which the mechanical properties of its stems best suited it. *S. × flevensis* is no longer cultivated in the area, but has been recorded there at least until the late 1990s (A. Corporaal pers. comm. to J. Bruinsma).

The South Forty-foot Drain presents another interesting situation. The drain runs south-north along the former confluence of spring-fed streams and freshwater marshes arising from the Lincolnshire Wolds and the inland limits of coastal marshes (Lansdown, 2017). Drainage of the marshes and conversion of the land to arable was achieved by the creation of a network of minor ditches and larger drains, together with canalisation of rivers such as the River Glen. It is likely that the extensive populations of *S. tabernaemontani* are a relic of populations growing in the former brackish marshes, while *S. lacustris* has probably expanded its range along the freshwater ditch system. It is also likely that *S. × flevensis* will have arisen *in situ* in this area. The South Forty-foot Drain supports a diverse aquatic flora, in part derived from the rich wetland flora of the ditch network, the River Glen and remnant marshes such as at Baston Fen Nature Reserve (Lansdown, 2017). The southern section of the South Forty-foot Drain, north of Guthram Gowt supports more than 25 aquatic plant species, ranging from nitrophiles such as *Ceratophyllum demersum*, *Lemna gibba* and *Stuckenia pectinata*, as well as filamentous algae such as *Cladophora glomerata*, *Ulva flexuosa* and *Vaucheria* sp(p). to species typical of calcareous fens such as *Myriophyllum verticillatum*, *Potamogeton trichoides* and *Ranunculus circinatus*. The area from which *S. × flevensis* was confirmed was characterised by *Berula erecta*, *Lemna gibba*, *L. trisulca*, *Sagittaria sagittifolia* and *Sparganium erectum* in the water, with *Carex acutiformis* and *Schoenoplectus lacustris* on the margin and extensive stands of *S. × flevensis* along the margins and extending into water to a depth of about 1 m.

Discussion

The taxonomic status of *Schoenoplectus lacustris* and *S. tabernaemontani* has long been disputed, with different authors treating them as subspecies of *S. lacustris* (e.g. Bakker, 1954; Sell and Murrell, 1996) or as different species (e.g. Otzen, 1962; Stace, 2019). One of the reasons for this inconsistency has been the widespread occurrence of plants intermediate between the concepts of the species, such that Grenier and Godron (1855-56) stated that "Aucun des caractères par lesquels on a voulu distinguer [*S. tabernaemontani*] du *S. lacustris* n'est constant" [none of the characters by which one might distinguish *S. tabernaemontani* from *S. lacustris* is constant]. However, cytological (Otzen, 1962) and molecular analysis (Saubin *et al.*,

2018) have shown that *S. tabernaemontani* is more closely related to *S. triqueter* than *S. lacustris* and there is therefore no justification for their treatment as elements of the same species.

S. lacustris and *S. tabernaemontani* are usually distinguished by the following characters (Table 1): the stem height is greater in *S. lacustris* and the stem is green, as opposed to glaucous, the glumes of *S. tabernaemontani* have red barbs which are lacking in *S. lacustris*, *S. lacustris* typically has three stigmas and trigonous achenes whereas *S. tabernaemontani* usually has two stigmas and the achenes are plano-convex.



Figure 4. Structures on the glumes of *Schoenoplectus* species: a (left) - barbs on the glume of *S. tabernaemontani*; b (centre) - teeth; and c (right) - thickenings on the glume of *S. lacustris* (specimens as for Fig. 2)

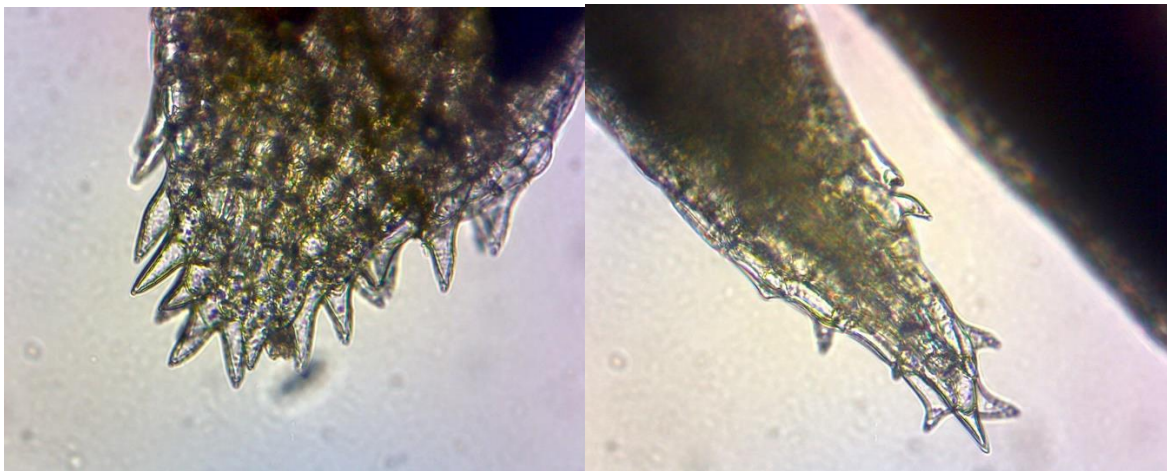


Figure 5 Apices of anthers of (left) *S. lacustris* and (right) *S. tabernaemontani* (specimens as for Fig. 2)

The structures on the glumes of *S. tabernaemontani* and their importance in distinguishing this species from *S. lacustris* have been referred to by a number of names, including papillae (Davis, 1968; Rose, 1989; Sell and Murrell, 1996; Jermy *et al.*, 2007; Stace, 2019), reddish resinous spots (Lun-Kai *et al.*, 2010), reddish barbs (Kukkonen, 1996) or reddish-brown, basally inflated barbs (Pignotti, 2003). The reason for these differences is likely to be that there are two or three different structures on the glumes of one or all of *S. lacustris*, *S. tabernaemontani* and *S. × flevensis*. *S. tabernaemontani* bears large numbers of barbs (Fig. 4a) with the base expanded and the pointed apex angled upward on the abaxial face of the glumes.

On the excurrent apex of the midrib, both *S. lacustris* and *S. tabernaemontani* may have varying numbers of teeth which appear similar to the barbs but taper gradually from the base (Fig. 4b). Finally, all three taxa have varying numbers and extent of red to blackish thickenings (Fig. 4c) extending along the midrib from the apex half to two-thirds of the way to the base, generally along the sides but in some cases scattered over the midrib. The diagnostic character for *S. tabernaemontani* is therefore the barbs and not other structures.

Bakker (1954) and others also refer to the presence of absence of a "beard" on the "connectiva" on the anthers of *S. lacustris* but not on those of *S. tabernaemontani*. However, as can be seen from the photograph (Fig. 5), both species have similar structures (clearly visible as teeth, rather than a beard at high magnification), but the apex of the anther of *S. lacustris* is broad and rounded with a fringe of teeth, whereas that of *S. tabernaemontani* is narrow and tapered to the apex with teeth all around.

Plants intermediate between *S. lacustris* and *S. tabernaemontani* have been widely reported (see above), but to-date "no proof of hybridisation has been given" (Jermy *et al.*, 2007). Unfortunately, it is difficult to know how to treat most of the published data, except perhaps for data presented by Lousley (1931) as different authors have applied different and inconsistent concepts of the morphological limits of *S. lacustris* and *S. tabernaemontani*.

There has been speculation that *Schoenoplectus hippolyti* (V.I.Krecz.) V.I. Krecz. ex Grossh. actually represents hybrids between *S. lacustris* and *S. tabernaemontani* and the type of *S. hippolyti* was considered to agree with Bakker's (1954) concept of *Scirpus lacustris* subsp. *flevensis* (A. Corporaal pers. comm. to J. Bruinsma). Material of *S. hippolyti* from the Astrakhan region of southern Russia was compared with *S. × flevensis* from the south Forty-Foot Drain. There is overlap in many characters, e.g. Stem glaucous-green, achenes 2-2.5 mm, stigmas 2-3. However, the glumes and spikelets of *S. hippolyti* are shorter than those of *S. × flevensis* (3-4 mm and 6.8-8 mm respectively) and have barbs resembling those of *S. tabernaemontani* (Fig. 2). The spikelets of *S. × flevensis* are also long, cylindrical and tapering toward the apex (Figure 6), while those of *S. hippolyti* are short and ovoid. In addition, most of the anthers of the specimen of *S. hippolyti* examined were fully formed and releasing pollen, whereas those of *S. × flevensis* were mainly withered and empty. *S. × flevensis* and *S. hippolyti* are clearly different.

Treating *S. lacustris* and *S. tabernaemontani* as subspecies of *Scirpus lacustris*, Bakker (1954) described *S. lacustris* subspecies *flevensis*, named for Lake Flevo which formerly occupied the area from which this taxon was collected. Lake Flevo was originally a freshwater lake before becoming linked to the sea in the Middle Ages (and named the Zuidersee), then enclosed in 1932 and renamed the IJsselmeer (J. Bruinsma pers. comm.). He applied this name to what he described as stable populations intermediate between *S. lacustris* and *S. tabernaemontani*, occurring in the Yssellake but he did not include other populations intermediate between *S. lacustris* and *S. tabernaemontani* from the Netherlands and Germany, which he considered to fall within the natural morphological variation of either *S. lacustris* or *S. tabernaemontani*. Bakker (1954) did note "it is still possible that the ssp. *flevensis* should in fact be a hybrid" and "it is thought that the ssp. *flevensis* originated from crossings between ssp. *lacustris* and ssp. *glaucus* (= *tabernaemontani*) followed by back-crossings with the parents which involved

introgressive hybridization". The name *Scirpus lacustris* subsp. *flevensis* D. Bakker is thus strictly applicable to a stable hybrid population occurring in the shallow water of the coastal area of the IJsselmeer between the Ketel (mouth of the IJssel) and the Ganzendiep (Bakker, 1954).

In his circumscription of *Scirpus lacustris* subsp. *flevensis*, Bakker (1954) provided a detailed description of the distinguishing characters which are summarised in Table 2. However, he recognised a total of four varieties within his concept of *Scirpus lacustris* subsp. *lacustris* (= *Schoenoplectus lacustris*), of which his var. *glaucoptis*, distinguished by its glaucous stem, is also likely to represent intermediate populations. He also recognised one variety and two forms within his concept of *Scirpus lacustris* subsp. *glaucus* (= *Schoenoplectus tabernaemontani*) of which his fo. *maior*, with larger stems (<2.75 m high and <6 cm diameter) which are glaucous or "nearly green" are also likely to represent intermediates (Lousley, 1931).

It seems clear that the *Scirpus lacustris* subsp. *flevensis* of Bakker (1954) represents one element of variation within hybrids between *Schoenoplectus lacustris* and *S. tabernaemontani*, although "The situation is, in all probability, greatly complicated by numerous back-crosses with the parents" (Lousley, 1931). We have retained the epithet "*flevensis*" in the binomial for the hybrid combination.

Other authors have provided descriptions of intermediate populations as follows:
Buchenau (1877): Hollerdeich, near Kattrepel, Germany. Stem grass-green; glumes reddish-brown, not asperous; stigmas 3; fruit poorly developed, intermediate between the parents.

Focke (1881): Bremen, Germany. Poorly fertile, intermediate.

Bakker (1954) (*Scirpus lacustris* subsp. *lacustris* var. *glaucoptis*): Zwarte Water and pool along Overijsselse Vecht near Dalfsen, Netherlands. Stems glaucous.

Bakker (1954) (*Scirpus lacustris* subsp. *glaucus* fo. *maior*). Brackish tidal estuaries in the south-west and the Yssellake, Netherlands. Stems glaucous, less often green; ≤2.75 m high, 6 cm diameter; inflorescence large and much branched.

Bakker (1954). Koelood, Oude Mass and Kamperisland, Netherlands. Leaf blades rather long; leaf-sheaths frayed; highly fertile; spikelets elongate; stigmas 3; glumes glabrous or nearly so; anthers with long-bearded connectiva.

Lousley (1931). R. Medway near Newhythe, United Kingdom. Stems 1.32 m high, very stout; panicle spreading; glumes asperous; stigmas 3; anther connectiva not bearded; achenes slightly trigonous.

Lousley (1931). G.C. Druce - Wytham ditches, Berkshire, United Kingdom. Stem glaucous; achene "more compressed than in typical *lacustris*"; stigmas 3.

Davis (1968). Istanbul, Turkey. Intermediate between parents but fully fertile "as shown by large amount of fruit set".

(A. Leslie pers. comm. 2020) P. Sell - Old chalk pit, Barrington, Cambridgeshire, United Kingdom. Stem glaucous but with glumes like *S. lacustris*.

(A. Leslie pers. comm. 2020). The new country park, beside Addenbrooke's Hospital, Cambridge, United Kingdom. Stems tall to at least 5ft (1.5 m), at least 15mm diameter; stigmas 2; glumes papillate.



Figure 6. Inflorescences of (left) *S. × flevensis* and (right) *S. hippolyti*

Table 2. Characters given by Bakker (1954) to distinguish between his three subspecies of *Schoenoplectus lacustris*

		subsp. <i>lacustris</i>	subsp. <i>flevensis</i>	subsp. <i>glaucus</i>
Rhizome	texture	hard	fairly hard	weak
	strength	brittle	tough	tough
	colour	red- or dark red-brown	yellow- or red-brown	yellow or yellow-brown
	cells	small	intermediate	large
Stem	dimensions	0.75-3.5 m high; 0.75-4 cm diameter	0.75-1.5 m high; 0.75-1.5 cm diameter	0.5-2-75 m high; 0.5-6 cm diameter
	colour	yellow- or dark-green or glaucous	glaucous	glaucous
	base	not club-shaped	not club-shaped	robust plants club-shaped
Dried flowering stems		yellow-green	yellow-green	yellow
Leaves		2-12; apices frayed	1-2; apices frayed	0-1; apices entire or slightly frayed
Spikelets		elongate or elongate-ovoid	elongate or elongate-ovoid	ovoid, elongate or elongate-ovoid
Glumes		glabrous or midrib not asperous; usually brown	asperous on the midrib, outer glumes also near the midrib; brown	all outer glumes asperous; red-brown
Number of stigmas		3	2-3 (60 : 40 % in each spikelet, 3 stigmas more frequent at apex)	2-3
Anther connective (apices)		bearded	bearded (shorter than <i>lacustris</i>)	very shortly bearded
Achenes	cross-section	bluntly trigonous	faintly trigonous or compressed	compressed
	length (exc. beak)	2.5-3 mm	about 2.5 mm	about 2.5 mm

All of these records are likely to involve hybrids between *S. lacustris* and *S. tabernaemontani*. It therefore seems likely that at the interface between coastal saline waters with freshwater habitats within the range of the parents, there is a good chance of populations of *S. × flevensis* occurring, as well as inland wherever *S. tabernaemontani* occurs. There is increasing potential for hybridisation between *S. lacustris* and *S. tabernaemontani* as both parent species are being planted outside their natural ranges and habitats. As a consequence, they are being increasingly brought into sympatry.

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