Ann. Bot. Fennici 46: 215–230 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 30 June 2009

Sagittaria × *lunata*, a binomial for the widespread North European hybrid between *S. natans* and *S. sagittifolia* (Alismataceae)

Christopher D. Preston[1] & Pertti Uotila[2]

[1)] *Centre for Ecology and Hydrology, Wallingford, Oxfordshire OX10 8BB, U.K.*
[2)] *Botanical Museum, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland*

Received 20 Feb. 2008, revised version received 11 Nov. 2008, accepted 13 Nov. 2008

Preston, C. D. & Uotila, P. 2009: *Sagittaria* × *lunata*, a binomial for the widespread North European hybrid between *S. natans* and *S. sagittifolia* (Alismataceae). — *Ann. Bot. Fennici* 46: 215–230.

The hybrid between the aquatic plants *Sagittaria natans*, of boreal Eurasia, and *S. sagittifolia*, of temperate Europe and W Asia, is widespread in the area of N Europe (Sweden, Finland, Russia) where the ranges of the two species overlap. The hybrid, which is variously intermediate between its parents, is described as *S.* × *lunata* C.D. Preston & Uotila. Its known distribution is mapped and its habitat, reproduction and dispersal are summarised. In Norden (= Fennoscandia and Denmark) it occurs in many watercourses in the absence of one or both parents, suggesting that it has a relict distribution, and it extends further north than *S. sagittifolia* and further north and south than *S. natans*. In the Finnish provinces at the northern end of the Gulf of Bothnia there is a hybrid complex which includes plants which approach *S. sagittifolia*, but only a single specimen of typical *S. sagittifolia* is known from these regions. *S. sagittifolia* forma *xanthandra* Holmberg, described from Sweden, appears to have been a non-persistent variant of *S. sagittifolia* with yellow anthers rather than a hybrid with *S. natans*. — Flora Nordica Notes 34.

Key words: distribution, new binomial, relic, sterile hybrid

Introduction

Sagittaria sagittifolia is widespread in temperate Europe and western Asia, penetrating more locally into the boreal zone, whereas *S. natans* is a boreal species which extends from eastern Norden eastwards across much of Asia (Hultén & Fries 1986). The ranges of the two taxa therefore overlap in N Europe and NW Asia. *Sagittaria sagittifolia* is a very distinctive species which has been known to European botanists since the mid 16th century. It was first recorded in Sweden in 1638 (Nordstedt 1920) and in Finland in 1683 (Tillandz 1683). *Sagittaria natans* was initially recognised in Europe as *S. sagittifolia* β *tenuior*, described by Wahlenberg (1826: 621) as growing "in fluviis maximis ut Klarelfven Vermlandiae et variis fluminibus Norrlandiae". Læstadius (1857) noted the elliptic leaf shape and yellow anthers of some North Swedish material of *Sagittaria* and wondered whether *S. natans* might be involved but it was not until the early 20th century that

Lindberg (1901) established the identity of the European plant with the Asiatic *S. natans*. He regarded *S. natans* and *S. sagittifolia* as two easily separable species, although soon after his paper was published Cajander (1906) treated S. *natans* as a subspecies of *S. sagittifolia*, without stating his reasons. Later botanists, including Samuelsson (1920), Hiitonen (1933) and Hylander (1953), recognised the two species, and attempted to ascribe all Nordic *Sagittaria* material to one or other of them. This view was also followed by Dandy (1976) in *Flora Europaea* and by Yuzepchuk (1934) and Tzvelev (1979) in the Russian Floras. The main characters separating the species are the nature of the mature leaves (elongate, unlobed or with short basal lobes and floating in *S. natans*, sagittate and emergent in *S. sagittifolia*) and the colour of the anthers (yellow in *S. natans*, purple in *S. sagittifolia*).

In the first half of the 20th century there was some speculation about the possibility of hybrids between the two *Sagittaria* species. Samuelsson (1920) did not discuss the possibility of hybridisation; he agreed with Lindberg that the species were easily separable although he could not accept that single specimens were always easy to determine. In discussing the variability of *S. sagittifolia* he noted that material with paler anthers and floating leaves was especially frequent in the northern part of the range of the species, but he did not consider that these plants were true intermediates. However, his comments on herbarium material at S suggest that he began to consider the possibility of hybridisation in later years. In Finland J. Montell, on an expedition to Kuusamo in 1937, collected a series of specimens from the Oulankajoki (all possibly gathered from sites which are now in Russia) which he labelled as *S. natans?* 'f. antheris ± violaceis' or 'f. antheris purpureis' (H), as 'var. *erythrandra* Mont.' (TUR-A) or 'var. *erythrandra* m[ihi]' (OULU, UME). The varietal name does not appear to have been published (Väre 2004) but it indicates that Montell had realised that one of the key characters of *S. sagittifolia*, its purple anthers, was in the Oulankajoki associated with plants which otherwise appeared to be *S. natans* (all these specimens are actually the hybrid). At the same time A. Vaarama was finding that the distinction between the two species was unclear further south. He collected material in Pohjois-Savo in 1935 which he labelled as *Sagittaria "natans × sagittifolia?"* but this specimen (H 226181) was determined as a modification of *S. sagittifolia* by H. Lindberg (it is also excellent material of the hybrid). In his published thesis on the aquatic plants of lake Kallavesi, Vaarama (1938) simply commented on the difficulty of separating the two species, but he later carried out a cytological study to investigate the possible occurrence of hybrids (Vaarama 1941). This, however, was inconclusive as both species proved to have the same chromosome number and a similar karyotype.

The presence of a hybrid between *S. natans* and *S. sagittifolia* was first convincingly demonstrated by Lohammar (1973). During fieldwork in Lule Lappmark, Sweden, in the hot summer of 1972 he was struck by large flowering stands of completely sterile *Sagittaria* which, on investigation, proved to be morphologically intermediate between the two species. He planned to follow his account of the morphology of the hybrid by starting "very extensive field studies", and he began by collecting a superb series of specimens from Sweden in 1973, but he was handicapped by failing health and died in January 1975, before he could publish a further account of the hybrid (Sjörs 1976). Suominen (1986) revised Finnish material of the three taxa, publishing detailed maps of their distribution. These demonstrated that the hybrid was widespread, and often occurred in the absence of at least one parent. Lohammar and Suominen's studies showed that both species had been interpreted too broadly by earlier botanists. In particular, Lindberg's and Samuelsson's concepts of *S. sagittifolia* can, in retrospect, be seen to have been much too broad, and Rataj (1972) also determined as *S. sagittifolia* many specimens from northern and eastern Finland which were actually attributable to the hybrid. Small-scale maps of the distribution of both species and the hybrid in Norden, prepared in the light of this taxonomic reassessment, were published in the first edition of *Den nordiska floran* (Mossberg *et al*. 1992). Outside of Norden, Tzvelev (2000) noted that hybrids between *S. natans* and *S. sagittifolia*, with violet anthers, were more frequent than *S. natans* in NW Russia.

P.U. has a long-standing interest in *Sagittaria* in the context of his studies of the aquatic flora

of Finland, arising at first from the difficulties he faced when attempting to name *Sagittaria* populations in the Kiiminkijoki in the late 1960s and early 1970s. He has considered for many years that it would be appropriate to give the widespread hybrid between *S. natans* and *S. sagittifolia* a binomial name. In 2006 C.D.P. examined much Finnish material of *Sagittaria* while preparing an account of the Alismataceae for *Flora Nordica* and independently came to this conclusion. We are therefore describing the hybrid under the epithet *lunata*, a reference to the lunate shape formed by the basal lobes of the floating leaves of some hybrid populations. The account that follows is based on specimens from Sweden, Finland and European Russia in the herbaria H, JYV, KUO, OULU, S, TUR, TUR-A, UME, UPS and VOA, supplemented by a very limited examination of fresh material.

Diagnosis

Sagittaria × ***lunata*** C.D. Preston & Uotila (*S. natans* Pallas × *S. sagittifolia* L.)

Hydrophytum inter S. natantem et S. sagittifoliam varie intermedium. A S. natanti (i) foliis fluitantibus saepius lobatis quam integris, (ii) foliorum fluitantium lobatorum lobis basilibus saepe quam lobi centralis dimidio longioribus, saepe curvatis vel divergentibus, sinum lunatum vel triangularem inter lobos facientibus, (iii) foliis emergentibus in plantarum congregationibus quibusdam praesentibus, (iv) antheris, ubi siccis, non pure flavis sed a colore flavo ex purpureo ad colorem purpureum variantibus differt. S. sagittifolia (i) folia submersa latiora et obtusiora, (ii) folia fluitantia in statu transitorio inter folia submersa et emergentia praesentia, sed in maturitate a foliis emergentibus dejecta, (iii) folia emergentia lobis nonnumquam angustissimus, (iv) antheras intense purpureas habet. S. × *lunata, S. natanti et S. sagittifoliae dissimiliter, plerumque sterilis est, sed aliquando fructus paucos vel (raro) multos bene formatos fert; fructus, ubi bene formati, S. sagittifoliae fructibus minores sunt.*

A hydrophyte which is variously intermediate between *S. natans* and *S. sagittifolia*. It differs from *S. natans* (1) in the more frequent occurrence of lobed rather than entire floating leaves, (2) in having basal lobes on the lobed floating leaves which are often more than half as long as the central lobe and are often curved or divergent, giving rise to a lunate or triangular sinus between them, (3) in the occurrence in some populations of emergent leaves, and (4) in anthers which when dried are not pure yellow but vary from yellow tinged with purple to purple. *Sagittaria sagittifolia* has (1) broader, more obtuse submerged leaves, (2) floating leaves which occur in the transitional phase between submerged and emergent leaves but are replaced by emergent leaves at maturity, (3) emergent leaves with lobes which are sometimes very narrow, and (4) deep purple anthers. *Sagittaria* × *lunata*, unlike *S. natans* and *S. sagittifolia*, is usually sterile, but sometimes has a few or (rarely) many well-formed fruits; when well-formed the fruits are smaller than those of *S. sagittifolia*.

Type: Finland. Etelä-Häme, Korpilahti: Kirkonkylä, Päijänteen Kirkkolahden perukan ja Tähtiniemen välinen ranta, Grid 27°E: 6879:473, UTM: MJ1, 6.VIII.1974 *J. Suominen 5000* (holotype H 449247; isotypes H 449248, 449249).

Description

Stolons robust. *Tubers* with an ellipsoid or ovoid body 12–23 × 6–13 mm and an apical beak. *Submerged leaves* sessile. Blade pale green to green, translucent, narrowly lanceolate to linear, 8–90 × 0.3–0.7(–1.0) cm, 16–120 times as long as wide. Lateral veins (0–)1(–2) on each side of the midrib. Secondary veins frequent, fairly conspicuous. Apex narrowly obtuse to acute. *Floating leaves* always present at maturity, petiolate. Petiole (6–)10–80(–126) cm. Blade entire, with one or two basal lobes or sagittate, green, often with a brownish tinge, or brown, (2.0–)2.6–19 × 0.35–4.5(–7.2) cm. Blade of entire leaves oblong-elliptical to narrowly oblong-elliptical, 3.5–12(–18.5) × 0.4–2.0(–2.5) cm, 3.6–13.0(–17.6) times as long as wide, the base cuneate, rarely truncate. Central lobe of lobed leaves lanceolate, ovate, ovate-oblong, ovate-elliptical or ovate-triangular, (1.0–)2.0–10.8 times as long as wide. Basal lobes of lobed leaves ± equal or markedly unequal and sometimes only one lobe present, ovate-triangular

or triangular, 0.4–7.5(–10.5) cm, 0.01–0.96 times as long as the central lobe, both edges straight or the outer edge convex and the inner straight or concave, the sinus between them broadly rounded or angular, the tips of the lobes obtuse, acute or acuminate. Apex rounded, obtuse or ± acute, very rarely mucronate. *Emergent leaves* sometimes present, petiolate. Petiole robust, much longer than the blade, (8–)30–73 cm. Blade sagittate, green. Central lobe oblong-lanceolate, ovate-triangular or triangular, (3.2–)5.5–11.5 × 1.2–5.0 cm, 1.4–6.1 times as long as wide. Basal lobes ± equal or rather unequal, narrowly lanceolate, lanceolate, ovate-triangular or triangular, (1.3–)2.5–8.4 × 0.5–2.5 cm, 0.26–0.93 times as long as the central lobe, both edges straight or the outer edge convex and the inner straight or concave, the sinus between the lobes rounded or angular, the tips of the lobes obtuse or acute, rarely acuminate. Apex rounded, obtuse or ± acute. *Peduncles* angular in cross-section but the angles not projecting as ridges, ± robust, (8.5–)15–65(–100) cm. *Inflorescences* (1.7–)3–14(–20) cm, with 2–5(–6) whorls of 3 flowers, the flowers in the lowest 1–3 whorls usually female or a mixture of female and male flowers, rarely all male, those in the whorls above male. *Bracts* (2–)3–6 mm. *Pedicels* of female flowers 1–15(–28) mm, of male flowers (4–)8–25(–47) mm. *Sepals* green with a narrow hyaline margin, usually with a marked purple tinge, 3–6 mm. *Petals* white, usually with a faint or distinct purple blotch, obovate to orbicular, (5–)7–11 × 6–10.5 mm. *Stamens* numerous; filaments yellow; anthers yellow with a slight purplish tinge to purple, (0.7–)0.8–1.1. *Fruits* often failing to develop, when developed 2.1–3.9(–4.2) × 1.6–3.6 mm, beak 0.3–0.7 mm, ventral or subventral, straight or curved.

The submerged, floating and emergent leaves of the hybrid and its parents are illustrated as Figs. 1–2, and a stand of the hybrid showing a characteristic range of floating leaf shape and colour is shown in Fig. 3. For further photographs of the hybrid, *see* Suominen (1986) and Väre *et al*. (2005, as *S. sagittifolia*).

Variation

Sagittaria × *lunata* is an extremely variable hybrid, ranging from plants which could easily be mistaken for *S. natans* to those which are much closer to *S. sagittifolia*. As with many aquatics, the extent to which these differences have a genetic as opposed to an environmental basis is unclear. The colour of the floating leaves varies even within a single individual, with some (and often most) leaves brown but others green. However, the consistent differences shown by populations of mature plants suggest that at least some of the variation of the hybrid is a result of the clonal spread of genetically distinct plants (Suominen 1986). This is particularly clear towards the southern edge of the range of the hybrid. For example, in Finland the few specimens from Etelä-Karjala, all from Kymi (Mussalo), are delicate plants, rather similar to *S. natans* but with pale purple anthers and highly sterile female flowers, some of which fail to open. Almost all the numerous specimens from Etelä-Häme, lake Päijänne (including the type) are of plants which tend to have well-developed submerged leaves, have numerous elongated floating leaves (the first being long and entire but the later ones having well-developed basal lobes), lack any emergent leaves and have highly sterile female flowers. In Oulun Pohjanmaa and Perä-Pohjanmaa the hybrid is much more variable, but many specimens collected from the Kiiminkijoki river system, Oulun Pohjanmaa, are very robust plants with well-developed submerged leaves, broad-lobed sagittate floating and emergent leaves with obtuse apices, robust inflorescences with a tendency for the carpels to develop a little after anthesis and even on one or two specimens to reach a reasonable size and be shed from the receptacle like the fruits of the fertile species.

Identification

In identifying plants of *Sagittaria*, it is important to understand the changes in morphology which the species undergo during their development, as well as the characters of the mature plants. The full sequence of changes is shown by *S. sagittifolia*. Plants germinating in water start with a rosette of short submerged leaves. These sometimes develop at least a single entire or

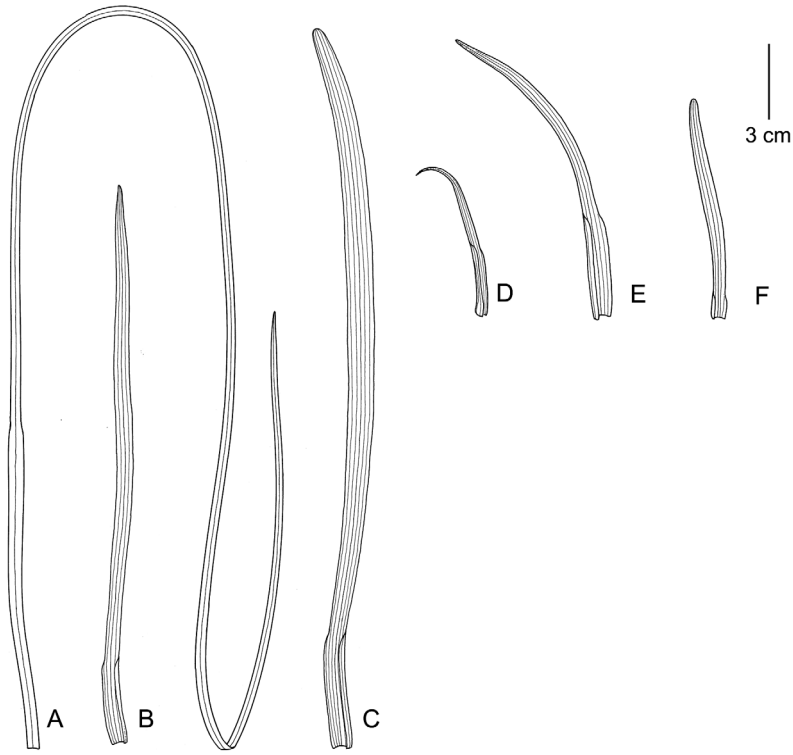

Fig. 1. Submerged leaves (**A**–**C**) and basal rosette leaves (**D**–**F**) of *Sagittaria natans* (**A**, **D**), *S.* × *lunata* (**B**, **E**) and *S. sagittifolia* (**C**, **F**). Drawn by Marja Koistinen from the following specimens at H: **A** 455027, **B** 021363, **C** 607461, **D** 225800, **E** 021442, **F** 607462.

only slightly sagittate floating leaf and further ± sagittate floating leaves may be produced before the mature, sagittate emergent leaves develop. Flowering stands of this species are dominated by emergent leaves, and any surviving floating leaves are generally moribund. *Sagittaria natans* differs in reaching maturity at the floating leaf stage; its floating leaves are therefore very numerous. This ontogenetic sequence interacts with habitat factors. In relatively deep water or in rapidly flowing water plants of *S. sagittifolia* may persist in a non-flowering state with only submerged leaves, which may become long and strap-like, and such populations can reproduce vegetatively by tubers. This tendency is apparently less marked in *S. natans*.

The characters of *S.* × *lunata* are compared to those of its putative parents in Table 1. The hybrid is variously intermediate between the parent species. *Sagittaria sagittifolia* differs from the hybrid in having broader, more obtuse submerged leaves, floating leaves which are never very elongated, numerous emergent leaves (which may sometimes have very narrow lobes) and intensely purple anthers, compared to the narrower, more acute submerged leaves of the hybrid, the frequent presence of elongated floating leaves, emergent leaves which (even if present) never have very narrow lobes and anthers which are variable in colour but combine in various ways the purple of *S. sagittifolia* and the yellow of *S. natans*. In the herbarium the anthers of the hybrid range from yellow with a faint purple blush to a distinct purple, although Lohammar (1973) states that in the field the fresh anthers of the hybrids are reddish in colour. *Sagittaria natans* differs from the hybrid in having floating leaves which are less frequently lobed, in never having emergent leaves (although terrestrial forms exposed by falling water levels may produce aerial leaves), in its more rounded peduncles and yellow anthers. The basal lobes of the floating leaves of *S. natans* are often straight-sided and the sinus between them tends to be narrow and parallel. The basal lobes of the hybrid are much more variable, and may have two straight sides, or the outer side may be convex and the inner either straight or concave.

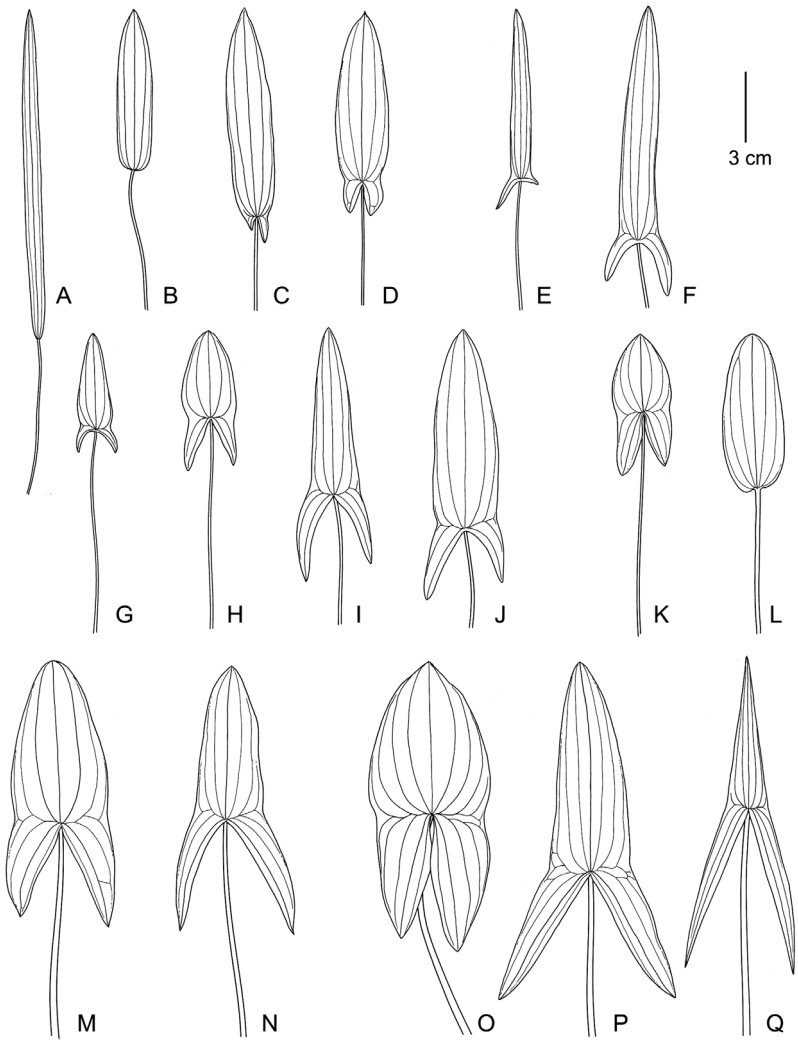

Fig. 2. Floating leaves (**A**–**L**) and emergent leaves (**M**–**Q**) of *Sagittaria natans* (**A**–**D**), *S.* × *lunata* (**E**–**J**, **M**, **N**) and *S. sagittifolia* (**K**, **L**, **O**–**Q**). Drawn by Marja Koistinen from the following specimens at H: **A** 225847, **B** 225825, **C** 225827, **D** 433998, **E** 449246, **F** 449253, **G** 226150, **H** 059634, **I** 000983, **J** 551843, **K** 226105, **L** 515226, **M** 713384, **N** 639899, **O** 052601, **P** 073769, **Q** 021382.

Fig. 3. A stand of *Sagittaria* × *lunata* in OP Kiiminki, the main village, in a pond formed from a previous river bed of the Kiiminkijoki. Photo: P. Uotila, 25.VII.2007.

The sinus is rarely narrow and parallel-sided; it may be lunate (if the lobes have concave inner and convex outer sides) or the lobes may diverge at an acute angle to give a triangular sinus. The hybrid differs from both parents in its sterility, with the carpels usually failing to develop or, even if they do, often producing a high proportion of clearly sterile fruits. The shape of the peduncle in cross-section and the petal colour cannot be observed on pressed specimens. The peduncle characters require careful interpretation even when fresh material is available. The more robust peduncles of *S. sagittifolia* and the hybrid are angular in cross-section, with five or six rather poorly defined sides, and in *S. sagittifolia* the angles sometimes project to form narrow ridges along the length of the stem (Fig. 4). The peduncles of *S. natans* are trigonous with rounded angles to almost circular in section, and unlike those of the other two taxa they can easily be rolled between the finger and thumb. However, thin peduncles of *S. sagittifolia* and the hybrid may resemble those of *S. natans*. Like most hybrids, the identification of populations

Table 1. A comparison of the characters of *Sagittaria natans*, *S. sagittifolia* and their hybrid *S. × lunata*.

Character		*S. natans*	*S. × lunata*	*S. sagittifolia*
Submerged leaves	width (mm)	2–6	3–7(–10)	4.5–21
	apex	narrowly obtuse to ± acute, often mucronate	narrowly obtuse to acute	obtuse
Floating leaves	occurrence at maturity	present	present	absent or few
	colour	brownish green or brown	green, often with a brownish tinge, or brown	green
	length/width of entire leaves	2.8–20(–27)	3.6–13(–17.6)	2.8–4.3(–5.8)
	length/width of central lobe of lobed leaves	(1.4–)1.7–8.2	(1.0–)2.0–10.8	1.2–3.6
	length longest basal lobe/central lobe	0–0.5(–0.67)	0–0.96	0–0.9
	sinus between basal lobes of lobed leaves	angular or rounded, sides often parallel	angular or broadly rounded, sides often rounded or divergent	angular, sides divergent
Emergent leaves	occurrence at maturity	absent	usually absent, sometimes present in shallow water	present
	length/width of central lobe	–	1.4–6.1	1.1–14.6
	length longest basal lobe/central lobe	–	0.26–0.93	0.44–1.44
	tip of basal lobes	–	obtuse or acute, rarely acuminate	± acute or acuminate
Peduncles	shape in cross section	bluntly trigonous or ± circular	angled	angled, often ridged
Petals	length (mm)	6–10	(5–)7–11	9–14
	colour of basal blotch	yellow	faint to distinctly purple	purple
Anthers	colour	yellow	yellow with a slight purple tinge to purple	deep purple
Fruit	development	usually fertile	usually sterile	usually fertile
	length (mm)	2.2–3.2(–3.5)	2.1–3.9(–4.2)	4.0–6.0

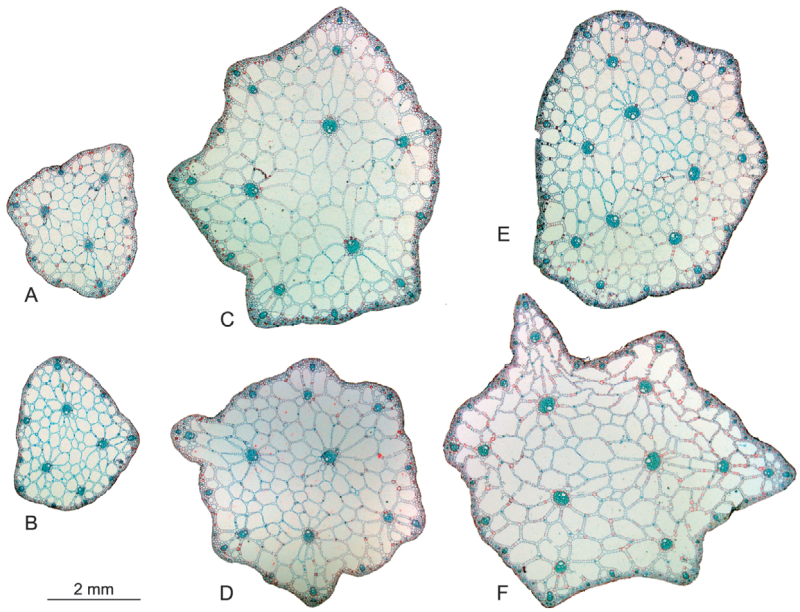

Fig. 4. Cross-sections of the peduncles of *Sagittaria natans* (**A**, **B**), *S.* × *lunata* (**C**, **D**) and *S. sagittifolia* (**E**, **F**). Sections were taken ca 5 cm below the lowest branches of the inflorescence. Fresh material was fixed in FAA or 50% ethanol, embedded in paraffin, and the sections were stained by safranin-alcian blue. F is slightly compressed from above (shown by the compressed aerenchyma), and therefore the upper furrow is somewhat too deep. Source of material: A ES Kangaslampi, Kurtto 6001 & Helynranta (H 809684); B PS Kuopio, Ihantola & Vainio (H 809685); C OP Kiiminki, Uotila 46846 (H 810681); D OP Kiiminki, Uotila 46847 (H 809265); E U Porvoo, Uotila 46917 (H 810829); F EH Hämeenlinna, Uotila 46916 (H 810826).

of *S.* × *lunata* in the field, or of well-collected specimens, is easier, and perhaps more certain, than that of fragmentary herbarium material.

The separation of *S.* × *lunata* and *S. sagittifolia* is especially difficult in the provinces at the northern end of the Gulf of Bothnia. We have reviewed a large series of specimens collected from Oulun Pohjanmaa and Perä-Pohjanmaa, including those determined and mapped as *S. sagittifolia* by Suominen (1986). There is only a single specimen of typical *S. sagittifolia* as it is represented in southern Finland, and elsewhere in Europe, with emergent leaves with narrow lobes, and a central lobe which is similar in size to the basal lobes. This was collected by E. Pallari from a pond in Oulujoki on 10 July 1938 (OULU 004775). All the other plants referred to *S. sagittifolia* from these provinces have rather broad lobes with the central lobe larger than the basal lobes, and their anthers are often a paler violet than those of typical *S. sagittifolia*. Such plants are illustrated (as *S. sagittifolia*) by Väre *et al*. (2005). It seems unlikely that the virtual absence of 'typical' *S. sagittifolia* reflects environmental conditions in the more northerly provinces, as *S. sagittifolia* with narrowly sagittate leaves does occur at similar latitudes by the White Sea in Russian Karelia. In reviewing the series of specimens we cannot separate the broader lobed plants determined as *S. sagittifolia* from those determined as the hybrid, although plants ascribed to the hybrid tend to be collected earlier in the year (July to mid-August) and have submerged leaves and floating leaves as well as emergent leaves, whereas those ascribed to the species were collected from mid August onwards and have emergent leaves alone. We consider that all this material is referable to the hybrid, and thus treat almost all *Sagittaria* plants in Oulun Pohjanmaa and Perä-Pohjanmaa except *S. natans* as belonging to a very variable hybrid complex. Some of these collections, previously ascribed to *S. sagittifolia* and now referred by us to *S.* × *lunata*, have a high proportion of apparently well-formed seed, notably specimens collected from the Kiiminkijoki in Haukipudas (Uotila

22112) and Kiiminki (Uotila 9441). The well-formed fruits are 3.3–4.2 mm long, intermediate in size between those of *S. natans* and *S. sagittifolia* (Table 1).

Distribution

A single collection from each of the provinces from which we have seen material of *S. × lunata* is cited below. For Finland and Sweden, the provinces are those defined by *Flora Nordica* (Jonsell 2004). The spelling of place names is modernised and Finnish specimens are cited under the communes to which they currently belong. If only vegetative material has been seen from a province, this is indicated by '(veg.)'.

Sweden. *Värmland*: Grava, Hynsjön, 15.VI.1896 G. Tiselius, S 3221 (veg.). *Uppland*: Nora, Östaviken, 4.VIII.1918 E. Almquist, S 6366, UPS V-220837. *Gästrikland*: Axmar, 10.VIII.1897 V. Arnell, UPS V-220752. *Dalarna*: Torsång, Lake Prästtjärn, 18.VII.1973 G. Lohammar, UPS V-220838, 220841. *Hälsingland*: Järvsö, at Lörstrand, in the river Ljusnan, 17.VIII.1973 G. Lohammar, UPS V-220844. *Medelpad*: Stöde, Lake Stödesjön, in the bay at Fanbyn, 26.VII.1973 G. Lohammar, UME, UPS V-220855. *Ångermanland*: Långsele, in the river Faxälven 1.5 km SW of the church, 27.VII.1973 G. Lohammar, UPS V-220859. *Härjedalen*: Sveg, Sveg, in the river Ljusnan about 200 m upstream from the road bridge across the river, 25.VIII.1973 G. Lohammar, UME, UPS V-220763. *Jämtland*: Stugun, Fiskviken, 12.VIII.1931 T. Lange, S 6379. *Västerbotten*: Degerfors, Lake Lill-Ramsjön, in the outlet bay, 1.VIII.1973 G. Lohammar, UME, UPS V-220769. *Norbotten*: Piteå, Mårtensholmen, in the former arm of the river Piteälven (5 km NW of the church of Öjebyn), 4.VIII.1973 G. Lohammar, UPS V-220781. *Åsele lappmark*: Åsele, nära Wilhelmina-färjan, 8.1912 J.G. Gunnarsson, S 3214. *Lycksele lappmark*: Lycksele, 3.VIII.1934 S. Nordenstam, S 3215, UPS V-220803. *Lule lappmark*: Jokkmokk, Lake Vaikijaure, in the bay at Haraudden (5.5 km NW of the church of Jokkmokk), 15.VIII.1972 G. Lohammar, H 1059104, OULU 505145, UME, UPS V-220811, 220812. **Finland**. *Etelä-Karjala*: Kotka, Kymi, Mussalo, Turankylänlahti, 5.VIII.1936 A. Ulvinen, H 225996. *Satakunta*: Pori, Kokemäenjoen suisto, Kahaluoto, Linderinkarin eteläpuolella, 29.VII.1995 J. Lampolahti & K. Nuotio, H 694217. *Etelä-Häme*: Korpilahti, Kirkonkylä, Päijänteen Kirkkolahden perukan ja Tähtiniemen väli, 6.VIII.1974 J. Suominen 5000, H 449247 (holotype). *Etelä-Pohjanmaa*: Närpiö, Öfvermark å, 29.VII.1912 A. Lindfors (TUR-A). *Pohjois-Häme*: Viitasaari, Ilmolahti, Särkilahden SW-ranta, 10.VIII.1955 H. Leivonen, H 226188. *Pohjois-Savo*: Leppävirta, Paukarlahti, Reinikkalansaari, 19.VII.1935 A. Vaarama, H 226181. *Pohjois-Karjala*: Joensuu, Linnunlahti, Ravirata, 11.VIII.1993 J. Räsänen N278, H 686943. *Keski-Pohjanmaa*: Lappajärvi, Salmela (Salmenniitty), 28.VII.1905 A. Nyström, H 226152. *Kainuu*: Suomussalmi, Pag. Piispajärvi, Runtinjärvi, 28.VII.1909 O. Kyyhkynen, H 000985. *Oulun Pohjanmaa*: Kiiminki, Kirkko, Kiiminkijoen lahdelma Rönkön kohdalla, 18.VII.1967 P. Uotila 2158, H 057596. *Perä-Pohjanmaa*: Simo, Asemakylä, Patokoski rapids of Simojoki river between farms Patokoski and Saarenpää, 21.VII.1979 T. Ulvinen & M. Kurttila, OULU 103269. *Koillismaa*: Kuusamo, Oulanka national park, Oulankajoki river ½ km upstream of Taivalköngäs waterfall, 1.VIII.1986 T. Ulvinen & M. Talasniemi, OULU 127311, UME. *Kittilän Lappi*: Kittilä, Raastenjärvi, eteläranta, 8.VIII.1960 E. Välitalo, OULU 004803. *Sompion Lappi*: Pelkosenniemi, Suvanto, Kitisen S-ranta, Mukkakoski, 27.VII.1960 K. Laaksonen, H 059636. *Inarin Lappi*: Inari, Akujärvi, Ylempi Akujärvi, 11.VIII.1973 C.E. Sonck, TUR 261626. **Russia**. Karelian Republic. *Karelia ladogensis*: Sortavala, Leppäsenlampi, 13.VII.1914 V. Pesola, H 498427. *Karelia olonetsensis*: Kuittinen, Mäkriänjoen poukama, 12.VII.1943 U. Häkkinen, H 226218. *Karelia pomorica occidentalis*: Muezerskii District, Rapids Logikoski, between Lake Kimasozero and Lake Njuk, 2.VIII.2006 P. Uotila 45763, H 805714. *Kuusamo*: Oulankadalen ca. 3 km från Paanajärvi, 15.VII.1937 J. Montell, TUR-A 386443. *Karelia keretina*: Pääjärven NW-nurkka Kostovaaran NE-puolella, 23.VIII.1942 N. Söyrinki, H 226123.

Mossberg *et al*. (1992) map the three taxa in the Nordic area (the maps in the *Sagittaria* account on p. 500 are, from top to bottom, *S. sagittifolia*, *S. natans* and the hybrid). The three taxa in Norden are mapped in UTM grid squares in Figs. 5–7. The maps of *S. natans* and the hybrid are based entirely on herbarium specimens. Most of these specimens have already been determined by J. Suominen and we have accepted his determinations unless we had a strong reason to change them. The map of *S. sagittifolia* also includes records from the southern part of its range which are not based on determined herbarium material, as in these areas the species is easily identified. For Norway the mapped records of this species are derived from a list of herbarium specimens and other records kindly supplied by R. Elven and for Denmark from the map published by Mikkelsen (1943). We have also included a number of records of *S. sagittifolia* from provincial Floras for Sweden south of Uppland. Suominen (1986) mapped the distribution of the three taxa in Finland and revised versions of these maps, based on herbarium material, are presented as Figs. 8–10.

The maps of the two parent species in Norden show that there is rather little overlap between them. *S. sagittifolia* has a lowland, southerly

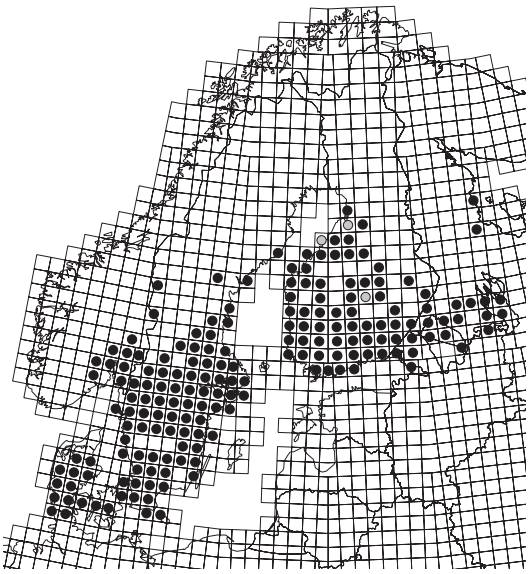

Fig. 5. The distribution of *Sagittaria sagittifolia* in Norden (plotted in 50 × 50 km squares of the Atlas Florae Europaeae grid system). Grey dots = location uncertain.

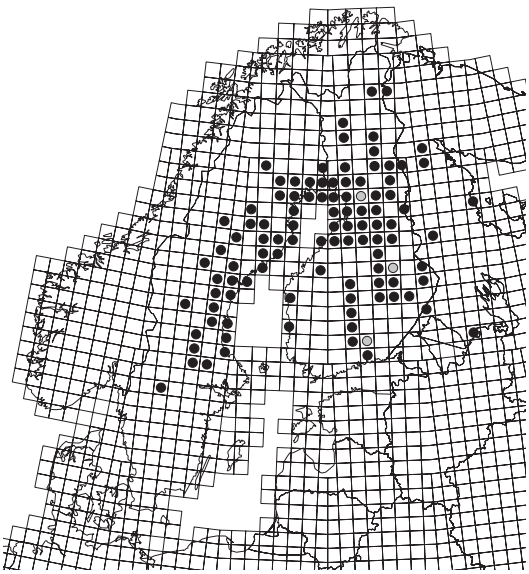

Fig. 6. The distribution of *Sagittaria* × *lunata* in Norden (plotted in 50 × 50 km squares of the Atlas Florae Europaeae grid system). Grey dots = location uncertain.

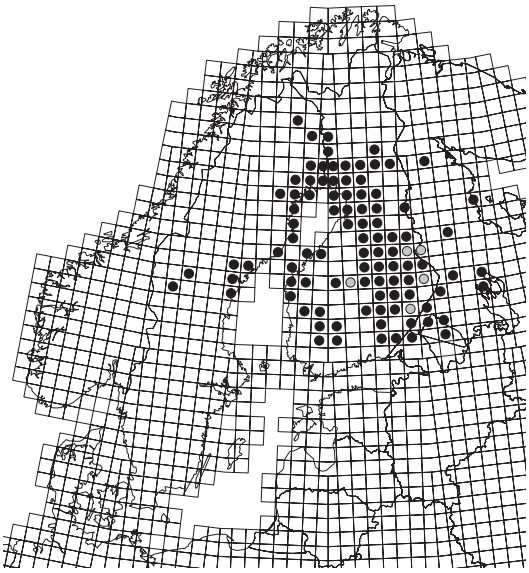

Fig. 7. The distribution of *Sagittaria natans* in Norden (plotted in 50 × 50 km squares of the Atlas Florae Europaeae grid system). Grey dots = location uncertain.

distribution, although within the main area of its range it is absent from some very acidic areas (e.g. northern Jutland, some parts of S Sweden) and from many of the Baltic islands (Öland, Gotland, the Åland islands). The northern limit of the species, running SW–NE, resembles that of *Hydrocharis morsus-ranae* and *Stratiotes aloides*, also species of lowland, relatively base-rich waters which extent much further north in Finland than in Sweden (Hultén 1971). By contrast, *S. natans* has a predominantly easterly distribution, even in Finland, extending only locally into western Finland and Sweden, and in Sweden it has a predominantly coastal range. The hybrid has a more extensive distribution in Sweden than *S. natans*, extending further south and being much more frequent away from the coastal zone. However, we have seen no recent specimens from the most southerly of the provinces in which the hybrid has been collected in the past, Värmland, Uppland and Gästrikland. This may, however, simply reflect the fact that there are few recent specimens from these provinces in public herbaria (T. Karlsson pers. comm.). In Finland the hybrid has a broadly similar distribution to *S. natans* at the 50-km square scale, although it is less frequent in the south-west.

The detailed distribution of the three taxa in Finland (Figs. 8–10) illustrates the extent to which the two more local taxa, *S. natans* and *S.* × *lunata*, tend to be restricted to particular water bodies. The concentration of *S.* × *lunata* in eastern Etelä-Häme and south-east Pohjois-Häme, in Lake Päijänne and adjacent lakes connected

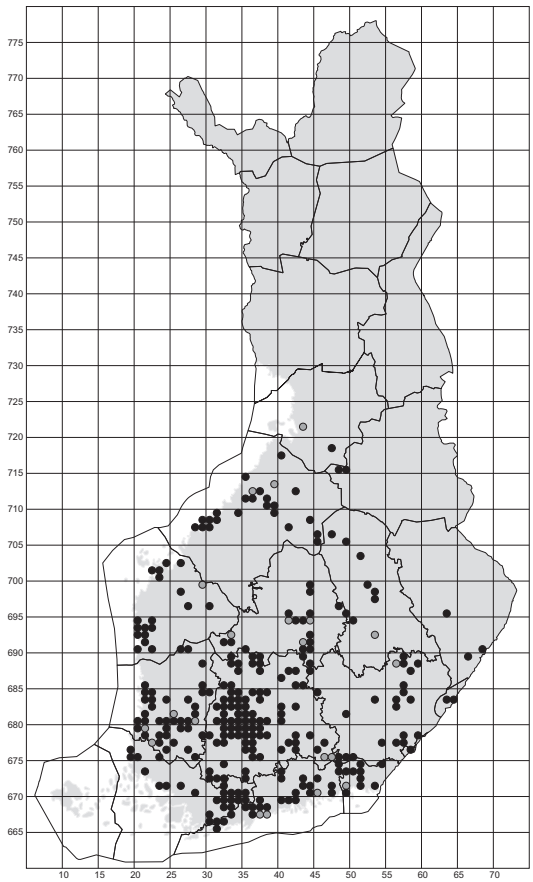

Fig. 8. The distribution of *Sagittaria sagittifolia* in Finland (plotted in 10 × 10 km grid squares of the Finnish uniform coordinate system). Grey dots = location uncertain.

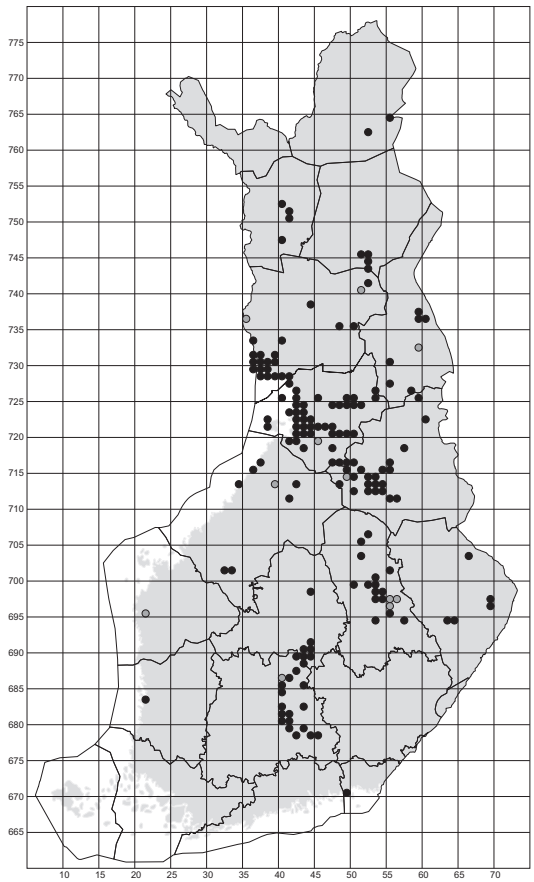

Fig. 9. The distribution of *Sagittaria Sagittaria* × *lunata* in Finland (plotted in 10 × 10 km grid squares of the Finnish uniform coordinate system). Grey dots = location uncertain.

to it, is very notable. *Sagittaria natans* is absent from this area of Etelä-Häme and may be absent from the province as a whole. There are three specimens in H which are clearly referable to this species but Suominen (1986) mapped them as doubtful as he considered that they might be mislabeled and we have mapped them with a different symbol in Fig. 10. *Sagittaria natans* also shows concentrations in areas from which the hybrid is absent, including one in eastern Satakunta (Lake Kulovesi and adjacent lakes) and others in Pohjois-Häme (Kyyjärvi–Karstula–Saarijärvi) and in Etelä-Savo (the southern part of Lake Saimaa watercourse). Rather unexpectedly, the hybrid extends further north in Finland than *S. natans* although much material from the northern provinces of both Sweden and Finland consists of vegetative rosettes which we have not attempted to identify with certainty, and the distribution of the two taxa in Lapland requires much more research. It is a case where the availability of a molecular diagnostic tool would be very useful.

In addition to the records from Norden cited above, it is likely that the hybrid occurs in Finnmark, Norway, but we have been unable to obtain conclusive proof of this. Wahlenberg (1812) reported *S. sagittifolia* from Finnmark ("in rivulis Varangriae") but there was no further record of this species from Finnmark until Økland (1962) reported a population which he discovered at Lake Vaggatem, Sør-Varanger, in the dry summer of 1960. Water levels were 25 cm below the normal August level at the time of

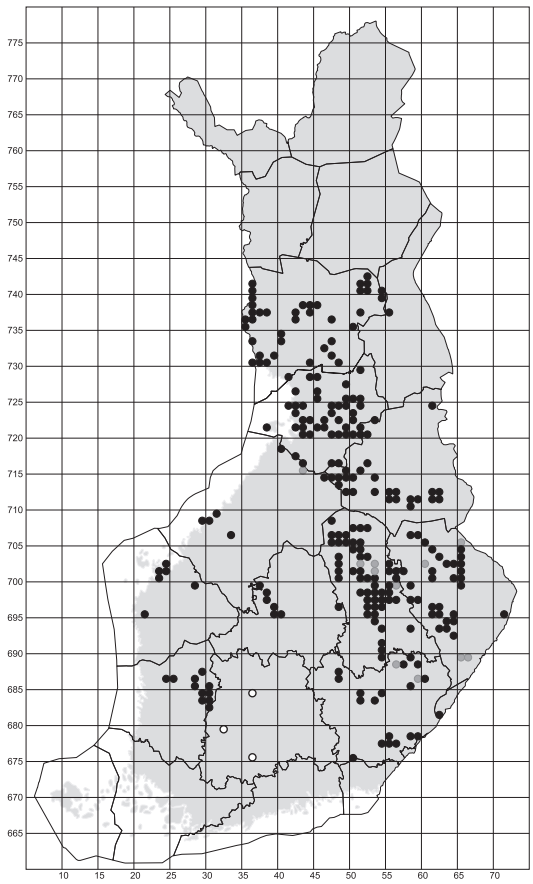

Fig. 10. The distribution of *Sagittaria natans* in Finland (plotted in 10 × 10 km grid squares of the Finnish uniform coordinate system). Grey dots = location uncertain. Open circles = possibly mislabeled.

his visit, and the *Sagittaria* plants grew on the strand line and in water up to 50 cm deep, and were flowering in the water. We have not traced Økland's specimen but it seems likely that it was the hybrid rather than *S. sagittifolia* as the hybrid grows nearby in Inarin Lappi, Finland, whereas a record of *S. sagittifolia* in this area would be very isolated. Further *Sagittaria* material was collected in Sør-Varanger by H. Edvardsen & B. Moe (Gjøkbukta, ved Noatun, UTM grid NS 8974, 17.VIII.1984, TROM) and T. Alm *et al.* (Øst for Nyrudneset, UTM grid NS8973, 27.VII.1994, TROM) but both collections are vegetative rosettes and we cannot say whether they are the hybrid or *S. natans*, although they cannot be *S. sagittifolia*.

Habitat

Sagittaria × *lunata* usually grows in water 0.5–1 m deep, although in places at depths as shallow as 10 cm, at the edges of lakes, in sheltered bays or the lotic shores of rivers or by the main channel of slow-flowing rivers, and in ponds in former river beds. At the northern end of the Gulf of Bothnia it grows in shallow water in sheltered bays, as well as coastal pools (sometimes with intermittent connection to the sea) and at the mouth of rivers. It is recorded from a range of waters from oligotrophic to eutrophic, and in slightly brackish conditions at its coastal sites, and over a range of soft substrates including fine sand and mud. Both the rivers and ponds in which the hybrid grows often undergo large and sometimes sudden increases in water level in response to heavy bursts of rainfall, and the water of the Gulf of Bothnia also fluctuates markedly as a result of changes in atmospheric pressure. The hybrid may be at a selective advantage in these ecological conditions.

Reproduction and dispersal

The carpels of the hybrid normally fail to swell, and the old female flowers with small heads of undeveloped carpels remain on the inflorescence. In some populations the lower female flowers do not open, so that when the upper male flowers are at anthesis the lower female flowers appear to be in bud. At the other extreme the carpels do swell to a limited extent in some populations, and even reach the state where a proportion of them develop into fruits resembling those of the parent species (though these are often accompanied by many unswollen carpels). In some cases these fruits clearly do not contain viable seeds, but there are specimens where at least half the fruits appear to have well-formed seeds, though their viability is unknown. The possibility that some are viable is presumably enhanced by the fact that both species have the same chromosome number. Lohammar (1973) noted reduced pollen fertility in the hybrid but more critical studies of the pollen fertility of both species and a range of hybrid populations, and of the viability of the seed produced by some hybrid plants, are clearly required.

The normal method of reproduction is by vegetative spread. The stolons of the hybrid are robust and may exceed 30 cm in length; they bear turions at their tips (although these are rarely represented on herbarium specimens). Spread by stolons results in dense patches of the hybrid. In Västerbotten S. Ericsson tells us that there are large populations of *Sagittaria* which persist as vegetative rosettes, and which he believes to be the hybrid growing in the absence of both parents. Lohammar (1973) described large-scale vegetative dispersal of the hybrid in Lapland when the water level rose after autumn rains, submerging the floating leaves and then uprooting masses of plants which formed floating rafts. Plants in these rafts developed stolons and small basal buds.

There is clear evidence for the persistence of the hybrid for decades in the same water body. In Sweden, for example, it was collected from the river Ljusnan in Sveg parish, Härjedalen, by S. J. Enander in 1901 (S) and at Järvsö parish, Hälsingland, by C. O. Schlyter in 1889 (UPS) and R. Jäderholm in 1891 (S). Lohammar refound it in both parishes in 1973 and also collected it at sites further downstream in Hälsingland.

Variants of *S. sagittifolia* with yellow anthers

Holmberg (1922) described a variant of *S. sagittifolia* with yellow anthers as forma *xanthandra*. In view of the importance of anther colour in identifying Nordic *Sagittaria*, the frequency and identity of such variants is obviously a matter of great relevance.

Holmberg's variety was based on material collected by E. Almquist from Dalarna, Sweden, at Lakes Trollbosjön and Bysjön. We have seen his collections, made at Trollbosjön in 1919 and at Bysjön in 1920, and further material collected by Samuelsson at Trollbosjön soon after Almquist's visit. Samuelsson (1920) describes the habitat of *Sagittaria* at Trollbosjön, where a large population grew in shallow water. G. Lohammar determined Almquist's material from Trollbosjön at S as cf. *S. natans* × *sagittifolia* and in 1969 K. Rataj determined the Samuelsson collection in H as this hybrid (although he named most hybrid material as *S. sagittifolia* and his subsequent monograph does not mention the occurrence of hybrids between these species). However, almost all the material with yellow anthers is of plants which have young, sagittate emergent leaves with very narrow lobes. This is a character of *S. sagittifolia* which we have never encountered in the hybrid. In addition, the fruits of the Trollbosjön plants appear to be swelling, suggesting that they are fertile. Although the plants lack the normal vigour of *S. sagittifolia*, appearing thin and rather feeble, they would appear to be this species rather than the hybrid. The specimen determined by Lohammar as the hybrid is unusual in having two floating leaves and only a single very young emergent leaf and this, if considered in isolation, might well be identified as the hybrid. Any possibility that these plants are a backcross between the hybrid and *S. sagittifolia* would appear to be ruled out by the anther colour itself, as the violet colour of *S. sagittifolia* is always evident to some extent in the hybrid and would certainly be expected in a backcross.

Samuelsson also collected *S. sagittifolia* with purple anthers on his visit to Trollbosjön in 1920. A further collection from Trollbosjön, made by J. Lundqvist in 1941 (S), appears to have pale purple anthers rather than the usual intense purple anthers of *S. sagittifolia*, but the flowers seem to have become mouldy as they dried and the anther colour is not that easy to make out. This specimen is certainly *S. sagittifolia* and appears to be fertile. Lohammer visited both Trollbosjön and Bysjön in 1973, presumably in search of the plant with yellow anthers, but only collected normal plants with purple anthers (specimens in UPS). We are not aware of any other records of true *S. sagittifolia* with yellow anthers from Norden (the variation in the anther colour of *S. sagittifolia* discussed by authors who did not recognise the hybrid must clearly be discounted). On the basis of this evidence, our provisional conclusion is that for some reason, either environmental or genetic, the usual purple pigmentation failed to develop in the anthers of plants at Trollbosjön and Bysjön, but that these plants did not represent a persistent population. There is no evidence that the presence of plants of *S. sagittifolia* with yellow anthers is currently a complicating factor which needs to be taken

into account in the identification of Nordic *Sagittaria*, and we have consequently disregarded this possibility in our treatment of the taxa.

The specimens of *S. sagittifolia* with yellow anthers which we have seen are listed below.

Sweden. *Dalarna*: Hedemora parish, Trollbosjön vid Trollbo båtställe, 28.VII.1919 E. Almquist, S (as 'var. med *gula* ståndarknappar'), UPS (annotated 'f. antheris flavis' by G. Samuelsson, 1920); Trollbosjön, 20.VIII.1919 G. Samuelssson, H 1041269, S, UPS (all as 'f. antheris flavis'). Stora Tuna parish, Bysjön, 28.VII.1920 E. Almquist, UPS.

Discussion

The occurrence of vegetatively reproducing, often more or less sterile hybrids is a feature of the aquatic vegetation of northern and western Europe. They are found in many of the major aquatic genera, including *Nuphar*, *Nymphaea*, *Potamogeton*, *Ranunculus* and *Sparganium*. Like *Sagittaria* × *lunata*, such hybrids often show a degree of independence from the parental species in their local distribution. The degree of complexity they introduce into the taxonomic understanding of the hybridising species varies from genus to genus. At one extreme, hybridisation can tend to obscure species differences, as is the case with hybrids between *Ranunculus flammula* and *R. reptans* (Uotila in Jonsell 2001). By contrast, some of the hybrids in *Potamogeton* (such as those involving *P. crispus* and *P. natans*) are recognisable entities which are highly sterile but quite distinct from either parent (Preston 1995). Both these situations may occur in the same hybrid, as is the case in *Nymphaea* where in some Finnish lakes the hybrid between *N. alba* and *N. candida* grows with its parents and is clearly distinct whereas in other lakes the determination of individual plants is impossible (Uotila in Jonsell 2001, Uotila 2001).

In much of its range *Sagittaria* × *lunata* can be distinguished without undue difficulty from the parent species, provided adequate material is to hand. Suominen (1986) regarded most populations of the hybrid as late-glacial relics. The fact that hybrid occurs in river systems where one or both parents are missing but is absent from water bodies where both parents grow together led him to suggest that in much of the range of the hybrid there was little evidence for recent hybridisation events. His hypothesis was that the hybrid had spread *as a hybrid* from the east, and was one of a number of aquatic plants (including *Butomus umbellatus*, *Ceratophyllum demersum*, *Myriophyllum spicatum*, *M. sibiricum* and most notably *Stratiotes aloides*) which spread to Finland from the east in the late glacial period, invading Lapland at a time when it was ice-free but the areas to the south and west were still covered by ice. He pointed out that the southern localities of the hybrid coincided with the position of the network of lakes which drained northwards into the Ancylus lake, the great freshwater meltwater lake whose northern part occupied the area of the Gulf of Bothnia during the Boreal period. (Since he wrote further localities for the hybrid have been discovered, but the major concentrations are still in these areas.) An alternative hypothesis is that the hybrid persists in areas in which *S. natans* formerly grew but no longer occurs. The two hypotheses are not mutually exclusive and the range of the hybrid might arise from a combination of both processes. A detailed molecular study of variation in European *Sagittaria* would be very valuable in testing the taxonomic treatment proposed here and in identifying the origins and relationships of the Nordic populations.

As discussed above, there are major difficulties in identifying *Sagittaria* material from the northern edge of the range of *S. sagittifolia* in Finland and Sweden. Here many specimens of *S. natans* and the hybrid can be identified with confidence but the distinction between the hybrid and *S. sagittifolia* is unclear. Suominen (1986) discussed the difficulties associated with material from the northern end of the Gulf of Bothnia and the Kiiminkijoki (the only river in the area from which he had a good series of specimens). He interpreted these taxonomic difficulties as indications that active hybridisation was taking place in this area, which appeared to be something of a 'melting pot' containing all three *Sagittaria* taxa. As discussed above, we consider that true *S. sagittifolia* is virtually absent from this area. Our hypothesis is that the area is not one where there is currently active hybridisation between the two parents, but that selection has favoured a range of hybrid morphotypes, including at some sites (including Kiiminkijoki) the vigorous, perhaps

partially fertile plants which resemble *S. sagittifolia* in having some submerged and floating leaves (which are often lost by the middle of August) and frequent emergent leaves.

There are other wetland plants which appear to be more taxonomically complex in this northern Gulf area than elsewhere in Europe. This is the only area in Norden where hybrids between *Thalictrum simplex* subsp. *boreale* and *T. flavum* are well documented (Jonsell in Jonsell 2001), and these lead to problems in separating the taxa in this area. *Ranunculus sceleratus* and *Ranunculus reptabundus* are another species pair in which hybridisation causes more difficulties of identification in the northern Gulf of Bothnia area than in the area by the White Sea (Uotila in Jonsell 2001). A further and more extreme example is the *Carex salina* group, which is exceptionally complex in this area (cf. Saxén 1938). In part these taxonomic difficulties might reflect a greater degree of hybridisation in northern latitudes, where the growing season is shorter and flowering periods are likely to overlap to a greater extent than in more southern populations. However, the particular difficulties associated with the Bothnian populations of several species pairs or complexes suggest that local factors play an important role. These may include the unusually dynamic aquatic environments of the coast and its associated rivers. The rivers in their natural state are highly mobile, with shifting channels, and the continuous land uplift leads on the coast to the isolation of shallow bays which become freshwater pools subject to the normal processes of vegetation succession. These physical processes occur in an area with close phytogeographical links to the White Sea, and thus an area where primarily European taxa encounter those with a more eastern distribution. It is perhaps not surprising that this combination of factors has some very interesting biological consequences.

Acknowledgements

We are grateful to Raino Lampinen for help with Finnish records of the three taxa and with distribution mapping, Stefan Ericsson for discussing his experience of *Sagittaria* in Sweden with us and for drawing our attention to the maps in *Den nordiska floran*, Philip Oswald for translating the diagnosis into Latin, and Marja Koistinen for drawing the illustrations. Juha Suominen, Outi Vainio & Risto Ihantola and Arto Kurtto & Leena Helynranta collected fresh material for us, Pirkko Harju prepared the cross-sections of the peduncles from this material, Tuuli Timonen photographed the sections and Leena Helynranta prepared Fig. 4 from these photos. We thank Thomas Karlsson, Torbjörn Petersson and Lennart Stenberg for help during visits to S, Mats Hjertson for similar assistance at UPS, the curators of the other herbaria cited for the loan of *Sagittaria* specimens and Reidar Elven for a list of Norwegian records. Juha Suominen kindly commented on a draft of this paper.

References

Cajander, A. K. 1906: *A. J. Melan Suomen kasvio*. — Suomalaisen Kirjallisuuden Seura, Helsinki.

Dandy, J. E. 1976: *Sagittaria* L. — In: Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds), *Flora Europaea* 5: 1–2. Cambridge University Press, Cambridge.

Hiitonen, I. 1933: *Suomen kasvio*. — Kustannusosakeyhtiö Otava, Helsinki.

Holmberg, O. R. 1922: *Skandinaviens flora 1*. — P.A. Norstedt & Söner, Stockholm.

Hultén, E. 1971: *Atlas över växternas utbreding i Norden*. — Generalstabens Litografiska Anstalts Förlag, Stockholm.

Hultén, E. & Fries, M. 1986: *Atlas of north European vascular plants north of the Tropic of Cancer*. — Koeltz Scientific Books, Königstein.

Hylander, N. 1953: *Nordisk kärlväxtflora 1*. — Almqvist & Wiksell, Stockholm.

Jonsell, B. (ed.) 2001: *Flora Nordica*, vol. 2. — Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm.

Jonsell, B. (ed.) 2004: *Flora Nordica*. General volume. — Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm.

Læstadius, L. L. 1857: [*Sagittaria* … som finnas i Norden]. — *Botaniska Notiser* 1857: 192.

Lid, J. & Lid, D. T. 2005: *Norsk flora*, 7 ed., ed. by R. Elven. — Det Norske Samlaget, Oslo.

Lindberg, H. 1901: *Sagittaria natans* Pallas. — *Meddelanden af Societas pro Fauna et Flora Fennica* 27: 66–72.

Lohammar, G. 1973: *Sagittaria natans × sagittifolia*. — *Svensk Botanisk Tidskrift* 67: 1–4.

Mikkelsen, V. M. 1943: Udbredelsen af Juncaginaceae, Alismataceae og Hydrocharitaceae i Danmark. — *Botanisk Tidsskrift* 47: 65–93.

Mossberg, B., Stenberg, L. & Ericsson, S. 1992: *Den nordiska floran*. — Wahlström & Widstrand, Stockholm.

Nordstedt, O. 1920: Prima loca plantarum suecicarum. — *Botaniska Notiser* 1920, supplement: 1–95.

Økland, J. 1962: Pilblad (*Sagittaria sagittifolia* L.) funnet i Pasvik, samt litt om vassdragsreguleringer. — *Blyttia* 20: 168–171.

Preston, C. D. 1995: *Pondweeds of Great Britain and Ireland*. — Botanical Society of the British Isles, London.

Rataj, K. 1972: Revision of the genus *Sagittaria*. Part I. (Old

World species). — *Annotationes Zoologicae et Botanicae*, *Bratislava* 76: 1–31.

Samuelsson, G. 1920: De nordiska *Sagittaria*-arterna. — *Svensk Botanisk Tidskrift* 14: 21–38.

Saxén, U. 1938: Die Varietäten von *Carex salina* Wg ssp. *cuspidata* Wg nebst ihren Hybriden an den Küsten des Bottnischen Busens, Finnland. — *Acta Botanica Fennica* 22: 1–30.

Sjörs, H. 1976: Gunnar Lohammar in memoriam. — *Svensk Botanisk Tidskrift* 70: 177–182.

Suominen, J. 1986: Katsaus keiholehtiimme. — *Lutukka* 2: 109–119.

Tillandz, E. 1683: *Catalogus plantarum quae prope Aboam in excultis*, *quam incultis locus hunc usque inventae sunt*. — Johanne L. Wallio, Aboae.

Tzvelev, N. N. [Цвелев, Н. Н.] 1979: Alismataceae Vent. — In: Federov, A. A. [Федеров, А. А.] (ed.), *Flora Partis Europaeae URSS* 4: 156–167. Nauka, Leningrad.

Tzvelev, N. N. [Цвелев, Н. Н.] 2000: *Manual of the vascular plants of North-west Russia (Leningrad*, *Pskov and Novgarod provinces)*. — St-Petersburg State Chemical-Pharmaceutical Academy Press, St. Petersburg.

Uotila, P. 2001: Suomen lumme- ja ulpukkatutkimus. — *Lutukka* 17: 35–48.

Vaarama, A. 1938: Wasservegetationsstudien am Grosssee Kallavesi. — *Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo* 13(1): 1–314.

Vaarama, A. 1941: Observations concerning the meiotic and mitotic chromosomes in *Sagittaria sagittifolia* L. and *S. natans* Pall. — *Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo* 16(2): 1–28.

Väre, H. 2004: Typification of names published by the Finnish botanist Justus Montell. — *Annales Botanici Fennici* 41: 435–444.

Väre, H., Ulvinen, T., Vilpa, E. & Kalleinen, L. 2005: Oulun kasvit: Piimäperälta Pilpasuolle. — *Norrlinia* 11: 1–512.

Wahlenberg, G. 1812: *Flora lapponica*. — Taberna Libraria Scholae Realis, Berlini.

Wahlenberg, G. 1826: *Flora suecica*. *Pars posterior*. — Suis impensis excudebant Palmblad & C., Upsaliae.

Yuzepchuk, S. V. [Юзепчук, С. В.] 1934: Alismataceae (Alismaceae) DC. — In: Komarov, V. L. [Комаров, В. Л.], *Flora URSS* 1: 278–291(‘192’). Institutum Botanicum Academiae Scientiarum URSS, Leningrad.