A monographic study of the genus Sparganium (Sparganiaceae). Part 1, Subgenus Xanthosparganium Holmberg

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A monographic study of the genus *Sparganium* (Sparganiaceae).
Part 1. Subgenus *Xanthosparganium* Holmberg

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Abstract

Cook, C. D. K. & Nicholls, M. S. 1986. A monographic study of the genus *Sparganium*. Part 1. Subgenus *Xanthosparganium* Holmberg. Bot. Helv., 96: 213–267.

A taxonomic revision of the genus *Sparganium* (Sparganiaceae) is presented with a key and full descriptions of each species including diagnoses, synonyms with typifications, distribution maps, variation and illustrations also containing information on fossils, anatomy, morphology, chromosomes, floral biology, dispersal, ecology, parasites, animal feeders, applied aspects and hybrids. Fourteen species and six subspecies are recognised. In part 1, subgenus *Xanthosparganium*, seven species are presented. One new name is used: ***Sparganium emersum*** subsp. ***acaule*** (Beeby ex Macoun) C. D. K. Cook & M. S. Nicholls.

Introduction

The only attempt at a worldwide revision of *Sparganium* was written by Graebner (1900). It was based almost entirely on the herbarium material in Berlin, most of which was destroyed in the second world war. Graebner worked in the Englerian fashion and recognised numerous taxa at varying ranks: 3 sections, 16 living and 16 fossil species, 4 subspecies, 5 proles, 28 varieties, 3 subvarieties and 4 hybrids. He described 12 new taxa and made 16 new nomenclatural combinations. Like Linneus before him, Graebner based his major taxa on vegetative characters. As virtually all species can grow submerged, floating and emergent many of Graebner's taxa represent no more than phenotypic states of a single taxon. Graebner also based some taxa on discordant elements, an additional source of confusion. This revision has simply not stood the test of time.

Wladislaw Rothert (b. 1863) formerly of the University of Kasan, later at Charkow, Odessa, Riga, Bogor, Warsaw and Krakow was preparing a monograph of *Sparganium*. He died in St. Petersburg (Leningrad) in 1916 before his monograph was published. We have not been able to trace his manuscript and it seems likely that it was destroyed during the upheavals in Russia at the time of Rothert's death. Two short accounts were published, one in 1910 on the species in Russia and the other in 1913 in Fedtschenko,

B. A., Flora Aziatskoi Rossii, 1: 17–37 St. Petersburg. Rothert made numerous notes on herbarium sheets in many different herbaria; we have often found these notes valuable for our studies. Rothert's herbarium is deposited in the Polska Akademia Nauk in Krakow; unfortunately, we have not been able to see this extensive collection but it apparently contains no holotypes and only three specimens collected by Rothert himself. C. D. K. Cook started studying *Sparganium* in 1956 and wrote some minor accounts in 1961, 1962 and 1963. After a quarter of a century's dormancy the genus has been, once more, actively studied.

Materials and methods

Our work is based mainly on herbarium and library studies with some field studies and experiments on living plants. Except for types and some otherwise important plants we have not cited herbarium sheets. We can give information about the material we have examined on request. We have also labelled herbarium specimens we have examined. Material from the following herbaria has been seen by us: State Herbarium of South Australia, Adelaide, Australia (AD); Botanischer Garten und Botanisches Museum, Berlin-Dahlem, W. Germany (B); Queensland Herbarium, Indooroopilly, Australia (BRI); Herbarium Australiense, Canberra City, Australia (CANB); Royal Botanic Garden, Edinburgh, UK (E); Conservatoire et Jardin Botaniques, Genève, Switzerland (G); Gray Herbarium of Harvard University, Cambridge, USA (GH); Royal Botanic Gardens, Kew, UK (K); Landesmuseum für Kärnten, Klagenfurt, Austria (KL); Kyoto University, Kyoto, Japan (KYO); Botanical Museum, Lund, Sweden (LD); Botanische Staatssammlung, München, W. Germany (M); Makino Herbarium, Metropolitan University, Tokyo (MAK); National Herbarium of Victoria, Melbourne, Australia (MEL); Lomonosov State University, Moscow, USSR (MW); New England Botanical Club Herbarium, Cambridge, USA (NEBC); National Herbarium of New South Wales, Royal Botanic Gardens, Sydney (NSW); Naturhistoriskariksmuseet, Stockholm, Sweden (S); University of Tokyo, Hongo, Tokyo, Japan (TI); University of Uppsala, Uppsala, Sweden (UPS); Institut für Systematische Botanik der Universität, Zürich, Switzerland (Z); Eidg. Technische Hochschule, Zürich, Switzerland (ZT).

Photographs of types and other important specimens were generously supplied by: the Komarov Botanical Institute of the Academy of Sciences, Leningrad, USSR (LE); New York Botanical Garden, New York, USA (NY).

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We would also like to thank the curators of the herbaria listed above for lending us their material.

Special terminology

In previous publications on *Sparganium* some terms have been widely used and have proved helpful although some are technically incorrect. The following specialized terms are used in this account:

Approximate – Referring to heads which overlap each other.

Axillary – Arising in the axis of a bract, exactly where the bract departs from the main stem, Fig. 1 (see also *Supra-axillary*).

Beak – The persistent part of the style.

Bract – A leaf subtending an inflorescence branch or head; it may be green and leaf-like or brownish and scale-like (Fig. 1).

Branch – A lateral stem bearing more than one head, Fig. 1 (see also *Peduncle*).

Endocarp – The innermost differentiated layer of pericarp, in other works often incorrectly called seed. Measurements made without the stalk.

Fruit – Measurements and shape descriptions made excluding the beak and the pedicel.

Head – An almost spherical, crowded group of sessile or subsessile flowers sharing a common base, in other works often called capitulum.

Inflorescence – The part of the plant bearing heads (see also *Head*).

Peduncle – The stalk bearing a single head (Fig. 1). The usage is technically incorrect (see p. 221) because the heads are compound inflorescences.

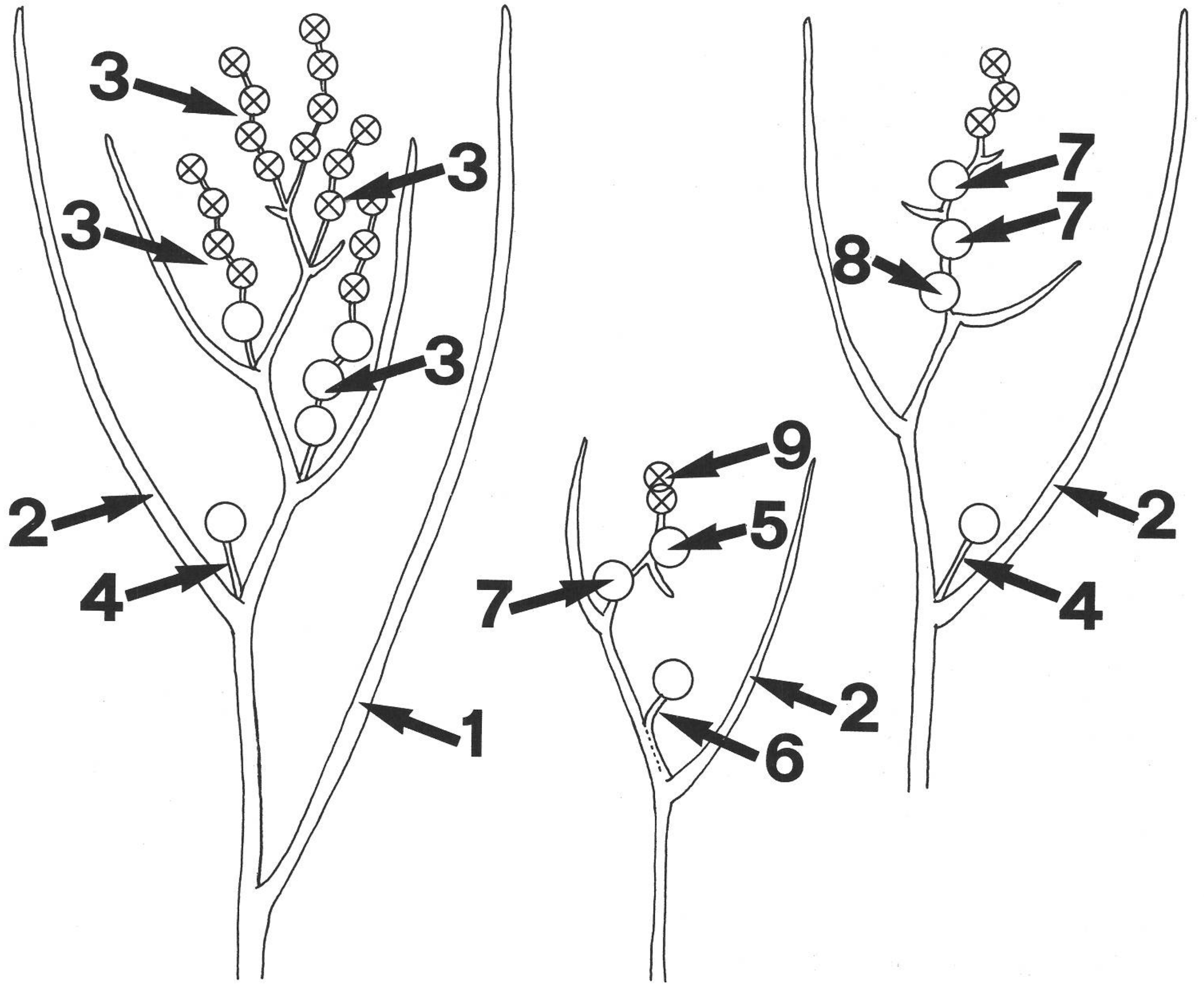


Fig. 1. Diagramatic representation of *Sparganium* inflorescences to illustrate special terminology: **1**. leaf; **2**. lowest bract; **3**. axillary branch; **4**. axillary peduncle; **5**. axillary head; **6**. supra-axillary peduncle; **7**. supra-axillary head; **8**. supra-axillary head concaulescent above the next node; **9**. approximate heads.

Perianth segments – The scale-like segments surrounding each flower. In other works sometimes called tepals; no distinction is made between bracts, bractioles, sepals or petals, see also p. 221.
Remote – Referring to heads which do not touch each other.
Supra-axillary – Arising on the main stem above the point where the bract departs from the main stem; branch, peduncle or head fused to main stem (concaulescent). Occasionally concaulescent up to or even above the next node, Fig. 1.

Classification

Sparganiaceae F. Rudolphi, Systema Orbis Vegetabilium, 27. October 1830.

One genus: *Sparganium.*

Following exhaustive investigations into the structure of the flower and inflorescence of *Sparganium* and *Typha,* Müller-Doblies, D. (1970) was convinced that *Sparganium* is so closely related to *Typha* that both should be united into the family *Typhaceae* (A. L. de Jussieu, Genera Plantarum, 25 October 1789).

We acknowledge that *Sparganium* and *Typha* share numerous features and that there is evidence of patristic relationship. However, they are clearly distinct from each other and have been so since, at least, the Oligocene (we rather distrust the records for both *Sparganium* and *Typha* from the Cretaceous). We therefore see no purpose in uniting both families; in fact, to do so will quite unnecessarily increase nomenclatural instability as nearly all floristic works in the last 150 years have recognized the two families as distinct.

Sparganium L. Species Plantarum, 971. 1 May 1753.

Type: Rydberg (N. Amer. Flora, 17: 5. 30 June 1909) designated *S. erectum* the type of the genus. This is unfortunate as *S. erectum* is based on a somewhat incomplete illustration in l'Obel, Plantarum Seu Stirpium Historia, 41. 1576 (see Cook 1985). We would prefer to base the genus *Sparganium* on *S. natans* which is, at least, based on an adequate specimen (sheet 1095/2, in Linn, see p. 234 and Cook 1985).

The following species were incorrectly described in the genus *Sparganium;* details are given by Cook (1985):
S. tenuifolia [sic] Poiret, Voyage en Barbarie, 2: 253. 1788, has been transferred to the genus *Carex* (under *Carex halleriana* Asso), see op. cit., p. 317.
S. pubescens Poiret, op. cit., has been transferred to the genus *Fuirena* (under *F. pubescens* (Poiret) Knuth).
S. trifidum Poiret in Poiret & Lamarck, Encyclopédie Méthodique, Botanique, Suppl. 4, 723. 1816, has been transferred to the genus *Dulichium* (under *D. arundinaceum* (L.) Britton).

Family and generic description

Aquatic or amphibious, monoecious, glabrous, perennial herbs.

Vessels with sclariform perforation plates; sieve tube plastids P-type with numerous cuneate protein crystalloids; oxalate raphides frequent; silica bodies absent.

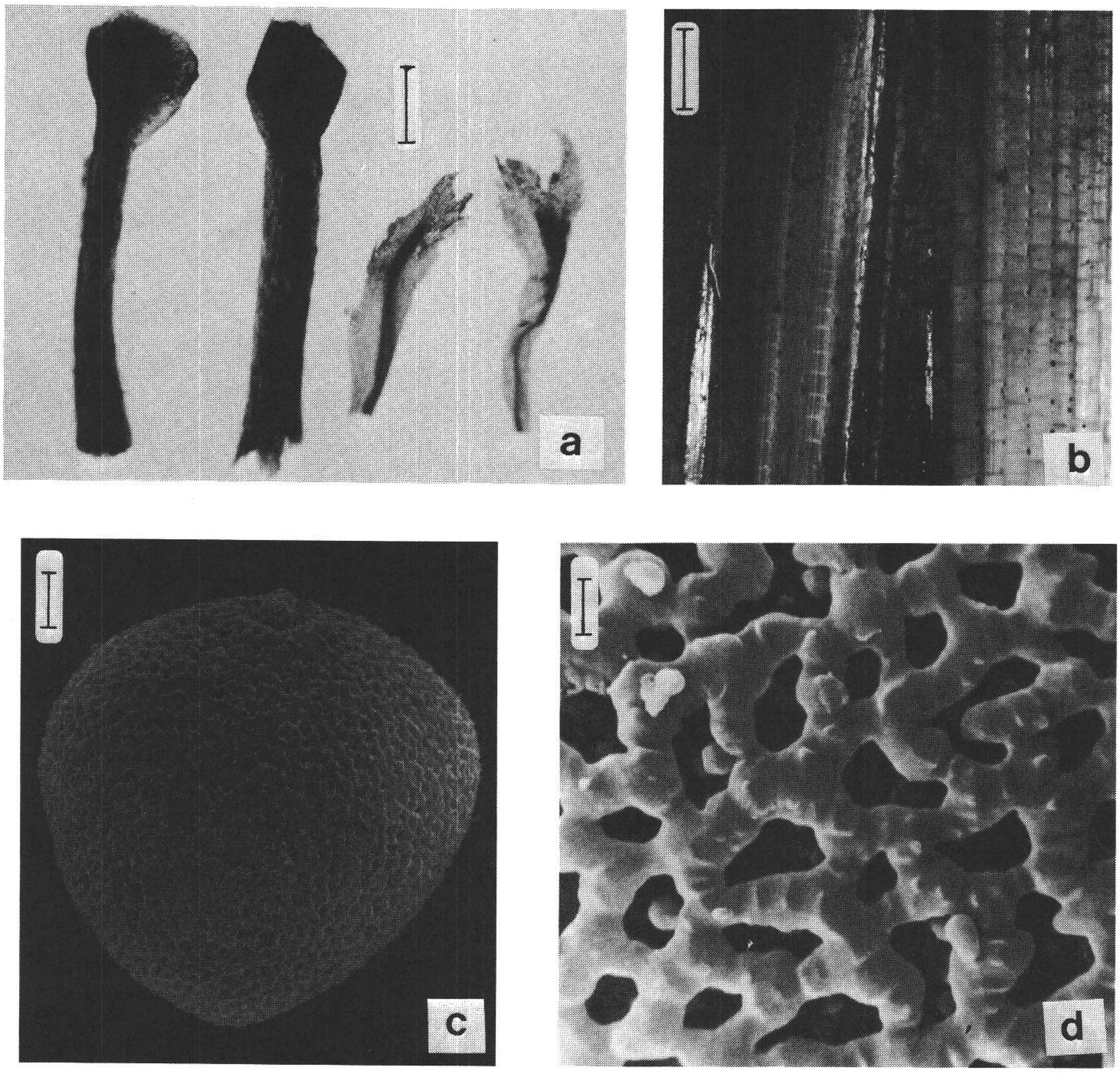


Fig. 2. *Sparganium:* a, perianth segments (left: *S. erectum* subsp. *neglectum;* right: *S. emersum* subsp. *emersum* scale bar: 1 mm); b, adaxial surface of leaf base of *S. erectum* subsp. *neglectum* showing glands, (scale bar: 1 cm); c, pollen grain of *S. erectum* subsp. *neglectum* (Scale bar: 5 μm); d, surface of pollen grain of *S. fluctuans* (scale bar: 1 μm).

Roots adventitious, fibrous, often inflated, simple or branched; root hairs not arising from specialised cells.

Stems stoloniferous to rhizomatous or cormous below, erect or floating and usually becoming emergent above, sympodial with reiterative monopodia, each monopodial part living for not more than 2 years.

Leaves distichous, exstipulate, sheathing below (sheath often tubular at base), not differentiated into petiole with blade, scale-like on underground parts otherwise linear; scale-like leaves brownish, translucent, thin and mostly remote; linear leaves submerged, floating or emergent, mostly basal and equitant or cauline and remote, more or less flattened to V-shaped or triangular in transverse section, sometimes carinate or keeled, with many longitudinal veins connected by transverse diaphragms; air chambers in 1 or usually more layers; stomata paracytic, the surrounding cells with sometimes intersecting oblique divisions; margins entire; apex rounded or apiculate.

Flowers unisexual, arranged tightly in 2 or 3 compact racemes in globose heads; heads usually unisexual, sessile or pedunculate, axillary or supra-axillary (concaulescent), or occasionally concaulescent up to or beyond the next node (Fig. 1), arranged in simple or branched racemes with female heads proximal to the males or occasionally the lowest branch bearing male heads only; male heads usually remote below becoming compacted above, caducous but naked axis usually persisting; inflorescence bracts leaf-like below, becoming reduced and scale-like in the middle and eventually absent above.

Floral bract usually indistinguishable from perianth segments; bracteoles absent.

Perianth segments radiate, (1–)3–4(–6), dry, scale-like, usually widened above (Fig. 2a), often irregular in shape and arrangement, sometimes superposed and sometimes united below.

Female flowers without staminodia, without nectaries; ovary superior of 1–3 (in fossil species to 7, Fig. 4a) united carpels; style 1, beak-like, often persisting in fruit or reduced; stigmas 1–3 (or perhaps more in fossil species), papillose, dry; ovules solitary, ventrally anatropous, pendulous, bitegmic with the outer integument longer than the inner, crassinucellar; megagametophyte development Polygonum-type; embryogenesis Onograd-type endosperm Helobial; embryo linear, straight and large, without chlorophyll.

Made flowers tightly packed in heads and difficult to recognise as individual flowers; stamens 1–8, often superposed; filaments mostly free, elongate, falling after anthesis; connectives somewhat widened above; anthers basifixed, oblong, 4-microsporangiate, dehiscing neutrorsly through longitudinal slits; endothecium with spiral thickening; tapetum 8-nucleate, at first amoeboidal, later pseudo-periplasmoidal; microsporogenesis successive; pollen single, monoporate, ulcerate, spheric to ellipsoidal (Fig. 2c), the surface reticulate (Fig. 2d), 2-cellular when released; pistillodia absent; nectaries absent.

Fruits sessile to shortly stalked, drupe-like, crowded in a burr-like head but released singly; mesocarp spongy; endocarp hard, with longitudinal ridges or smooth, with distinct micropylar plug.

Seeds with a membranous testa and starchy endosperm surrounding the embryo.

Distribution

The genus *Sparganium* is found almost throughout the temperate and arctic regions of the northern Hemisphere. In the Tropics there are isolated occurrences in the mountains of central Sumatera and New Guinea. In the southern temperate regions it occurs in southeastern Australia and New Zealand (see Fig. 3). Most species are found in the northern boreal zone and the regions of greatest species diversity are in North America and eastern Asia. There are no local endemics and nearly all species have large more or less continuous distribution patterns; only *S. glomeratum* (see p. 242) and *S. subglobosum* show major disjunctions. *Sparganium* seems to be absent from most of the Himalayas, being recorded only in the extreme west and extreme east. All fossil finds are within the range occupied by *Sparganium* today. Only one species seems to have become established outside its native area in recent times; it is *S. erectum* which is perhaps introduced in Australia.

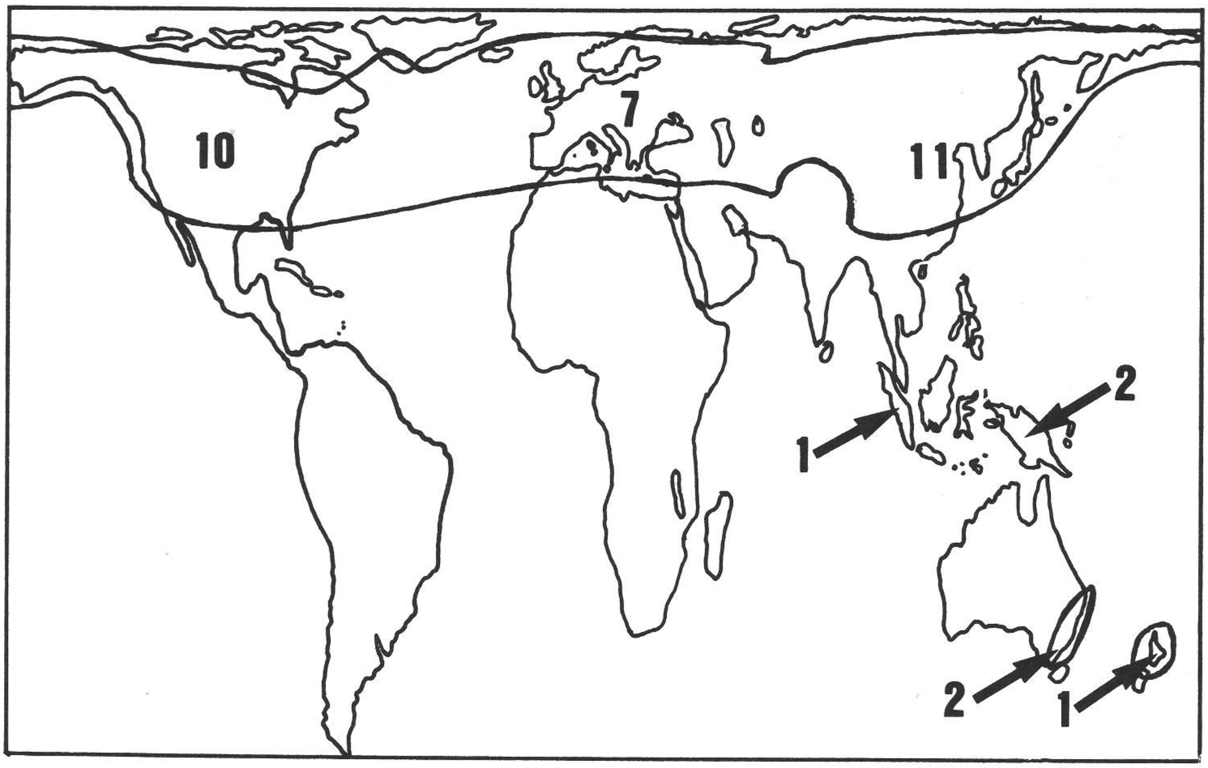


Fig. 3. World-wide distribution of *Sparganium*. The numbers represent the number of species in that region.

Fossils

Records of pollen and fruits have been reported from the Cretaceous. These records are based on very doubtful evidence although Mai (1984) is inclined to accept the report of Velenovský & Viniklář (1926) of supposed fruiting heads of *Sparganium* from Czechoslovakia. The earliest reliable record of *Sparganium* in an imprint of an inflorescence from the Middle Eocene of Wyoming named *S. antiquum* (Newberry) Berry. In his paper Berry (1924) draws a reconstruction which we feel must be wrong, the lower portion based on *Pontederites hesperia* Knowlton should not have been combined with the inflorescence which is probably *Sparganium*. We have not, however, examined the original fossil material. Without qualification Muller (1984) cites the Paleocene for the first *Sparganium* fruits and for Typhales pollen.

By the Oligocene there is fossil material from the Old World that is convincingly attributable to the genus *Sparganium*, both pollen (Abuziarova 1970) and macrorests. A superficial search through the literature has revealed that there are at least 44 fossil species of *Sparganium* described. At least 34 of them are certainly *Sparganium* but we are not convinced they are all distinct from each other or that they are all distinct from recent species.

Among the fossil species both subgenera (*Sparganium* and *Xanthosparganium*) are already distinct by the Oligocene. Most of the Oligocene species are clearly distinct from the species of today. The endocarps although shorter than some recent species were often much wider with numerous locules (*S. balticum* Dorofeev (Fig. 4a), 4–7, locules; *S. multiloculare* Reid & Chandler, 2–5; *S. sobolevii* Dorofeev, 2–4, but surface smooth). Another species *S. costatum* Dorofeev from Oligocene beds near Tomsk had a

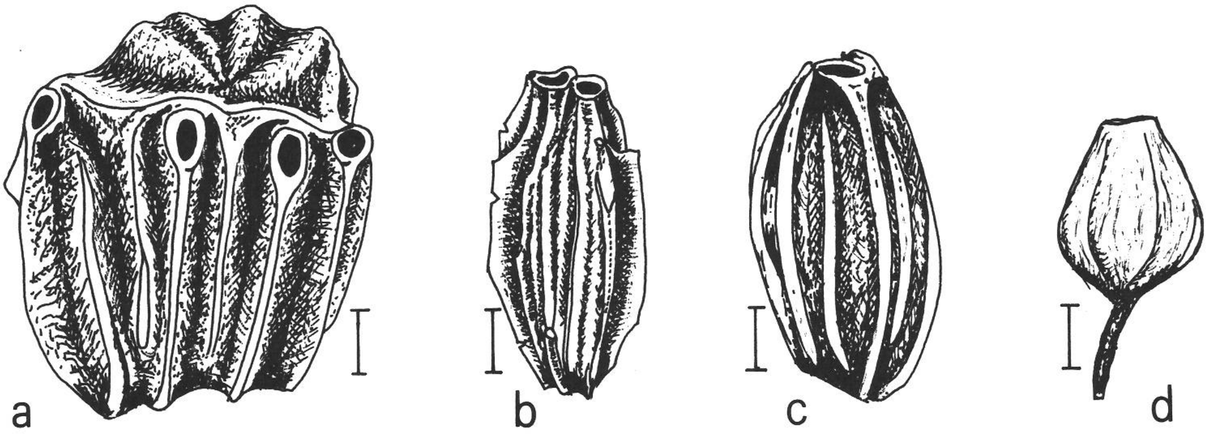


Fig. 4. Drawings of *Sparganium* endocarps: a, *S. balticum;* b, *S. costatum;* c, *S. erectum* subsp. *neglectum;* d, *S. emersum* (scale bar: 1 mm).

winged endocarp quite unlike any recent species (Fig. 4b). By the Miocene the endocarps of the majority of the described fossil species are very difficult to distinguish from recent species and even Dorofeev (1979) who has himself described no less than 33 fossil species recognises *S. erectum* (Fig. 4c) as going back to the Miocene.

Anatomy and morphology

a) Vegetative parts

The general anatomy and morphology of the vegetative parts of *Sparganium* are well-summarized by Loew in Kirchner et al. (1908) and by Meyer in Solereder & Meyer (1933); the essential features of diagnostic value have been incorporated into the formal descriptions.

The growth is essentially sympodial, each horizontal axis (rhizome or stolon depending on the species) is a monopodium which bends upright at the tip where it becomes thickened and develops into a hard rather woody corm. After the first winter each corm usually develops several axillary monopodia and then dies with or without developing an inflorescence. Photosynthetic leaves develop only from corms; the rhizomes or stolons bear non-photosynthetic, scale-like leaves. The leaves are distichous which has the consequence that the lateral monopodia tend to leave the mother corm at angles approaching 180°.

The lateral monopodia grow horizontally through their subtending leaves, they do not appear to be dorso-ventrally organised and do not, under normal conditions, branch. If damaged these horizontal axes are capable of further growth through the development of buds in the axils of the scale leaves. Stems and roots are ventilated internally by a system of large chambers bridged by porous diaphragms.

Germination takes place submerged in water. The juvenile leaves of all species are aquatic and cannot tolerate emergence. Depending upon the species and local ecological conditions the leaves may remain submerged or, later in ontogeny, become floating or emergent. During the juvenile phase it is not possible to distinguish the species. The submerged leaves have a relatively simple system of longitudinal compartments with porous transverse diaphragms. The compartments between the diaphragms are partly schizogenous and partly lysigenous in origin.

The architecture of *Sparganium* leaves has been described by Kaul (1972, 1973, 1976). In a large and erect species such as *S. eurycarpum* the emergent leaves are deltate in transverse section with palisade tissue on all three sides. Within the leaf every fourth diaphragm has a vascular bundle and is heavily photosynthetic, the other diaphragms are translucent and consist of thin stellate cells (actinochyma). Floating leaves are isobilateral with adaxial palisade only and there are even more thin, essentially non-photosynthetic diaphragms than thick photosynthetic ones.

If all diaphragms were thick and heavily photosynthetic and had small intercellular spaces, the amount of light reaching the interior would be diminished and as Kaul (1972) suggests this pattern of alternating translucent and photosynthetic diaphragms allows the linear leaves of *Sparganium* with a relatively small surface area to utilise more light than leaves without such internal structures.

On the adaxial surface of the upper portion of the sheathing part of the leaf there are curious longitudinal rows of emergent glandular cells (Fig. 2b). These glands are brownish and are sometimes visible to the naked eye. In *Typha* similar looking glands secrete slime, this does not appear to be the case in *Sparganium*. The statement by Graebner (1900) that these glands are lacking in *Sparganium* is false.

b) Floral parts

The morphology of the floral parts of *Sparganium* has been exhaustively described by Müller-Doblies, Ute (1969), Müller-Doblies, Dietrich (1970) and Müller-Doblies, Ute & Müller-Doblies, Dietrich (1977). The primary inflorescence is a simple or branched raceme, the female and lateral male heads are twice racemose but the terminal male heads are three-times racemose or consist of several virtually united lateral heads. The structure of the heads can be followed only by examination of the total ontogeny.

The female flowers have as a rule one bract and (2–)3–4(–5) perianth segments. There is no fundamental difference between the bract and the perianth segments (Fig. 2a); differences such as size, innervation and ontogenetic succession may be reduced and in extreme cases totally de-differentiated. The male flower is essentially like the female but has 1 to 8 stamens and lacks traces of pistillodium.

The heads are usually unisexual but some female flowers in essentially male heads are not uncommon, they are, however, very rarely fertile. Heads partly male and partly female are uncommon. Intersex flowers are found from time to time but the female component is usually sterile. The plants are usually bisexual but in most species pure male plants have been found.

Although morphologically incorrect, the term "branch" is used in this and all other known accounts for axillary shoots bearing more than one head and the term "peduncle" for axillary shoots terminating in solitary heads. The "peduncles" are strictly speaking lateral branches because they are branched below the inflorescence, each head is, strictly speaking, made up of two or three compact racemes (dicephalus or tricephalus). Genuine terminal heads were not found by Müller-Doblies, Ute (1969).

Chromosomes

The published chromosome numbers are presented on Table 1; because of the high uniformity no efforts have been made to check voucher specimens and we have not made any chromosome investigations ourselves. About 65 plants have been counted

Table 1. *Sparganium* chromosome numbers.

Name (in publication)	Number	Locality	Voucher	Ill.	Reference
S. angustifolium					
(*angustifolium*)	$2n=30$	None given, presumably Scandinavia	?	–	Löve & Löve 1942
(*angustifolium*)	$2n=30$	Iceland	?	–	Löve & Löve 1956
(*affine*)	$2n=30$	None given, presumably Poland	?	?	Bijok & Młynek 1965
(*angustifolium*)	$2n=30$	Canada: Manitoba, Macbride Lake, s.d., *J. C. Ritchie 1075*	WIN	–	Löve & Ritchie 1966
(*multipedunculatum*)	$2n=30$	Canada: Manitoba, New Iceland, Vannes, s.d., *Löve & Löve 5566*	WIN	–	Löve & Löve 1975
(*angustifolium*)	$2n=30$	Czechoslovakia: Slovàkia, Západné Tatry, Rohačské plesá, s.d., *Májovský & Murin s.n.*	SLO	–	Murin & Májovský 1978 b
(*angustifolium*)	$2n=30$	Canada: Manitoba, Brokenhead River, near Vivian, s.d., *Löve & Löve 5272*	WINor COLO	–	Löve & Löve 1981
S. emersum					
(*simplex*)	$2n=30$	Germany: Schleswig-Holstein	?	?	Scheerer 1940
(*simplex*)	$2n=30$	None given, presumably Scandinavia	?	?	Hagerup 1941
(*simplex*)	$2n=30$	None given, presumably Scandinavia	–	–	Löve & Löve 1942
(*simplex*)	$2n=30$	USSR: Kamchatka, near Kozyresvsk, 24 July 1959, *Sokolovskaya s.n.*	LECB	–	Sokolovskaya 1963
(*simplex*)	$2n=30$	Poland	?	?	Bijok & Młynek 1965
(*simplex*)	$2n=30$	Canada: Queen Charlotte Islands, *? coll.*	?	?	Taylor & Mulligan 1968
(*simplex*)	$2n=30$	USSR: Leningrad Distr., Lake Buoksa, s.d., *Sokolovskaya s.n.*	LECB	–	Sokolovskaya 1972
(*emersum*)	$2n=30$	Czechoslovakia: Západné Beskydy, Zázirivá, s.d.,	SLO	–	Váchová in Májovský 1976
S. erectum s.l.					
(*ramosum*)	$2n=30$	Germany: Schleswig-Holstein, an der Kronsbek bei Neudorf, s.d., *? coll.*	?	+	Wulff 1938
(*ramosum*)	$2n=30$	None given, presumably Scandinavia	–	–	Löve & Löve 1942
(*ramosum*)	$2n=30$	None given, presumably Poland	?	?	Bijok & Młynek 1965
(*erectum*)	$2n=30$	Denmark: Bestmose Isl. of Bornholm, s.d., *K. Larsen 6039-Bn19*	AAU	–	Larsen 1965
(*erectum*)	$2n=30$	Netherlands: Utrecht, Vuntus, nr. Loodsrecht, s.d., *Gadella & Kliphuis s.n.*	U	–	Gadella & Kliphuis 1973

(*erectum*)	2n = 30	Czechoslovakia: Jur pri Bratislave, Podunajská nižina, Šur, s.d., *V. Feráková s.n.*	SLO	–	Feráková in Májovský 1974
(*ramosum*)	2n = 30	India: Kashmir, Nagin Lake, s.d., *Mehra & Pandita 73*	PAN	–	Mehra & Pandita 1979
subsp. ***erectum***					
(*polyedrum*)	2n = 30	None given	–	–	Löve & Löve 1948
(*erectum*)	2n = 30	Czechoslovakia: Bratislava, Podunajská nižina, s.d., *V. Feráková s.n.*	SLO	–	Murin in Mákovský 1978 a
subsp. ***microcarpum***					
(*microcarpum*)	2n = 30	None given	–	–	Löve & Löve 1948
subsp. ***neglectum***					
(*neglectum*)	2n = 30	None given	–	–	Löve & Löve 1948
(*neglectum*)	2n = 30	Bulgaria: Smoljan, "Big Lake", 13 Sept. 1963 *? coll.*	?	–	Kožuharov & Kuzmanov 1964
(*neglectum*)	2n = 30	Poland: pow. Cieszyn, Debowiec, s.d., *? coll.*	?	+	Bijok & Adamkiewicz 1971
(*neglectum*)	2n = 30	Poland: pow. Cieszyn, stawy Ochaby, s.d., *? coll.*	?	+	Bijok & Adamkiewicz 1971
(*neglectum*)	2n = 30	Poland: pow. Milicz, stawy Milicz, s.d., *? coll.*	?	+	Bijok & Adamkiewicz 1971
subsp. ***stoloniferum***					
(*stoloniferum*)	2n = 30	None given, presumably Japan	–	+	Harada 1949
(*stoloniferum*)	n = 15 II	None given, presumably Japan	–	+	Harada 1949
S. eurycarpum	2n = 30	Canada: Manitoba, Brokenhead River, Vivian, *Löve & Löve s.n.*	WINor COLO	–	Löve & Löve 1981
subsp. ***coreanum***					
(*macrocarpum*)	2n = 30	None given, presumably Japan	–	+	Harada 1942
(*coreanum*)	2n = 30	None given, presumably Japan	–	+	Harada 1942
S. fallax					
(*yamatense*)	2n = 30	None given, presumably Japan	–	+	Harada 1949
(*yamatense*)	n = 15 II	None given, presumably Japan	–	+	Harada 1949
S. glomeratum					
(*glomeratum*)	2n = 30	None given, presumably Scandinavia	–	–	Löve & Löve 1942
(*glomeratum*)	2n = 30	None given, presumably Japan	–	+	Harada 1949
S. gramineum					
(*friesii*)	2n = 30	None given, presumably Scandinavia	–	–	Löve & Löve 1942

Table 1 (continued)

Name (in publication)	Number	Locality	Voucher	Ill.	Reference
S. hyperboreum					
(*hyperboreum*)	2n = 30	None given, presumably Iceland	–	–	Löve & Löve 1948
(*hyperboreum*)	2n = 30	Greenland	?	?	Jörgen et al. 1958
(*hyperboreum*)	2n = 30	Canada: Queen Charlotte Islands, s.d., *? coll.*	?	?	Taylor & Mulligan 1968
(*hyperboreum*)	2n = 30	USSR: Anadyrskoe, Nagorbe, R. Komarinasa, s.d., *? coll.*	?	–	Zhukova & Tikhonova 1971
(*hyperboreum*)	2n = 30	USSR: Rud Jagodnyj, s.d., *? coll.*	?	–	Zhukova & Petrovsky 1976
(*hyperboreum*)	2n = 30	USSR: northern Pekul'veyem River, s.d., *? coll.*	?	–	Zhukova 1980
(*hyperboreum*)	2n = 30	Canada: north-east	?	?	Gervais 1981
(*hyperboreum*)	2n = 30	Canada: Manitoba, New Iceland, opposite Hekla Island, s.d., *Löve & Löve 3329*	WINor COLO	–	Löve & Löve 1981
S. japonicum					
(*japonicum*)	2n = 30	None given, presumably Japan	–	+	Harada 1949
(*japonicum*)	n = 15 II	None given, presumably Japan	–	+	Harada 1949
S. natans					
(*minimum*)	2n = 30	Germany: Schleswig-Holstein, Schwabstedter Moor, s.d., *? coll.*	?	–	Wulff 1938
(*minimum*)	2n = 30	Iceland	?	–	Löve & Löve 1956
(*minimum*)	n = 15	Canada: Queen Charlotte Islands, 9 August 1964, *Calder & Taylor s.n.*	G	–	Taylor & Mulligan 1968
(*minimum*)	2n = 30	Poland: pow. Giżycko, Bagiennice, s.d., *? coll.*	?	+	Bijok & Adamkiewicz 1971
(*minimum*)	2n = 30	Poland: pow. Mrągowo, Łukniany, *? coll.*	?	+	Bijok & Adamkiewicz 1971
(*minimum*)	2n = 30	Czechoslovakia: Západné Beskydy, Zázriva, s.d., *Králik & Váchova s.n.*	SLO	–	Váchova in Májovský 1976
(*minimum*)	2n = 30	Canada: Manitoba, Porcupine Mt., s.d., *Löve & Löve 3280*	COLO		Löve & Löve 1981
(*minimum*)	2n = 30	Finland: Ab Nauvo, *Seili Arohonka, 177208*	TUR	–	Arohonka 1982
S. subglobosum					
(*stenophyllum*)	2n = 30	Japan: Botanic Garden of Kyoto University, s.d., *? coll.*	?	+	Harada 1949
(*stenophyllum*)	2n = 45	Botanic Garden of Kyoto University, s.d., *? coll.*	?	+	Harada 1949
(*stenophyllum*)	n = 15 II	Japan: Prov. Kida of Sikoku, s.d., *? coll.*	?	+	Harada 1949
(*stenophyllum*)	2n = 30	Japan: Prov. Musasi, Inada-Inoborito s.d., *? coll.*	?	+	Harada 1949
(*stenophyllum*)	n = 15 II	Japan: Prov. Musasi, Inada-Inoborito, s.d., *? coll.*	?	+	Harada 1949

and with one exception all have $2n=30$. The exception was a single sample of *S. subglobosum* from the botanic garden of Kyoto University, Japan; it had $2n=45$ but Harada (1949) mentioned that other plants of the same species from the same place had $2n=30$. Meiosis has been reported from six plants, all had 15 bivalents and no irregularities.

The chromosomes of *Sparganium* are (0.7–)0.9–1.5(–2.0) µm long and can be classified as relatively small. Some published illustrations show more or less equal-sized chromosomes while others show differentiation into shorter and longer. Most illustrations do not clearly show the centromere, however, Bijok & Adamkiewicz (1971) found about half the chromosomes to be metacentric while the other half was acrocentric with an arm ratio of about 1:3.

Floral biology

The flowers are congested into globose unisexual heads with males borne above females. Exceptionally, some essentially male heads have female or intersex flowers which rarely develop fruit; male flowers in essentially female heads are very rare. Occasionally part of the head is male and part female.

Within a head, anthesis is more or less simultaneous. The heads are clearly protogynous in spite of the fact that many early publications, including Graebner (1900) have reported *Sparganium* to be protandrous. In some of the large branched plants the lowest female head has frequently passed its receptive stage before the first male heads shed pollen. The lowest female heads sometimes bear less fruit than the others; this is particularly noticeable in *S. erectum.* No agamospermous or self-incompatibility mechanisms have been found.

Pollen transfer is by wind. *S. erectum* is occasionally visited by representatives of syrphid flies of the Melanostoma-Platycheirus group according to Leereveld (1984). Pollen is a principle source of food for these flies and analyses of the crop and gut contents showed that the syrphid *Pyrophaena granditarsa* may feed almost exclusively on the inflorescence of *S. erectum* in northwestern Holland. Pinkess (1980) noted that not only syrphids but that bumble bees and honey bees also collect *Sparganium* pollen. Pinkess (1980) and Leereveld (1984) claim that zoophilous pollination may sometimes result from this activity but have not tested it experimentally. We have observed insects collecting pollen on *S. erectum* but female heads are visited very rarely and then for very short times.

We have studied pollen flow in a stand of *S. erectum* in an artificial pool at the University of Zürich by emasculating plants at known distances from the nearest male inflorescence and recording the number of seeds set. Emasculated plants separated from the nearest male inflorescence by a distance of 1 m set less than 25% of the seeds set of intact plants, though even plants separated by 2 m or more set some seeds. The significance of this finding in *S. erectum* which forms large clones is unclear. Although no precise measurements were made it seems that the stigmas remain receptive for at least two days and that wind pollination over distances of several metres or more may occur.

Dispersal

Both Guppy (1906) and Praeger (1913) observed that the fruits of *Sparganium* may remain floating for more than a year under experimental conditions. The fruits are coated with a hydrophobic material soluble in detergent. Our observations in nature are that after being frozen in ice the exocarp usually ruptures and the spongy mesocarp soon decays in spring liberating the endocarp which sinks. In nature the fruits rarely remain floating for more than 6 months.

Floating fruits may be dispersed by water movements induced by gravity or by wind. Being hydrophobic the fruits readily stick to objects in the water and some fruits are probably dispersed by boats and epizoically on aquatic animals, particularly larger birds. The fruits of *Sparganium* are important food for water birds (Martin & Uhler 1939). In the summary of his work Guppy (1906) stated that seeds that have passed through the alimentary canal of a duck have a higher germination rate; Cook (1962) found no difference in germination rate in seed fed to chickens.

Ecology

Sparganium is found in a wide variety of permanent or seasonally aquatic habitats. The seedlings of all species develop only when submerged in water and thus standing water is necessary for establishment by seed; the rhizomes and corms of some species can, however, perennate terrestrially so that *Sparganium* may inhabit bogs or moors without standing water. In all species the leaves die down in winter and the plants hibernate embedded in the substrate as corms or rhizomes.

The germination and seedling development of *S. erectum* are described and illustrated by Cook (1962). The seed, or more correctly endocarp, is very uniform in structure throughout the genus and is well described by Dietz (1887) and Saccardo (1895). The seed is enclosed in a hard scleridial endocarp with a plugged micropyle. The plug has a somewhat complicated development described by Hegelmaier (1874). Germination only takes place under water or in a fully saturated atmosphere and appears to be fully dependent on dislodging the micropyle or breaking the endocarp. No dormancy has been reported. The first stage in germination consists of an elongation of the cotyledon stalk. This elongation is due to the seed taking up water and can be demonstrated on dead seeds. The first visible indication that the second or vital stage has started is that the tip of the cotyledon stalk turns green and starts swelling as the embryo grows. If seeds without micropylar plugs are left in the dark the cotyledon stalk elongates in a somewhat disorganized spiral without any growth of the embryo. If a seedling is taken from the dark and put into the light there is growth of the embryo and orientation toward gravity. This acquired geotropic response is irrespective of the direction of light and is retained if seedlings are replaced in the dark.

The seedlings of all species of *Sparganium* are very similar and it is not possible to distinguish the species on the basis of the juvenile leaves. *S. natans* develops flowers in the juvenile phase and is thus essentially a submerged species. Other species, such as *S. angustifolium* or *S. gramineum,* develop floating leaves after the submerged juvenile stage; the floating leaves have clearly differentiated ab- and adaxial surfaces. These species flower at the floating-leaved phase. Others, such as *S. erectum* and *S. eurycarpum,* develop erect emergent leaves directly after the submerged juvenile phase. The erect, emergent leaves also show ab- and adaxial differentiation and may be phylogenetically tied to floating leaves. These species flower only at the erect emergent-leaved phase and they are essentially terrestrial plants following their brief aquatic juvenile phase. Most other species occupy positions intermediate between these three extremes (submerged, floating and erect) and show varying degrees of "aquaticness".

Species such as *S. emersum, S. fallax* and *S. subglobosum* show considerable plasticity and can flower in floating and emergent phases.

The flexibility in leaf form of some species has enabled them to occupy places subject to rapid changes in water level. The relatively deep roots, rhizomes and stolons also make the plants difficult to dislodge and they are capable of withstanding severe floods and spates. These very phenotypically plastic species are usually poor competitors and rarely build large stands. The less flexible species, either erect-emergent, floating or submerged, are relatively strong competitors and may become dominant over large areas.

The evolutionary trend from small aquatic species to large terrestrial species is clear and is reflected in the order of species in this work. However it is difficult to distinguish between the processes of paedogenesis (sexual maturity in the juvenile phase) and neoteny (retention of juvenile characters in the adult). Although it is popular today to interpret the evolution of flowering plants in terms of reduction, there is no evidence that *S. natans* is more than a neotenous or paedogenetic derivative of *S. eurycarpum,* in terms of life-form it may well be the most primitive.

Parasites and animal feeders

Despite the fact that no comprehensive survey has been attempted, an extraordinary large number of parasites and animal feeders have been recorded on *Sparganium* (13 beetles, 7 moth larvae and 24 fungi). Cook (1962) presented a list based on work done in Britain on *S. erectum* and Müller-Doblies, U. & Müller-Doblies, D. (1977) in Hegi's Flora of Central Europe extended and added to this list.

a) Animal feeders or parasites

Coleoptera. Chrysomelidae: *Donacia appendiculata* Ahr., *D. aquatica* L., *D. bicolor* Zschach, *D. cineria* Hbst., *D. marginata* Hoppe, *D. simplex* F., *D. sparganii* Ahr., *D. tomentosa* Ahr., and *D. vulgaris* Zschach; Cryptophagidae: *Cryptophagus sparganii* St.; Curculionidae: *Thryogenes festucae* Hbst.; Mycetophagidae: *Telmatophilus sparganii* Ahr. (a monotypic genus) and *Typhaea caricis* Ol.

Lepidoptera. Noctuidae: *Archanara algae* Esp., *A. sparganii* Esp., *Eustrotia candicula* Schiff., *Phytometra festucae* L.; Pyralididae: *Haemylis sparganiella* Thb., *Hydrocampa stagnata* Don., and *Laelia coenosa* Hb. Several aquatic molluscs, some rodents, ruminants and birds eat the shoots, rhizomes and fruits but none apparently are dependent on *Sparganium.*

b) Plant parasites (including some essentially saprophytic species that are sometimes weakly parasitic)

Chytridomycetes: *Cladochytrium sparganii-ramosii* Büsgen, and *Urophlyctis ramosa* Büsgen.

Ascomycetes: *Acanthophiobolus helmithosporus* Berl., *Leptosphaeria clava* (Cooke & Auersw.) Sacc., *L. duplex* (Sow.) Sacc., *L. riparia* Sacc., *L. sparsa* (Fuck.) Sacc. var. *meizospora* Feltg., *Metasphaeria sparaganii* Fautrey, *Phaeosphaeria eustoma* (Fuck.) L. Holm, *P. typharum* (Desm.) Karsten, *Pleospora sparganii* Cooke, *Sordaria sparganicola* Phill. & Plowr., *Sphaerella taediosa* Pass., and *S. thais* Sacc.

Deuteromycetes: *Hendersonia sparganii* Niessl., *Macrosporium sparganii* Lindau, *Ramularia sparganii* Lindroth, *Septoria sparganii* Pass., and *Stagonospora sparganii* (Fuck.) Allescher.

Basidiomycetes: Agaricales: *Psathyrella typhae* (Kalchbr.) Pears & Dennis; Tremellales: *Dacryopsis typhae* Höhn; Uredinales: *Uromyces sparganii* Clint & Pech.; Ustilaginales: *Entyloma sparganii* Lagerh., and *Melanotaenium sparganii* Lagerh.

Applied aspects

Sparganium is not of great economic importance. In northwestern Europe *S. erectum* and *S. emersum* are sometimes considered to be undesirable weeds in small rivers, canals or drainage ditches. However, the negative aspects (reduction of water flow and eventual blockage) should be weighed against the benefits, as *Sparganium* may protect the banks from erosion. Also it is a valuable food for wild fowl and offers shelter to numerous aquatic or wetland animals. The Klamuth Indians of Oregon used the starchy corms for food but only for subsistence. It is not given important medicinal properties in western Herbals and Pharmacopoeias. In China, according to Duke & Ayensu (1985), it is used to dissolve clots or correct enterrhagia, also as an abortifacient, emmenagogue, lactagogue, sedative and to stimulate blood circulation and to cure cancer of the cervix and liver, lymphosarcoma and relieve abdominal and chest pains. We have no first-hand experience of its efficacy. Although often found in decorative pools it is rarely offered for sale in plant catalogues.

Key to Sparganium

1A. Perianth segments more or less translucent, without a thickened dark-brown to black pad of tissue near the apex; margin at apex distinctly erose (see Fig. 2a) .... subgenus *Xanthosparganium*
  2A. Distal part of leaves and lower bracts convex or flat but never keeled or triangular in transverse section, usually floating or submerged.
    3A. Male heads 1–4, crowded and overlapping at anthesis (appearing as 1 elongated head terminating the main axis); beak of fruit absent or more or less erect, not curved or deflexed, inflorescences simple.
      4A. Styles less than 0.5 mm long; stigmas not more than 0.5 mm long; beaks absent or nipple-like .... 1. *S. hyperboreum*
      4B. Styles more than 0.5 mm long; stigmas more than 0.5 mm long; beaks elongate (not nipple-like), at least 0.5 mm long.
        5A. Lowermost bract shorter than or scarcely exceeding the inflorescence; all female heads usually axillary ..... 2. *S. natans*
        5B. Lowermost bract very much longer than the inflorescence; some female heads usually supraaxillary.
          6A. Male heads clearly separated from the uppermost female head; female heads remote (not congested); stigmas usually more than 0.8 mm long; anthers usually more than 0.9 mm long .... 3. *S. angustifolium*
          6B. Male heads contiguous with the uppermost female head; the upper female heads crowded; stigmas not more than 0.8 mm long; anthers usually less than 0.9 mm long. 4. *S. glomeratum*

3B. Male heads 2–6, the lower ones remote, not overlapping at anthesis; beak of fruit usually curved or deflexed, inflorescences branched or simple.

  7A. Stigmas not exceeding 0.8 mm long; beaks not more than 1.5 mm long; fruit shiny, not more than 3 mm long; endocarp not more than 2.5 mm long; leaves usually less than 5 mm wide; inflorescence simple or with one branch (Eurasia) .... 5. *S. gramineum*

  7B. Stigmas 1 mm or more long; beaks 2 mm or more long; fruits dull, 3 mm or more long; endocarp 3 mm or more long; leaves usually more than 4 mm wide; inflorescence usually with more than one branch N. America) .... 6. *S. fluctuans*

2B. Distal part of the leaves and lower bracts keeled or triangular in transverse section, usually erect and emergent.

  8A. Male heads 1–2, when 2 then overlapping at anthesis; lowermost male head contiguous with uppermost female head (without a sterile internode); stigmas up to 0.8 mm long .... 4. *S. glomeratum*

  8B. Male heads 3–10, at least the lower one remote at anthesis; lowermost male head separated from uppermost female head by a sterile internode; stigmas more than 0.8 mm long.

    9A. Female heads usually remote, the lower often pedunculate; lower bracts shorter or about equalling the inflorescence; fruit beak shorter than the fruit body in length; fruit body 3.5–5.5 mm long .... 7a *S. emersum* subsp. *emersum*

    9B. Female heads crowded and usually sessile (the lowermost sometimes remote and pedunculate); lower bracts conspicuously longer than the inflorescence; fruit beak equal to or exceeding the fruit body in length; fruit body 3–4 mm long (N.E. America) 7b. *S. emersum* subsp. *acaule*

1B. Perianth segments not translucent, with a thickened darkbrown to black pad of tissue near the apex; margin at apex emarginate to entire or nearly so (see Fig. 2a) .... subgenus *Sparganium*

  10A. Stigmas less than 1.5 mm long; inflorescence simple or branched, when branched rarely more than 2 branches bear female heads; endocarps more or less smooth .... *S. americanum* group

    11A. At least 2 female heads supra-axillary and at least one concaulescent up to or beyond the next internode (inflorescence simple; female heads widely spaced) .... 8. *S. fallax*

    11B. Female heads axillary or on lateral branches, occasionally 1 head supra-axillary but never concaulescent to next internode (inflorescence simple or branched; female heads spaced or upper approximate).

      12A. Fruit obovoid to almost globose, shiny and light brown and below, subsessile or with an up to 1 mm long pedicel; endocarp rarely more than 3 mm long; stigma rarely more than 1 mm long; lowermost bract shorter or as long as the inflorescence (inflorescence usually branched, lowest branches bearing both male and female heads or male heads only) (E. Asia, Australasia) 9. *S. subglobosum*

      12B. Fruit ellipsoidal or fusiform, shiny or dull above and dull below, with pedicels more than 1 mm long; endocarp 3.5 mm or more long; stigma usually more than 1 mm long; lowermost bract very much longer than the inflorescence (inflorescence branched or simple).

13A. Fruits less than 5 mm long with beaks less than 4.5 mm long, dull and dark-brown above below; fruiting heads less than 25 mm diameter; endocarp 4 mm or less long.

14A. Upper female heads approximate; fruit without dark brown glands, not pitted; beak not more than 4 mm long; pedicels usually 3 mm or more long; inflorescence never branched (E. Asia) .... 10. *S. japonicum*

14B. Upper female heads remote; fruit with dark-brown glands and pits; beak 3 mm or more long; inflorescence simple or branched (when branched the branch or branches bearing both male and female heads), (N. America) .... 11. *S. americanum*

13B. Fruits more than 5 mm long with beaks more than 4 mm long, shiny and light-brown above, dull and pitted below; fruiting heads 25 mm or more in diameter; endocarp more than 4.5 mm long (inflorescence simple or with lowermost branch bearing male heads only; anthers 1.0–1.6 mm long) (N. America) .... 12. *S. androcladum*

10B. Stigmas more than 1.5 mm long; inflorescence usually branched with more than 2 branches bearing female heads, if less then endocarps with longitudinal ribs.

15A. At least some female heads borne sessile on main axis; endocarps more or less smooth with shallow longitudinal furrows but not ribbed; fruits with 1–4 mm long pedicels; female heads axillary or supra-axillary.

16A. Fruiting heads less than 25 mm diameter: fruits rarely more than 5 mm long, dull and pitted above and below; stigmas rarely more than 2 mm long; lowermost branch bearing both male and female heads .... 11. *S. americanum*

16B. Fruiting heads more than 25 mm diameter; fruits more than 5 mm long, shiny above and dull, pitted and glandular below; stigmas more than 2 mm long; lowermost branch bearing male heads only .... 12. *S. androcladum*

15B. Female heads borne on axillary branches or peduncles, very rarely sessile on main axis but if so then axillary; endocarps with longitundal ribs; fruits sessile or pedicels up to 1.5 mm long .... *S. erectum* group

17A. Less than half the ovaries bilocular; less than half the stigmas bifid .... *S. erectum* sensu lato

18A. Fruits obpyramidal, flattened above, contracted very abruptly into a beak; viewed from above distinctly angled .... 13a. *S. erectum* subsp. *erectum*

18B. Fruits fusiform to spherical, domed to conical above, tapering into a beak, viewed from above not or indistinctly angled.

19A. Fruits with distinct shoulders, upper and lower parts differing in form, colour and texture.

20A. Upper part of the fruit light-brown to straw-coloured, conical to domed but not distinctly wider than lower part; slightly constricted below the shoulder; fruits sessile or subsessile .... 13b. *S. erectum* subsp. *stoloniferum*

20B. Upper part of fruit brown to black, matt or shiny near the shoulder, domed and inflated, wider than the lower part, distinctly constricted below the shoulder; fruits with pedicels up to 1.5 mm long .... 13c. *S. erectum* subsp. *microcarpum*

19B. Fruits without distinct shoulders, upper and lower parts alike in form, colour and texture.

21A. Fruits ellipsoidal to fusiform, gradually tapering into a beak; beaks at least 2 mm long .... 13d. *S. erectum* subsp. *neglectum*

21B. Fruits widely ovoid to almost spherical, abruptly tapering into a beak; beaks less than 2 mm long .... 13e. *S. erectum* subsp. *oocarpum*

17B. More than half the ovaries bilocular; more than half the stigmas bifid .... 14. *S. eurycarpum* sensu lato

22A. Fruits flattened above; fruiting heads 15–32 mm diameter; endocarps 7–10 mm long (N. America) .... 14a. *S. eurycarpum* subsp. *eurycarpum*

22B. Fruits domed or pyramidal above; fruiting heads rarely exceeding 20 mm diameter; endocarps 6–7 mm long (N.E. Asia) .... 14b. *S. eurycarpum* subsp. *coreanum*

Species of subgenus Xanthosparganium

1. **Sparganium hyperboreum** Beurling ex Laestadius, Wikström's Årsberättelse, 1850, Bihang: 4. 1853 or 1854; in Beurling, Öfversigt Kongl. Vetenskaps-Akad. Förhandl. (Stockholm), 9 (8): 192. 13 October 1852 the names are cited without description using "Laest. in schaed". Type: Sweden, Torne Lappmark, *Laestadius* (lectotype: chosen here, S, sheet bearing "*S. hyperboreum* Laest. var. *natans,* Kengis, Laestadius"; a possible isolectotype in S is dated 1842 by Laestadius; see Cook, Bot. Jahrb. Syst., 107: 275. 1985 for details of typification).

= *S. natans* var. *submuticum* C. J. Hartman, Handbok Skand. Flora, ed. 4: 312. October 1848 ≡ *S. submuticum* (C. J. Hartman) L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12: 108. October 1889. Type: lectotype to be chosen from material in LD.

= *S. submuticum* forma *platyphylla* [sic] L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 108. October 1889. Type: lectotype to be chosen from material in LD.

= *S. williamsii* Rydberg, N. Amer. Flora, 17: 10. 30 June 1909. Type: Canada, Yukon Terr., Klondyke Bottom, 9 & 23 July 1899. *R. S. Williams* (holotype: NY).

Slender plants with vegetative parts submerged, or floating, or in summer sometimes emergent. Stolons short, up to ca. 10 cm long and ca. 0.8–1.2 mm diameter. Scale leaves up to 9 mm long and 1 mm wide.

Basal leaves usually floating or emergent, relatively thick, opaque, yellowish-green, (5–)10–40(–80) cm long and (0.5–)1–3(–5) mm wide, flat, without a distinct midrib and without a keel even at the base, gas chambers in one layer sometimes higher than wide; sheaths not inflated; apex rounded, not thickened.

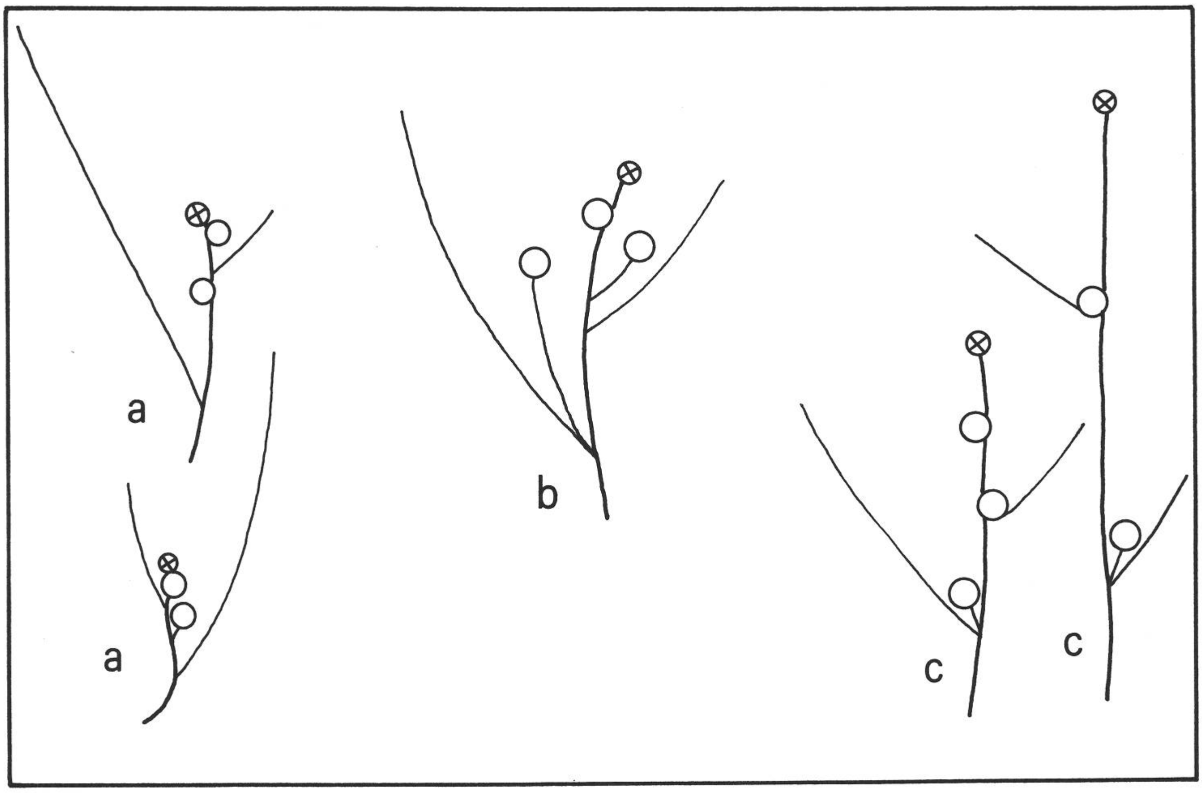


Fig. 5. Diagrammatic representation of inflorescence of: a, *Sparganium hyperboreum;* b, *S. hyperboreum* × *S. natans;* c, *S. natans.*

Flowering stems (5–)10–30(–60) cm long, 0.8–2 mm diameter, with rarely more than 4 elongated sterile nodes below the inflorescence, decumbent or ascending, usually floating, flexuous or rarely erect and emergent.

Inflorescence bracts with very slightly inflated bases and hyaline margins; the lowermost bract 2–6(–14) cm long, distinctly exceeding the inflorescence (Fig. 5 a). Uppermost bract absent in fruiting plants.

Inflorescence simple, 2.5–4.5 cm long.

Female heads (1–)2–3(–4), usually congested or adjacent (not remote), the lower one or two usually supra-axillary with peduncles adnate below to the main axis (see Fig. 5 a); the peduncle of the lowest head mostly exceeding 5 mm, often arched; in fruit (5–)7–11(–14) mm diameter.

Male head terminal, solitary, (or 1 or 2 contiguous heads appearing as 1), adjacent to the uppermost female head or with an internode less than 5 mm long.

Male flowers with filaments 4–5 mm long; anthers oblong, (0.3–)0.4–0.8 mm long.

Female flowers with perianth segments slender, linear-spathulate, with erose tips, one third to one half but rarely more as long as the fruit, attached at the base of the fruit or along a short pedicel; stigmas 0.3–0.5 mm long, elliptic to almost orbicular, obliquely attached to a less than 0.5 mm long style.

Fruits ellipsoid to obovoid-fusiform, (1.5–)3–4(–5) mm long, (1–)1.5–2.5 mm diameter, often constricted around the middle, brown or yellowish, dull-surfaced, tapering below to an obconic base with short pedicel, rather abruptly tapered distally to an acute or rounded summit with a minute beak, 0–0.5 mm long (see Fig. 6 a); endocarp widely ellipsoidal often rounded with a somewhat asymmetrical apex and elongate but

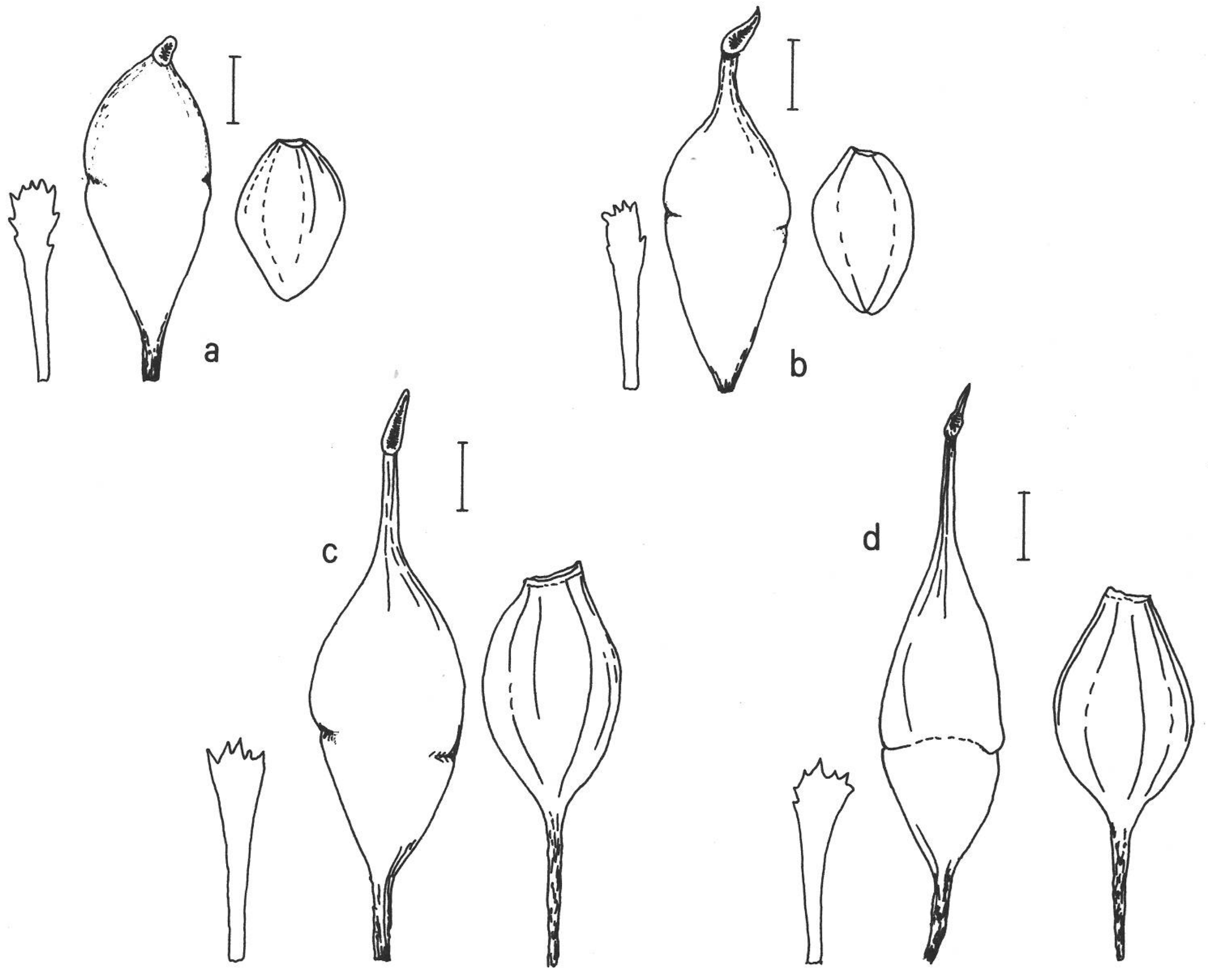


Fig. 6. Perianth segments, fruits and endocarps of: a, *Sparganium hyperboreum;* b, *S. natans;* c, *S. angustifolium;* d, *S. glomeratum* (scale bar: 1 mm).

blunt base; 2–2.5 mm long, 1.–1.7 mm diameter, smooth or with few, very fine, longitudinal furrows.

Diagnostic features

It can be distinguished from all other species of *Sparganium* by its fruit which has a minute, nipple-like beak. It is patristically related to *S. natans* with which it occasionally hybridizes (for description of hybrid see p. 237 and Table 2).

Distribution

It is found in arctic and boreal N. America and Eurasia. It extends from Scandinavia eastwards through Russia and Siberia to Kamchatka and Hokkaido. In N. America it reaches from the Pacific coastal forests of the Yukon into Alaska and across to the Atlantic coast extending southwards to S. Newfoundland, Anticosti Island and Cape Breton Island. It is also found in S. W. Greenland and Iceland. It is almost confined to the Taiga but occasionally extends into the Tundra and is known from a small region in the southern Alps in N. Italy, (see Maps 1 & 2). In the Alps it grows at an altitude of between 2250 m and 2350 m elsewhere it is rarely found above 1000 m. Fossil fruits have been reported from Poland so it is likely that the alpine populations represent genuine glacial relicts.

Ecology

Unfortunately, we have not had the opportunity to study living material of *S. hyperboreum.* According to the literature it is found in flat-bottomed pools and ditches in the Taiga, Tundra and high Alpine Zones, prefering cold water. Glück (1938) gives description of the ecology of the alpine populations. It appears to be rather indifferent to water quality being reported in calcium rich and calcium poor water; however, it is found in neither very oligotrophic nor highly eutrophic conditions.

It is essentially a plant of shallow water but grows at depths of up to about 80 cm but is rarely found in flowing water and is not resistant to much wave action. The leaves are usually completely submerged or partly floating but unlike *S. natans* it apparently rarely develops truly aerial leaves and rarely flowers in a terrestrial state. The leaves die in autumn and it overwinters as a corm. It is found growing with species such as *Utricularia ochroleuca* Hartman, *Subularia aquatica* L., *Hippuris vulgaris* L., *Potamogeton alpinus* Balbis, *P. filiformis* Persoon, *P. gramineus* L. and *Ranunculus trichophyllus* subsp. *eradicatus* (Laest.) C. D. K. Cook.

Variation

The variation is well described by Harms (1973) and the pattern he describes for N. America is similar in the Old World except that hybridization is local and hybrids are rare. We agree that *S. hyperboreum* occasionally hybridizes with *S. natans* (See p. 237). We are not, however, convinced that introgressive hybridization takes place although perhaps occasionally back crosses are found. *S. hyperboreum* has been recorded to make hybrids with *S. angustifolium* (e.g. Lid 1952, Benum 1958) and *S. emersum* (Lid 1952). There is no experimental evidence and we do not find the morphological evidence convincing.

2. **Sparganium natans** L., Species Plantarum, 971. 1753. Type: "in Europae borealis lacubus, paludibus" (lectotype: Linn. Savage Cat. No. 1095.2; see Cook, Bot. Jahrb. Syst., 107: 272. 1985); non L., Flora Lapponica, 345.1737, nec L., Flora Suecica, 771. 1745.

= *S. minimum* J. Ray, Historia Plantarum, 1910. 1688; nom. illeg., pre-1753 (cited by Linneus as a synonym of *S. natans*) ≡ *S. minimum* J. Hill, British Herbal, 507. 1756; nom. illeg., binomial names not used consistently (ICBN Art. 23) ≡ *S. natans* L. var. *minimum* C. J. Hartman, Handbok Skand. Flora, ed. 1: 43. Oct. 1820 ≡ *S. minimum* Wallroth, Erster Beitrag Fl. Hercyn., 2: 294. 1840 ≡ *S. minimum* E. M. Fries, Summa Veg. Skand., 2: 560. 1849; based on J. Ray. Type: the description in J. Ray, Historia Plantarum, 1910. 1688.

= *S. natans* var. *subdecumbens* Laestadius, Wikström's Årsberättelse, 1850, Bihang: 4. 1853 or 1854. Type: Sweden, "lacu Rättar-Dammen prope Drottningholm",? *Laestadius* (holo- or lectotype: S, n.v.)

= *S. natans* var. *suberectum* Beurling ex Laestadius, Wikström's Årsberättelse, 1850, Bihang: 4. 1853 or 1854. Type: Sweden. "in Lapponica Umensi, *Dr. Ångström*", (holo- or lectotype: S?)

=*S. rostratum* Larsson, Fl. Wermland, 260. 1859≡*S. minimum* E. M. Fries forma *rostrata* [sic] (Larsson) L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 108. October 1889≡*S. minimum* E. M. Fries var. *flaccidum* subvar. *rostratum* (Larsson) Graebner in Engler, Pflanzenreich, 2 (IV. 10): 23. 1900. Type: Sweden, specimen not yet located.

=*S. ratis* Meinshausen, Bull. Soc. Imp. Nat. Moscou, N.S., 3: 174. 1890; emended in Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4: 39. December 1893≡*S. minimum* E. M. Fries var. *oligocarpon* (Ångström) subvar. *ratis* (Meinshausen) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora, 1: 293. 15 June 1897; Type: USSR, "Ingrien kleiner Waldseen im Nordgebiete, July" coll.? *Meinshausen* (lectotype: chosen here, the specimen labelled "Typus" by N. Tzvelev in 1958: LE; isolectotypes: L, MW).

=*S. septentrionale* Meinshausen, Bull. Soc. Imp. Nat. Moscou, N.S., 3: 174. 1890; emended in Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4: 39. December 1893≡*S. minimum* E. M. Fries var. *oligocarpon* (Ångström) subvar. *septentrionale* (Meinshausen) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora, 1: 293. 15 June 1897. Type: USSR, "Ingrien, nur im Nordgebiete in rieselden kalten Quellbächen der Torfmoore" "mit *Malaxis paludosa* nicht häufig" (lectotype: chosen here, specimen with "in paludibus Malaxide paludosae, rarius. Julio" coll.? *Meinshausen,* the specimen labelled "Typus" by N. Tzvelev in 1958: LE; isolectotypes: LD, MW).

=*S. flaccidum* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4: 37. December 1893≡*S. minimum* E. M. Fries var. *flaccidum* (Meinshausen) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 292. 15 June 1897. Type: USSR, "Ingrien in tieferen Sümpfen mit faulenden, dunklen Gewässern untergetaucht" (lectotype: chosen here, specimen with "in fossis profundis aquis putredis submersum, Jul." *Meinshausen* with "N12/2296A" written on the sheet: LE; isolectotypes: LD, MW).

=*S. perpusillum* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S. 4: 38. December 1893≡*S. minimum* E. M. Fries var. *perpusillum* (Meinshausen) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 293. 15 June 1897. Type: USSR, "Ingrien" "am Gestade des finnischen Meerbusens, im Nordgebiete (ipse)" (lectotype: chosen here, the specimen labelled "Lachtam" collected 9 July 1891 by *Meinshausen:* LE; isolectotype: LD).

–*S. minimum* var. *strictum* (distinct from var. *typicum*) Luersson ex Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 293. 15 June 1897, based on Luersson, Schrift. Phys-ökon. Ges. Königsberg, 29: 59. 1888 und 1889, nomen nudum. Type: Poland, "Ostpreußen Gutten bei Johannisburg, *Luersson* (holotype: destroyed in B?).

Slender plants with vegetative parts usually submerged or floating. Stolons up to ca. 20 cm long and 1–2 mm diameter. Scale leaves up to 12 mm long and 2 mm wide.

Basal leaves when submerged or floating, thin, translucent, deep green, 6–40(–60) cm long and (1.5–)2–6(–10) mm wide (or when terrestrial 7–20 cm long and 2.5–4 mm wide), flat to somewhat concave but without a distinct midrib and without a keel even at the base, gas chambers in one layer and wider than high; sheaths not inflated; apex rounded, not thickened.

Flowering stems (6–)8–40(–100) cm long, 1–3 mm diameter., with (4–)5–8(–9) elongated sterile nodes below the inflorescence, decumbent or ascending, usually floating, flexuous or rarely erect and emergent.

Inflorescence bracts with usually somewhat inflated bases with hyaline margins; the lowermost bract 1–5(–8) cm long, scarcely exceeding the inflorescence (Fig. 5 c), the uppermost leaf-like or scale-like.

Inflorescence simple, 1.5–8 cm long.

Female heads 1–3(–4), usually remote, axillary or rarely supra-axillary; the uppermost sessile, the lowermost sessile or with an up to 28 mm long but usually less, more or less straight peduncle; in fruit (5–)7–10(–15) mm diameter.

Male head terminal, solitary, (of 1 or 2 contiguous heads appearing as 1, remote from the uppermost female head, internode exceeding 5 mm long.

Male flowers with filaments 3–5 mm long; anthers oblong, (0.3–)0.4–0.5(–0.8) mm long.

Female flowers with perianth segments elliptic to cuneate-spathulate with erose tips, scarcely clawed below, one half to two thirds as long as the fruit, attached at the base of the fruit or along a short pedicel; stigmas (0.3–)0.5–0.8 mm long, ovate, obliquely attached to a 0.5–1.5 mm long style.

Fruits elliposid to narrowly obovoid-fusiform, (1.5–)2–4(–6) mm long, 1.0–2.5 mm diameter, only slightly if at all contracted near the centre, greenish or brownish, dull-surfaced, tapering below, sessile or with a pedicel not exceeding 1 mm long, rather abruptly tapered distally to an acute summit with a conic based, slender beak, 0.5–1.0(–1.5) mm long; endocarp ovoid, 2–2.5 mm long, 1.2–1.4 mm wide, uniformly narrowed below, smooth or with very fine longitudinal furrows (Fig. 6 b).

Diagnostic features

Inflorescence simple; female heads axillary; male head solitary and remote; leaves flat, thin, translucent and dark-green; the lowest bract scarcely longer than the inflorescence. Like *S. hyperboreum* but female heads remote and separated from the male head by an at least 5 mm long internode; fruit with a slender beak. See Table 2 for further information.

Distribution

It is found in arctic and boreal N. America and Eurasia. It extends from Newfoundland to Alaska, south (on higher ground) into Oregon, Utah, Colorado and New Jersey. It is characteristic of Great Lakes conifer-hardwood and western subalpine-montane forest regions. Across much of N. America the northern limit of *S. natans* coincides well with the northern limit of trees (Harms 1973).

Table 2. Comparison of *Sparganium hyperboreum, S. Natans* and their hybrid.

Character	*S. hyperboreum*	Hybrid	*S. natans*
Leaf width	1–3 (–5) mm	2–5 mm	2–6 (–10) mm
Leaf thickness	Thick, opaque	Thick, opaque	Thin, translucent
Leaf colour	Yellowish	Light-green to brown	Dark-green
Female heads dispersion	Congested above	Remote	Remote
Female peduncle adnation	Adnate	Adnate	Axillary
Female lowest peduncle length	> 5 mm	3–7 mm	< 3–8 mm
Distance between ♂ and ♀ heads	< 5 mm	4–10 mm	> 5 mm
Fruit colour	Yellowish	Light-green to brown	Dark-green
Fruit beak length	< 0.5 mm	0.5–1.0 mm	About 1 mm

In Europe it extends from southern Scandinavia (with isolated stations above 65° N) southwards to the Pyrenees, N. Appennini and S. Bulgaria. In Scandinavia it is found up to almost 1000 m and in the Alps up to about 2300 m. In Asia it extends across Siberia from Yenisei (66° N) south to Omsk. It is also recorded from the Caucases, Sajan Mountains and northern Japan, see Maps 3 & 4. The Japanese record is based on a single specimen: 'Azuma', 13 July 1893. *Faurie 10368* (K).

Ecology

S. natans is found in sheltered bays or inlets of lakes, in pools, ditches and drainage channels. It is a characteristic species of peat diggings, is rarely found in flowing water and is not resistant to much wave action.

It is essentially a species of shallow water rarely being found more than 60 m deep, although it has been recorded at depths of more than 1 m. It flowers best in water 20–40 cm deep. In deeper water it develops fewer inflorescences and each inflorescence tends to have fewer heads. Both leaf surfaces are wettable and it does not develop true floating leaves. The upper leaves and inflorescence bracts are sometimes aerial. In summer *S. natans* can develop terrestrially but the terrestrial state is a rather shy flowerer and it is readily killed by excessive drought or frost and therefore rarely develops ripe fruit. The aerially developed leaves are shorter, more glossy and deeper green than the submerged ones.

The species shows a preference for slightly acid, mesotrophic to somewhat oligotrophic water with a base-rich substrate. It has been observed to tolerate salinities of up to 0.22% in Finland. It is usually found in peat-rich muds preferring aerobic conditions (Gyttja) and rarely grows in clay or sandy soils.

It usually grows in rather loose stands and is rarely dominant over large areas although it is the characteristic species of the association "Sparganietum minimi" within the Class "Ultricularietae intermedio-minoris". The leaves die in winter and it overwinters as a small corm. The stolons rarely develop more than 3 to 5 internodes in a year; it is likely that the effective spread is through seeds.

In open water *S. natans* is frequently found growing with *Potamogeton* species, such as *P. polygonifolius* Pourret & Figeac, *P. alpinus* Balbis, *P. natans* L. and *P. gramineus* L. It often grows in loose stands of *Phragmites* and *Carex rostrata* Stokes between the upright stems. It sometimes grows with *S. angustifolium* but rarely grows intermingled as it occupies the shallower water or shaded parts of pools. In similar pools without *S. natans*, *S. angustifolium* is capable of growing in shallow water and shade; when *S. angustifolium* is absent *S. natans* can invade the deeper water. It is also occasionally found growing with *S. emersum.*

Notes

S. natans has been reported to hybridize with *S. angustifolium* (Lid 1952), *S. emersum* (see p. 255) and *S. hyperboreum* (Lid 1952). None of these hybrids have been experimentally verified. From morphological and ecological evidence we are convinced that *S. natans* × *S. hyperboreum* exists; the two other putative hybrids are doubtful and we are not convinced that they exist.

Hybrid

1 × 2. *Sparganium hyperboreum* × *S. natans.* This hybrid is like *S. hyperboreum* in having supra-axillary female heads but distinguished by wider (2–5 mm) leaves and

green-brown fruits with beaks ca. 0.5–1.0 mm long. The upper (distal) female heads are often more remote than in "pure" *S. hyperboreum* and the internode between the uppermost female and the male head can be up to ca. 10 mm long (Fig. 5 b). The combination of supra-axillary female heads and beaked fruits is characteristic (see Table 2).

Despite hybridization, each of the parents retain their essential integrity and pose few taxonomic problems. The hybrid is infrequent through much of the world (see Maps 3 & 4); the distribution of the parents is mostly allopatric. The main exception is in C. Alaska and N.W. Canada where this distinction breaks down (probably due to the topography) and putative hybrids are found. In the Old World hybrids are much rarer. They have been recorded from Bygland and Anot in Norway by Lid (1959) and from Troms Fylke by Benum (1958).

The hybrid appears to be fertile. Harms (1973) suggests that introgression may occur but we feel that he is using the term rather loosely. Some backcrossing or segregation may occur but most hybrids look like first generation progeny.

3. **Sparganium angustifolium** Michaux, Flora Boreali-Americana, 2: 189. 1803≡*S. natans* var. *angustifolium* (Michaux) Pursh, Flora Amer. Septentrionale, 1: 34. December 1813≡*S. simplex* var. *angustifolium* (Michaux) Engelmann in Gray, A., Manual Bot. Northern U.S., ed. 5, 481. 1867≡*S. emersum* var. *angustifolium* (Michaux) R. L. Taylor & B. McBryde. Canad. J. Bot., 56: 193. 1978. Type: Canada, Lake Mistassini, *Michaux* (holotype: P n.v.).

=*Isoetes lacustris* var. *fluitans* Döll, Rheinische Flora, 40. June 1843. Type: none found, perhaps in KR.

=*Sparganium affine* A. Schnizlein, Die Pflanzenfamilie der Typhaceen (Nordlingen), 27. 1845. Type: lectotype to be found perhaps in ER or REG.

=*S. oligocarpon* Ångström, Bot. Not. 1853: 149. 1853.≡*S. minimum* E. M. Fries var. *oligocarpon* (Ångström) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora, 1: 292. 1897. Type: Sweden, "at Lycksele et Betsele Lapponiae Umensis", July., *Ångström* (lectotype to be chosen in S, isolectotypes: S. UPS and in other herbaria).

=*S. vaginatum* L. M. Larsson, Flora Wermland och Dal, 259. 1859. Type: Sweden, "Wermland, vester om Liljendal i Bergsladen" *L. M. Larsson* (holotype: C, n.v.).

=*S. borderi* [sic] W. O. Focke, Abhandl. Naturwiss. Ver. Bremen, 5: 409. April 1877; ≡*S. affine* subsp. *borderi* (W. O. Focke) Weberbauer ex Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 288. 15 June 1897; (Graebner clearly intended it to be a subspecies, the "B" is misprinted in roman and should have been put in italic). Type: France, "Hautes Pyrénées, Tremouse", *Bordère* (holotype: BREM n.v.; topotypes: "Tremouse, July 1886, *Bordère*" B, Z).

=*S. simplex* var. *multipedunculata* [sic] Morong, Bull. Torrey Bot. Club, 15: 79. 2 March 1888≡*S. simplex* proles *longissimum* var. *multipedunculatum* (Morong) Graebner in Engler, Pflanzenreich, 2 (IV. 10): 17. September 1900≡*S. multipedunculatum* (Morong) Rydberg, Bull. Torrey Bot. Club, 32: 598, 1905≡*S. emersum* var. *multipedunculatum* (Morong) Reveal, Taxon, 19: 797. 1970≡*S. angustifolium* subsp. *emersum* var. *multipedunculatum* (Morong) Brayshaw, Occasional Papers British Columbia Provincial Museum, 26: 115. 1985. Type: USA, Montana, Great Falls, s.d., *R. S. Williams* (holotype: NY).

=*S. affine* var. *zosteraefolium* [sic] L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 110. October 1889≡*S. affine* subvar. *zosterifolium*

[sic] (L. M. Hartman) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 288. 15 June 1897. Type: none cited, Sweden, Medelpad Prov., Sundsvall par., 20–25 September 1886. *L. M. Neumann* (holotype: UPS).

= *S. affine* var. *deminutum* L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 110. October 1889 ≡ *S. affine* subsp. *borderi* [sic] var. *deminutum* (L. M. Neuman) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 289. 15 June 1897. Type: "Ligger i Linnés herb. unter namnet *Sp. natans β*" it is not known which specimen Neuman saw; *S. natans* var. *β* L. was based on *S. minimum* Ray (1688), Neuman is probably referring to *S. angustifolium* Michaux from his description.

= *S. affine* var. *microcephalum* L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 110. October 1889 ≡ *S. affine* subsp. *borderi* [sic] var. *microcephalum* (L. M. Neuman) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 289. 15 June 1897. Type: Plate 1, Fig. 1 B & 1 C in Bot. Not. 1852.

= *S. subvaginatum* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4 (36): 34. December 1893, pro parte ≡ *S. simplex* var. *angustifolium* subvar. *subvaginatum* (Meinshausen) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. simplex* var *subvaginatum* (Meinshausen) Graebner in Engler, Pflanzenreich, 2 (IV. 10): 17. September 1900 ≡ *S. emersum* forma *δ subvaginatum* (Meinshausen) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971 published 1972. Type: "Finnland, Archipelago Aboensi-Krànskor", pr. Kelo, *Ruprecht;* Ins. Sitcha, *Mertens;* Rocky-Mountains, reg. alpina, *C. C. Parry* (lectotype to be chosen).

= *S. kawakamii* Hara, J. Jap. Bot., 14: 53, 54. January 1938. Type: USSR, Kurilskiye Ostrova, "Ins. Etorofu, Ponto, Rubetsu, 25 August 1898, *Kawakami* (holotype: MAK, 13 8613; ? isotype: "Herb. Agr. Hokk. Imp. Univ.").

Slender plants with vegetative parts usually submerged or floating rarely emergent but when so then very small. Stolons up to ca. 35 cm long and ca. 3 mm diameter. Scale leaves up to 16 mm long and 3 mm wide.

Basal leaves usually submerged below and floating distally, (20–)30–80(–250) cm long, (1.5–)2–4(–10) mm wide, flat or rounded abaxially, without a distinct midrib and without a keel even at the base; abaxial surface of floating portion of leaf with one layer of 6–8 gas chambers, the submerged portion with 2 or rarely 3 layers of gas chambers, the sheath with 2 or 3 layers.

Flowering stems (7–)30–100(–175) cm long, 1–3 mm diameter, with 2–4 elongated sterile nodes below the inflorescence, decumbent or ascending, usually floating, flexuous or rarely erect and emergent.

Inflorescence bracts inflated at base with hyaline margins; lowermost bract (5–)10–20(–60) cm long, (1.5–)2.5–4.0(–4.5) times as long as inflorescence (Fig. 7 a); the bract of the uppermost female head 1.5–20 cm long and usually exceeding the inflorescence, the bract of the lowest male head often green and leaf-like. Inflorescence simple, 1–9 cm long.

Female heads (1–)2–4(–5), remote, the lowest axillary or supra-axillary and peduncled the other axillary or supra-axillary and usually sessile; the free part of the peduncle 5–25(–55) mm long; in fruit (8–)10–20(–24) mm diameter.

Male heads (1–)2–3(–4), usually crowded and appearing as one elongated head terminating the main axis (Fig. 7 a), usually remote from the uppermost female head with an internode (0–)10–20(–50) mm long.

Female flowers with perianth segments spathulate, translucent, with erose tips, scarcely clawed below, about two thirds as long as the fruit, attached at the base of the

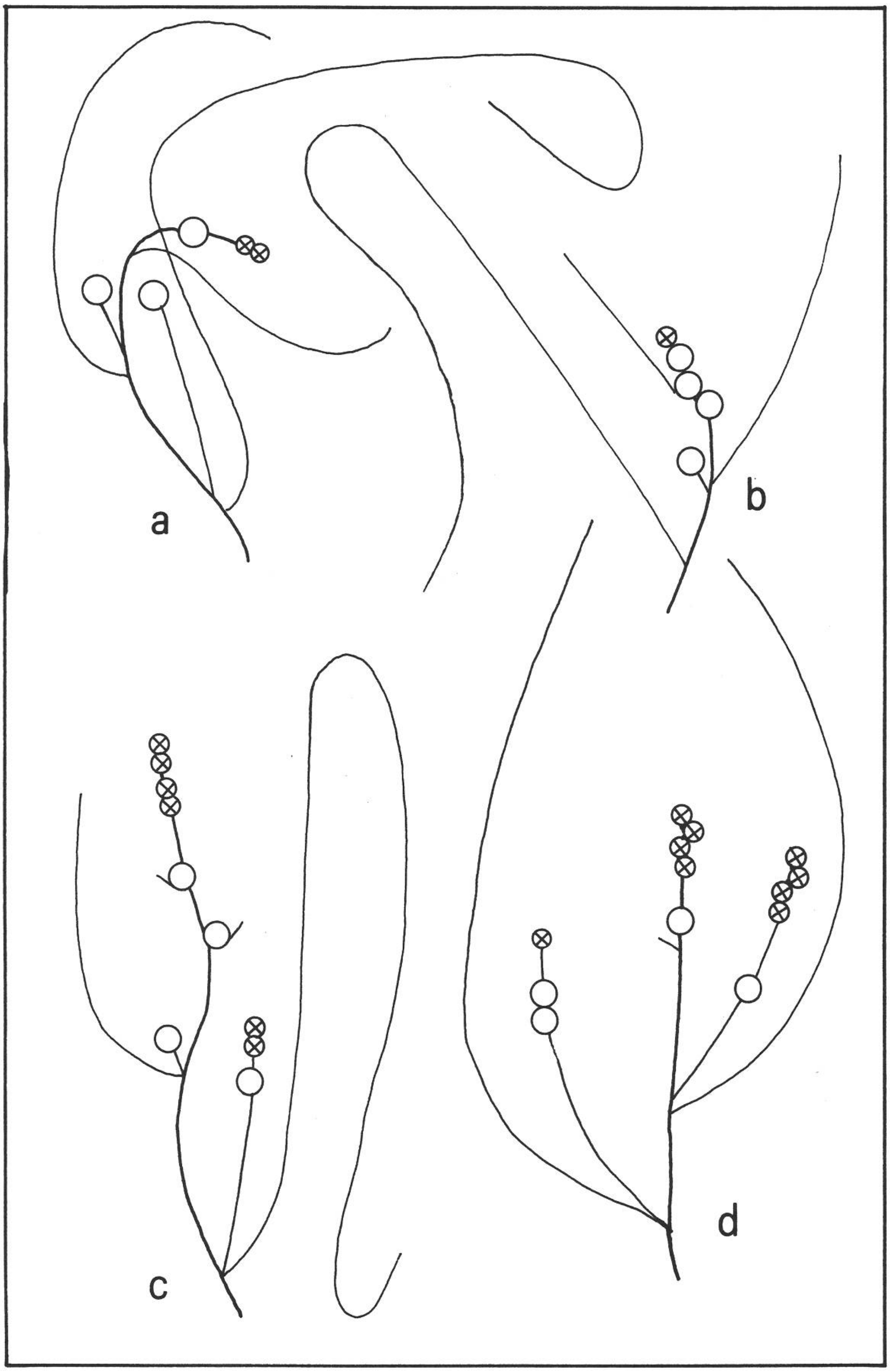


Fig. 7. Diagrammatic representation of inflorescences of: a, *Sparganium angustifolium;* b, *S. glomeratum;* c, *S. gramineum;* d, *S. fluctuans* (scale bar: 1 mm)

fruit or along a short pedicel; stigmas (0.6–)0.8–1.0(–1.2) mm long, lanceolate-ovate, obliquely attached to a 1.5–2 mm long style.

Male flowers with filaments 3–5 mm long; anthers narrowly oblong, (0.8–)0.9–1.0(–1.2) mm long.

Fruits ellipsoid to fusiform, 3–5.5 mm long and 2–2.5 mm diameter, brownish, usually somewhat constricted near the centre, tapering below to an obconic base with a (0.8–)1.0–1.5 mm long pedicel, tapered distally to an acute summit with a conic-based, 1.5–2.0(–2.2) mm long beak; endocarp ovoid, 2.5–4.0 mm long, ca. 2.5 mm diameter, tapered below into a ca. 2.5 mm long stalk, smooth with some fine longitudinal furrows (Fig. 6c).

Diagnostic features

Inflorescence simple; at least some female heads supra-axillary; male heads up to 3, continuous, clearly separated from uppermost female head, at anthesis appearing as 1 elongated head; stigmas upto 1 mm long; lowest inflorescence bract inflated at base, usually at least twice as long as the the inflorescence; leaves usually floating, plano-convex.

Distribution

S. angustifolium is a holarctic species with a circumboreal distribution. It is commoner in suboceanic regions and is rare (or perhaps poorly collected) in continental Eurasia. It shows a somewhat arctic-alpine distribution pattern in Europe and N. America (see Maps 5 & 6).

In N. America it extends from the Aleutian Islands and Alaska to Newfoundland, reaching southwards to California, Idaho, Montana, Wyoming and Utah on higher ground, growing at about 3000 m in Colorado; only in western N. America does it extend beyond 60° N but even then rarely grows beyond the arctic circle. It is present in Greenland and Iceland. In Europe it is widespread and common in the North, extending beyond the arctic circle (reaching 71° N in Norway). In central and southern Europe it is confined to higher land in the Alps and the mountains of Portugal, Spain (2000 m in Sierra de Gredos) and Macedonia. In European Russia it is found in Karelia-Lappland, Dvina-Pechora, Ladoga-Il'nen and the Upper Volga. In eastern Asia it is found in Kamchatka, Sakhalin southwards to Hokkaido and the mountains of Honshu.

Ecology

S. angustifolium is confined to and can be used as an indicator of acid oligotrophic water. It occupies a variety of different habitats from large lakes to small pools, ditches and streams. Among the species of *Sparganium* it is the most tolerant of deep water usually being found in 30–150 cm of water but occasionally growing to 2.5 m or more. It develops true floating leaves with wettable abaxial and unwettable adaxial surfaces. These floating leaves are plano-convex in transverse section with considerable aerenchyma and 6–8 gas chambers. The stems are relatively thin, flexible and non-buoyant. The sheaths of the cauline leaves and inflorescence bracts are often inflated and filled with gas; these buoyant sheaths probably play an important role in keeping the inflorescence above the surface of the water. Usually most of the photosynthetic surface is exposed to air (adaxial surface of floating leaves). In summer *S. angustifolium* is capable of growing terrestrially with short, weakly erect and unwettable leaves.

S. angustifolium can spread by stolons and is sometimes locally dominant with the floating leaves covering quite large areas. Within these dense stands very few other species are found; the commonest associated species outside the dense stands are:

Isoetes lacustris L., *I. echinospora* Durieu or *I. macrospora* Durieu, *Potamogeton alpinus* Balbis, *Littorella uniflora* (L.) Ascherson or *L. americana* Fernald, *Scirpus (Eleogiton) fluitans* L. and *Lobelia dortmanna* L. It is sometimes found growing with *Sparganium natans* and *S. glomeratum,* it apparently sometimes hybridizes with the latter.

In autumn the leaves of *S. angustifolium* die and it overwinters as corms. Local spread is by stolons and perhaps also by seed. It is often infected with the larvae of *Hydrocampa stagnata* (a small moth: Pyralididae) which may well reduce its vigour; it is readily eaten by many other moth and beetle species (see p. 227).

Variation

S. angustifolium is a relatively invariable and constant species. In deep water the lower female heads are usually borne on long peduncles (Fig. 7 a) with highly inflated bract-bases. In very shallow water or on land the female heads are usually sessile and the bract-bases are not inflated.

This variation is most likely to be phenotypically induced but has led to some taxonomic confusion. Deep water plants occasionally carry the epithets *"multipedunculatum"* or *"subvaginatum"* while those having the shallow-water or terrestrial state are often called *"S. borderei"*. Fertile hybrids are formed with *S. emersum* (see p. 255) and *S. gramineum* (p. 247) which in some regions may lead to taxonomic difficulties.

Hybrids

S. angustifolium has been reported to hybridize with *S. hyperboreum* (Lid 1952; Benum 1958), *S. natans* (Rothert 1910, Lid 1952) and *S. glomeratum* (Rothert 1913, Lid 1952). Although these hybrids are likely we are not convinced they exist and material determined as hybrid is usually attributable to one or other of the putative parents. Hybrids with *S. emersum* (p. 255) and *S. gramineum* (p. 247) do exist and are fertile.

4. **Sparganium glomeratum** (Beurling ex Laestadius) L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Flora, ed. 12, 111. October 1889 ≡ *S. erectum* var. *γ glomeratum* Beurling ex Laestadius, Bihang till Wikström's Årberättelse, 1850: 2. 1853 or 1854. Type: Sweden, Hernösand, 1843, *Laestadius* (lectotype: chosen here, sheet with "*S. glomeratum*" in Beurling's own handwriting and "*S. simplex* var. *glomeratum*" in Laestadius' handwriting: S; isolectotype; S). In Beurling's publication in "Öfversigt Kongl. Vetenskaps-Acad. Förhand (Stockholm), 9 (8): 192. 13 October 1852" the epithet "*glomeratum*" is a nomen nudum citing "Laest. in schaed" for further details see Cook (1985).

= ?*S. fluitans* (E. M. Fries) E. M. Fries, Summa Vegetabilium Scand., 559, 1849 ≡ *S. simplex* var. *β fluitans* E. M. Fries, Flora Hallandica, pt. 1, 139. 1817. In 1849 Fries clearly bases *S. fluitans* on his "var. *fluitans*" from 1817. It is not possible to identify var. *fluitans* on the basis of its diagnosis in Flora Hallandica (pusillum, foliis decumbentibus natantibus, sequentis multo latioribus & brevioribus, basi 3-quetris). A type specimen must have been collected in Halland by 1817; no such specimen has been found even after a diligent search by Dr. Roland Moberg (UPS). In 1849 Fries wrote a new description of *S. fluitans* which bears almost no relation to his earlier diagnosis. This new description probably refers to *S. glomeratum* Laestadius; he also cites "Herb. normale XVI" (presumably a misprint for XV). From this evidence it is fairly clear that *S. fluitans* E. M. Fries and *S. glomeratum* Laestadius refer to the same species. The earlier name is *S. fluitans* which is not only semantically unsuitable but has not been used for about a hundred years. Following the present interpretation of the Code of Botanical Nomenclature *S. fluitans* would not be accepted as a nomen rejiciendum and *S. glomeratum* would not be accepted as a nomen conservandum. We beg the botanical community to use *S. glomeratum* until a more sensible code of nomenclature exists.

= *S. glehnii* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4 (36): 34. December 1893. Type: USSR, "Sachalin, Sümpfe bei der Ansiedlung Tunai, 29 July, *Glehn* (holotype: LE, MHA or MW, not found by us but seen by Rothert, 1910).

Robust but relatively small plants usually emergent with erect leaves and stems, rarely floating or submerged. Stolons up to at least 10 cm long, 1–1.5 mm diameter. Scale leaves ca. 10–18 mm long.

Basal leaves submerged or erect and distally emergent but rarely floating; submerged leaves thin and delicate, flat rarely more than 5 mm wide; emergent or floating leaves (20–)30–50(–60) cm long, (2–)4–9(–18) mm wide, in transverse section flat to very shallowly triangular distally, becoming shallowly triangular to deltate below with a winged abaxial keel, with 1 or below sometimes 2 layers of 6–8 gas chambers, not inflated at base.

Flowering stems (10–)30–40(–60) cm long, 2–4 mm diameter with 1–3(–4) elongated sterile nodes below the inflorescence, erect, robust, distinctly shorter than the leaves.

Inflorescence bracts usually straight and erect but remaining at an acute angle to the axis (Fig. 7b), inflated at base with hyaline margins; lowermost bract (15–)20–30(–35) cm long, at least 3 times as long as the inflorescence; bract of the lowest male head usually brown and scale-like or sometimes absent. Inflorescence simple and compact.

Female heads (2–)3–5(–6), crowded, sessile or the lowest pedunculate and often remote, the rest usually supra-axillary, the lower ones often appearing above the next node or opposite the next bract; in fruit (10–)12–16(–20) mm diameter.

Male heads 1–2, more or less contiguous with the uppermost female head (Fig. 7b).

Female flowers with perianth segments oblong to oblong-spathulate, with erose tips, clawed below, one third to half as long as the fruit, attached to a short pedicel; stigmas 0.6–0.8 mm long, lanceolate, obliquely attached to a 1.5–2.0 mm long style.

Male flowers with filaments 5–6 mm long; anthers narrowly oblong, 0.7–0.9 mm long.

Fruits narrowly fusiform, (3.0–)3.5–5.0(–6.0) mm long, 1.2–2.0 mm diameter, distinctly or indistinctly constricted near the centre, green-brown, shiny-surfaced, tapered below to an obconic base with a 0.5–2.0 mm long pedicel, tapered above to an acute summit with a conic based, 1.5–2.0 mm long beak; endocarp ovoid, 3.5–4.0 mm long, ca. 2 mm diameter, tapered below into a 2–3 mm long stalk, smooth with some very fine longitudinal furrows (Fig. 6d).

Diagnostic features

Inflorescence simple; female heads crowded, the upper ones usually sessile, supra-axillary, often appearing above the next node or opposite the next bract; male heads 1–2, contiguous with uppermost female head; stigmas less than 0.8 mm long; mature fruit shiny with a straight beak; lowest inflorescence bract carinate to apex, at least 3 times as long as the inflorescence.

Distribution

S. glomeratum has a disjunct distribution (see Map 7 & 11). It is common and abundant in lowland and southern regions of Norway, Sweden and Finland, rarely reaching beyond 63°30′N (at Kuolajärvi it reaches to 67° N); eastwards it extends from White Russia to the Urals. It is apparently absent from Siberia and central Asia but reappears in the east where it grows in Manchuria, Liaoning, Jirin, N. Korea, Kamchatka and Japan (in Hokkaido and the mountains of central Honshu). There are some isolated records from eastern Tibet and Yunnan in S.W. China. There are also reports of *S. glomeratum* in N. America. We can confirm the record from Goose Bay. Labrador, Canada (20 July 1950, *Gillet & Findlay 5390* – LU). The records of Lakela (1941) from Lake Country, Minnesota and Porsild (1950) from Dawson in the Yukon we have not been able to confirm and we doubt their validity (Map 11).

Ecology

S. glomeratum is essentially a species of shallow water in pools, small ponds, streams and ditches that have varying water levels and that may dry out in summer. The leaves are usually erect and mostly aerial; the aerial portions of the leaves are unwettable on both surfaces. It is rarely found in large lakes but if so then it is confined to the edges in very shallow water. It shows a preference for mesotrophic neutral water, not being found in acid oligotrophic water and also avoiding calcium-rich waters. From the point of view of water quality it occupies a position between *S. natans* and *S. emersum.* In Scandinavia it is widespread east of the Kattegat but is by no means common only occasionally is it locally abundant; it is found growing with species such as: *Scirpus (Eleogiton) fluitans* L., *Eleocharis mamillata* (Lindb. f.) and *Ranunculus reptans* L. Among the northern species it is the first to flower and develop fruits; fruiting specimens have been collected as early as July.

Variation

The characteristic arrangement of the male and female heads is remarkably constant throughout the range of the species making *S. glomeratum* a highly distinctive member of the genus. Compared with other species of *Sparganium* it is not very variable. In Japan, however, some plants have narrow leaves which are flat (not keeled) and floating. These plants have been given varietal rank (var. *angustifolium*) by Graebner (1900); Hultén (1964) suggested that these plants belonged to another species. All floral characters are typical for *S. glomeratum* and without further biosystematic work we feel it unwise to give these plants formal taxonomic recognition.

Hybrids

Lid (1952) reports that *S. glomeratum* hybridizes with *S. angustifolium* and *S. emersum* in Norway. Yuzepchuk (1934) in Komarov reports *S. glomeratum* × *S. emersum* from Karelia-Lappland and Kamchatka. We have seen no convincing material of these hybrids, we doubt that the former exists but *S. glomeratum* × *S. emersum* way well exist but would be difficult to distinguish from *S. angustifolium* × *S. emersum.*

5. **Sparganium gramineum** J. G. Georgi, Bemerkungen einer Reise im Russischen Reich im Jahre 1772, 1: 232. 1775. Type: USSR, Buryatskaya ASSR, "in den Seen der oberen Angara, der Tanaga und dem Turtil", *Georgi* (we have failed to find any type

specimens in LE and MW but they were known to Rothert, 1910) non Wallroth, Erster Beitrag Fl. Hercyn., 2: 297. 1840.

= *S. lanceolatum* J. G. Georgi, Bemerkungen einer Reise im Russischen Reich im Jahre 1772, 1: 233. 1775. Type USSR, Buryatskaya ASSR, the same as *S. gramineum* (we have failed to find any type specimens in LE and MW but they were known to Rothert, 1910).

= *S. friesii* Beurling, Bot. Not. 1854: 136. September–October 1854. Type: Sweden, Strömstad (lectotype: chosen here, "in lacu Strömvattnet, Jul. 1854, *P. J. Beurling*" S; isolectotype: S; paratype: "Ströms-än Julio 1954" manu *Beurling*, S.)

Slender plants with vegetative parts usually submerged or floating. Stolons not well developed (or rarely collected), short, ca. 3 mm diameter. Scale leaves up to 1 cm or more long, thin translucent. Basal leaves submerged below and floating distally, up to 120 cm or more long, (1–)2–3(–6) mm wide, not inflated at base, flat to plano-convex or semi-terete, with hyaline margins at base, without a distinct midrib; apices rounded.

Flowering stems 40–50(–200) cm or perhaps longer, 2–3 mm diameter, flexible, mostly submerged but emergent at tip; inflorescence simple or usually branched; main axis bearing (3–)5–7 female and 2–6 male heads; lowest lateral branch axillary bearing 1–3 female and (0–)1–2(–3) male heads, no other branches bear male heads; female and male heads separated by a (1–)2–4 cm long internode.

Inflorescence bracts at base inflated and with hyaline margins; lowermost bract up to 60 cm long, one to two times as long as the inflorescence (Fig. 7c); bracts of uppermost female heads and all male heads scale-like or absent.

Female heads always axillary, sessile or the lower shortly pedunculate, each remote and not touching, in fruit 10–20 mm diameter.

Male heads distinctly separated from female ones by a (1–)2–4 cm long internode, all more or less contiguous (Fig. 7c); axis remaining more or less straight after anthesis.

Female flowers with perianth segments oblong to spathulate, 2.5–3.5 mm long, erose at apex, translucent or with brown midrib, attached at base of pedicel, not obviously united below, at maturity about half as long as fruit; pedicel ca. 1 mm long; stigmas 0.6–0.7 mm long, ovate to triangular, obliquely attached.

Male flowers with filaments ca. 5 mm long; anthers (0.7–)0.8–0.9(–1.0) mm long.

Fruits ovoid, 2–3 mm long, 1.5–2 mm diameter, rarely constricted around middle, dark brown often with purple flecks, shiny-surfaced; tapering below to an obconic base with a 0.5–1.0 mm long pedicel; tapering above to conic-based beak; beak persistent, abruptly deflexed from base, 0.8–1.5 mm long; endocarp ovoid, ca. 2–2.5 mm long, somewhat constricted by ca. 6 shallow longitudinal furrows, bluntly conic at micropyle, elongated below into a peristent pedicel (Fig. 8a).

Diagnostic features

Leaves floating (apparently never erect), long and usually less than 5 mm wide; inflorescence simple or with a single branch; female heads axillary and remote, sessile or with the lowest shortly pedunculate; male heads 2–6, separated from the uppermost female by an internode at least 1 cm long; stigmas less than 0.8 mm long; fruit shiny with a short, abruptly deflexed, ca. 1 mm long beak.

Distribution

S. gramineum has a somewhat disjunct distribution (Map 8). In Scandinavia it is centred in S. and E. Sweden and S. Finland, mostly in low lying regions but reaching

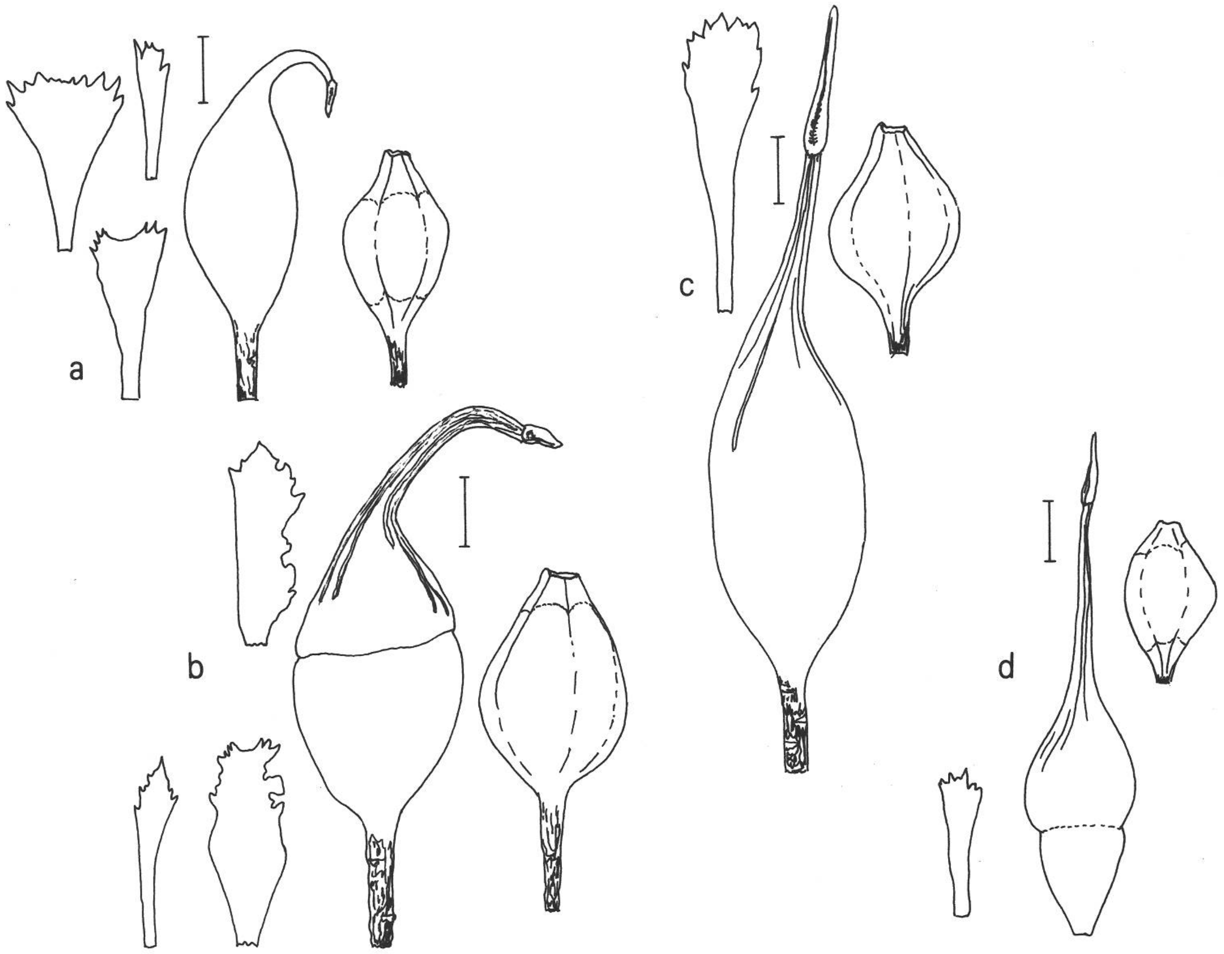


Fig. 8. Perianth segments, fruits and endocarps of: a, *Sparganium gramineum;* b, *S. fluctuans;* c, *S. emersum* subsp. *emersum;* d, *S. emersum* subsp. *acaule* (scale bar: 1 mm).

346 m in Dalarna Jamtland and 292 m in Lappland. There are some isolated reports from E. Norway, extending to ca. 67° N.

In European Russia it grows from Leningrad and Novgorod north to Archangelsk and eastwards to Upper Volga (Moscow). It is absent from much of C. Russia but reappears in Siberia from Irkutskaya Oblast (around Lake Baikal) and Kamchatka.

Ecology

S. gramineum is more or less confined to oligotrophic lakes and is not or very rarely found in pools or ditches. It seems incapable of developing aerial leaves and may not be able to accommodate to changing water levels. The distal parts of the leaves float on the surface but they are apparently not so dorso-ventrally specialised as *S. angustifolium.* The submerged part of the leaf is often very thin and almost resembles a petiole. It is very gregarious and often develops very large populations; the floating leaves, which usually lie parallel, may cover the surface of the the water. It is usually found in water from 40 cm to 150 cm deep with the consequence that it is rarely found near the banks. In depths of more than 1 m it often does not develop flowers and it is then virtually impossible to distinguish it from *S. angustifolium.* It has been recorded up to 3 m deep. It is unable to tolerate more than very small quantities of calcium, nitrogen and phosphorous and is not found in brackish waters; it is a good indicator for oligotrophic water.

It is occasionally found growing with *S. angustifolium* with which it sometimes hybridizes. The hybrid apparently outcompetes the *S. gramineum* often leaving populations of *S. angustifolium* mixed with *S. angustifolium* × *S. gramineum*. *S. gramineum* also crosses with *S. emersum;* this hybrid is more tolerant of eutrophic conditions and rarely co-habits with pure *S. gramineum.*

Hybrid

5 × 3. *Sparganium gramineum* × *S. angustifolium*

From the morphology alone it is not possible to distinguish this hybrid from 5 × 7, *S. gramineum* × *S. emersum* (see p. 257). As *S. emersum* is a species of eutrophic waters it is to be expected that the latter hybrid is less common but the opposite seems to be the case. The hybrids tend to resemble *S. gramineum* but have longer stigmas and some supra-axillary heads. They are rather variable and characteristically have a somewhat irregular arrangement of the male heads (Fig. 9 a & b). The hybrids are apparently fertile and the variability may result from segregation of self-fertilized hybrids or occasional backcrossing to either parent. These hybrids are relatively common in Scandinavia and regions where the distributions of the parent species overlap (see Map 9).

6. **Sparganium fluctuans** (Engelmann ex Morong) B. L. Robinson, Rhodora, 7: 60. 1905 ≡ *S. androcladum* var. *fluctuans* Engelmann ex Morong, Bull. Torrey Bot. Club, 15: 78. 2 March 1888. Type: USA Pennsylvania, "ponds at the base of the White Mountains, *Oakes*" (holotype: MO n.v.).

– *S. simplex* Hudson var. *fluitans* Engelmann in A. Gray, Manual Bot. Nothern U.S., ed. 5, 481. 1867; nom. illeg., based on the type of *S. fluctuans;* non E. M. Fries, nec Döll, nec Godron & Grenier, nec Wirtgen. Type: USA, Pennsylvania, "ponds at the base of the White Mountains, *Oakes*" (holotype: MO n.v.).

Slender plants with vegetative parts usually submerged or floating. Stolons up to 20 cm or more long and 2–3 mm diameter.

Scale leaves up to 1 cm or more long, thin, translucent.

Basal leaves submerged below and floating distally, (20–)60–80(–100) cm long, (3–)4–8(–12) mm wide, not inflated at base, flat, thin, translucent, cross-reticulate abaxially, without a distinct midrib; apex rounded-acute.

Flowering stems (20–)60–100(–150) cm long, 1.5–3 mm diameter, mostly submerged, flexible, floating and emergent at tip; inflorescence usually branched with main axis bearing (0–)1(–2) female and (3–)4–6 male heads; lateral branches usually axillary (individual heads may be supra-axillary) bearing 1–2(–3) female and (1–)2–4 male heads (at distal end of inflorescence it is difficult to distinguish between main axis and branches, Fig. 7 d); female and male heads separated by a distinct, (5–)10–20(–30) mm long internode.

Inflorescence bracts slightly inflated at base, usually with hyaline margins; lowermost bract (4–)6–18(–25) cm long, shorter than or sometimes slightly exceeding (up to 1.8 times) the inflorescence; bracts of uppermost female head and all male heads scale-like or absent.

Female heads axillary or supra-axillary, sessile, irregularly spaced along the axis or branches (Fig. 7 d) at least some touching or almost touching, in fruit 15–23 mm diameter.

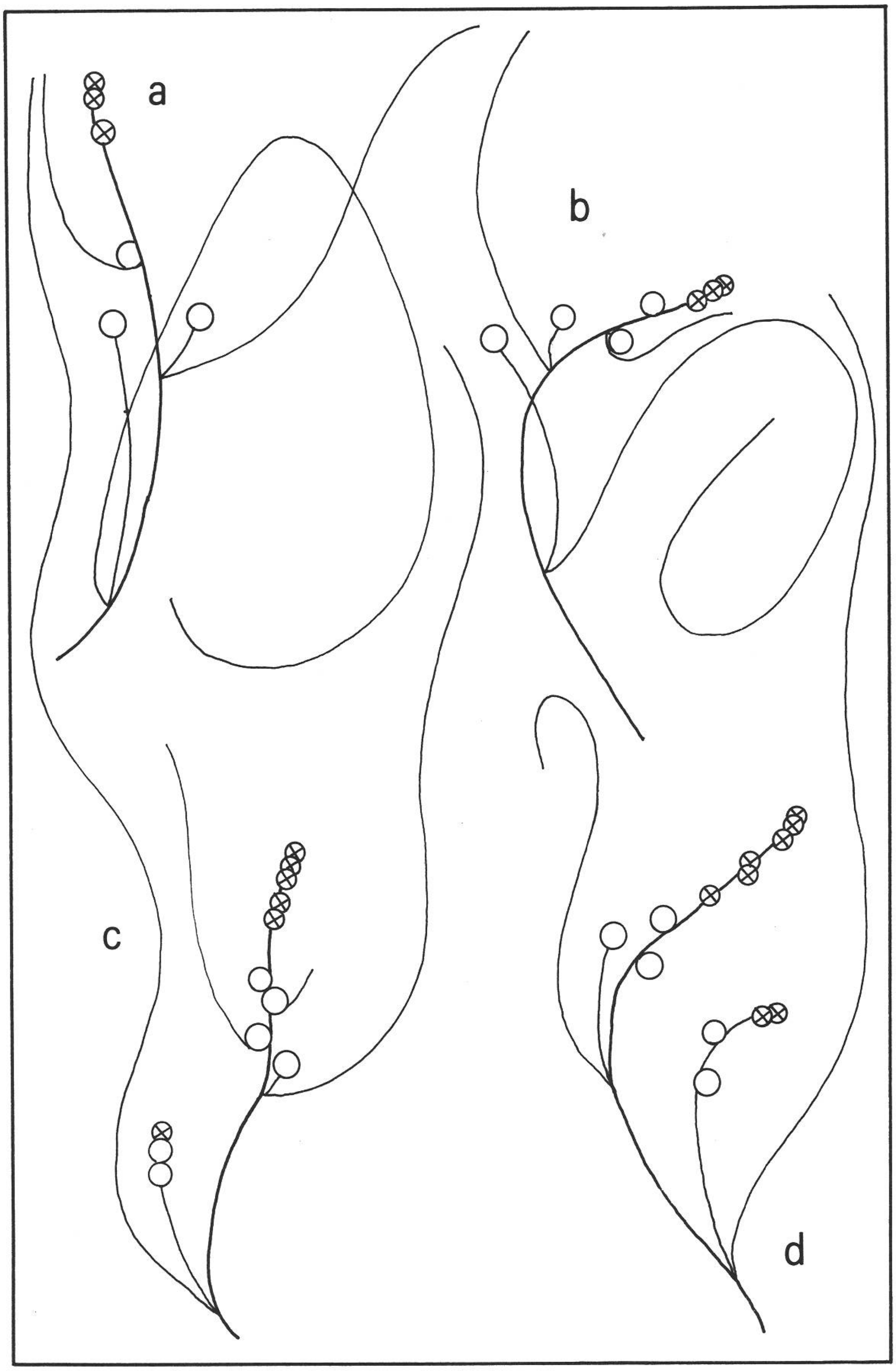


Fig. 9. Diagrammatic representation of inflorescences of: a, b, *Sparganium angustifolium* × *S. gramineum;* c, d, *S. emersum* × *S. gramineum.*

Male heads ca. 10–15 mm diameter, the lower ones distinct from each other, after anthesis leaving a zig-zag stalk, usually ebracteate.

Female flowers with perianth segments linear-oblong, 2–3.5 mm long, erose at apex, with dark brown tip and midrib, attached to the middle or below the middle of the pedicel, not clearly united below, at maturity about half as long as the body of the fruit; pedicel ca. 1–3 mm long; stigmas (0.4–)0.7–0.8(–0.9) mm long, lanceolate-ovate, obliquely attached.

Male flowers with spathulate, ca. 3 mm long, dark-tipped perianth segments; filaments ca. 6 mm long; anthers (0.5–)0.6–0.7(–0.9) mm long.

Fruits obovoid to ovoid or fusiform, (2.7–)3.0–4.0(–5) mm long, ca. 2–2.5 mm diameter, usually constricted somewhat above the middle, dark brown, matt, dull-surfaced; tapering below to an obconic base with persistent 1.5–3 mm long pedicel; rounded above with a robust curved, 2–3.5 mm long beak; endocarp ovoid, ca. 3.5 mm long and 2.25 mm diameter, somewhat constricted by ca. 6 very shallow longitudinal furrows, flattened at the micropyle, elongated below into a persistent pedicel (Fig. 8 b).

Diagnostic features

Superficially resembling *S. gramineum* but generally more robust; inflorescence more branched with more heads on each branch; leaves usually more than 4 mm wide; beak curved, longer than 2 mm; stigmas usually more than 1 mm long; fruit usually more than 3 mm long with a pedicel exceeding 1.5 mm; anthers smaller, rarely exceeding 0.8 mm long. Easily distinguishable from the *S. americanum* group by the thin, translucent perianth segments.

Distribution

S. fluctuans is confined to boreal North America (Map 11) from Newfoundland westwards to northern Alberta and central British-Columbia extending southwards in the east to the northern counties of Pennsylvania.

Ecology

According to published accounts (Crow & Hellquist 1981, Brayshaw 1985) it is found in cold water ponds, lakes and slow rivers, often in relatively deep (1–2 m) water. It grows in oligotrophic usually somewhat acidic waters. It is reported to be uncommon in British Columbia and it is on the "rare and endangered plant list" for Connecticut.

Variation and hybrids

S. fluctuans is a distinct, rather invariable species that could be considered to be the New World vicariant of *S. gramineum.* Unlike *S. gramineum* it does not seem to hybridize with any other species.

7 A. **Sparganium emersum** A. Rehmann, sensu stricto, Verhand. Naturforsch. Ver. Brünn, 10: 80. 1872 ≡ *S. simplex* proles *longissimum* subvar. *emersum* (Rehmann) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 286. 15 June 1897 ≡ *S. simplex* proles *longissimum* var. *γ emersum* (Rehmann) Graebner in Engler, Pflanzenreich, 2 (IV.10): 17. September 1900 ≡ *S. angustifolium* subsp. *emersum* (Rehmann) T.C. Brayshaw, Occasional Papers British Columbia Provincial Museum, 26: 115. 1985. Type: USSR, Ukraine, "Im Flussbette des Row bei Bar in Podolien", 1868, *A. Rehmann 154* (holotype: not found ?BRNM or BRNU; isotypes: B, K – paratype: Iter cilicico kurdicum, *J. Kotschy 468:* K).

= *S. erectum* L. var. *β* (*non ramosum*) L., Sp. Pl., 971. 1753. Type: Europe, specimen in Clifford's Herbarium (BM).

= *S. simplex* var. *gracilis* [sic] Meinshausen, Bull. Soc. Imp. Nat. Moscou, N.S., 3: 170. 1890 ≡ *S. simlex* var. *angustifolium* [sensu Morong] subvar. *gracile* [sic] (Meinshausen) Graebner in Ascherson & Graebner. Synopsis Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. simplex* var *γ gracile* (Meinshausen) Graebner in Engler, Pflanzenreich, 2 (IV.10): 17. September 1900 [Graebner's citations loc. cit. are incorrect] ≡ *S. emersum* forma *gracile* (Meinshausen) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972; non *S. natans* forma *gracilis* L. M. Neuman in C. J. Hartman & C. Hartman, Handbok Skand. Fl., ed. 12, 109. October 1889. Type: USSR, "Ingrien" "im nordlichen Torflande" (lectotype: chosen here, the specimen collected in July 1860 with "Teste Prof. Rothert" stamped on the label, LE).

= *S. splendens* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4 (36): 32. December 1893 ≡ *S. simplex* var. *splendens* (Meinshausen) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. emersum* forma *splendens* (Meinshausen) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972. Type: USSR, "nur in Süd Gebiete Ingriens gefunden" (lectotype: chosen here, sheet bearing label "*Sparganium splendens* m. n.sp" and another label with handdrawn crown and "n.sp exellentissima" written on it, LE). Some iso- or syntypes may represent the hybrid *S. angustifolium* × *S. emersum.*

= *S. simile* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4 (36): 34. December 1893 ≡ *S. simplex* var. *splendens* subvar. *simile* (Meinshausen) Graebner in Ascherson & Graebner. Syn. Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. simplex* var. *ϱ simile* (Meinshausen) Graebner in Engler, Pflanzenreich, 2 (IV.10): 17. September 1900 ≡ *S. emersum* forma *simile* (Meinshausen) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972. Type: USSR, "monte Calmytolohey in deserto Siungorico, 1771, *Falk*" (holotype not found in LINN, LE, MW).

= *S. subvaginatum* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg, N.S., 4 (36): 34. December 1893, pro parte ≡ *S. simplex* var. *angustifolium* subvar. *subvaginatum* (Meinshausen) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. simplex* var. *δ subvaginatum* (Meinshausen) Soó, Acta Bot. Acad. Sci. Hung., 17 (1–2): 124. dated 1971, publ. 1972. Type: Finland, Archipelago Aboensi-Krànskor, pr. Kelo, *Ruprecht;* Ins. Sitcha, *Mertens;* Rocky Mountains, reg. alpina, *C. C. Parry* (lectotype to be chosen).

= *S. diversifolium* Graebner, Schriften Naturf. Ges. Danzig., N.F., 9 (1): 335, 1896, pro parte. Type: Poland "Bielawa-Bruch . . . Slawoschin . . . Lübtower See, leg. A. Triechel . . . Wobrow, leg. *Graebner*" (holotype: ?destroyed in B). In a letter to Fernald (cited in Rhodora, 24: 29. 1922) Rothert wrote "Graebner's name [*S. diversifolium*] comprises chiefly *S. simplex* × *minimum* [*S. emersum* × *natans*] and slender forms of *S. simplex;* besides, I have seen specimens of *S. affine* [*S. angustifolium*], *S. minimum, S. glomeratum* and *S. affine* × *minimum* determined by G. himself as *S. diversifolium,* not a single one of all these fitting his description." We have also seen different taxa determined as *S. diversifolium* by Graebner in B.

= *S. chlorocarpum* Rydberg, North American Flora, 17: 8. 30 June 1909 ≡ *S. angustifolium* subsp. *emersum* var. *chlorocarpum* (Rydberg) T. C. Brayshaw, Occasional Papers British Columbia Provincial Museum, 26: 115. 1985. Type: USA, Iowa, Emmet Country, "rare in marshes", September 1898, *Alta Cratty s.n.* (holotype: NY).

= *S. diversifolium* proles *wirtgeniorum* Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 290. 15 June 1897 ≡ *S. wirtgeniorum* (Graebner) Rouy, Fl. France, 13: 339. 1912. Type: Germany, Rheinland, "Laacher See, Rodder Maar, Mülheim b. Köln, Viersen" *Wirtgen* (holotype: ? destroyed in B).

= *S. simplex* proles *longissimum* subvar. *inundatum* Schur ex Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 286. 15 June 1897 ≡ *S. simplex* proles *longissimum* var. *β inundatum* (Schur ex Graebner) Graebner in Engler, Pflanzenreich, 2 (IV.10): 17. September 1900. Type: Austria, "im Prater bei Wien, *Schur*" (holotype: ? destroyed in B).

- *S. simplex* Hudson, Flora Anglica, ed. 2, 2: 401. 1778 ≡ *S. erectum* var. *α simplex* (Hudson) Laestadius, Bihang Wikstöm's Årberättelse, 1850: 1. 1853 or 1854 ≡ *S. emersum* subsp. *simplex* (Hudson) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972; nom. illeg., based on *S. natans* L., see Cook (1985).
- *S. simplex* var. *longissimum* E. M. Fries, Bot. Not., 1868: 71. 1868 ≡ *S. simplex* proles *longissimum* (E. M. Fries) Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora, 1: 285. 15 June 1897 ≡ *S. longissimum* (E. M. Fries) Fritsch, Exkursionsfl. Österreich, ed. 2, 29. 1909; nom. illeg., based on *S. erectum* var. *β boreale* Laestadius.
- *S. simplex* var. *angustifolium* Beckmann, Abhandl. Natforsch. Ver. Bremen, 10: 505. 1889; nom. illeg., combination made in 1867 by Engelman for "*angustifolium*" Michaux.
- *S. emersum* forma *natans* (Glück ex) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972; nom. illeg., Glück's "Formen" represented phenotypically induced states.
- *S. emersum* forma *submersum* (Glück ex) Soó, Acta Bot. Acad. Sci. Hung., 17: 124. dated 1971, publ. 1972; nom. illeg., Glück's "Formen" represented phenotypically induced states.

Robust to slender, submerged, floating or erect herbs.

Stolons up to ca. 50 cm long, (1–)2–3(–4) mm diameter. Leaves of fertile plants usually erect and partially emergent, (10–)20–50(–80) cm long and (1.5–)4–10(–12) mm wide, usually distinctly carinate from base to apex, with 1–3(–5) layers of up to 12 gas chambers.

Plants in deep or swiftly flowing water usually remain sterile; leaves of sterile plants submerged of floating, flat to somewhat keeled, up to 220 cm long and 18 mm wide.

Flowering stems simple, erect, 20–60(–80) cm long or when floating up to ca. 180 cm long, with 1–3 sterile nodes between the corm and the inflorescence.

Inflorescence bracts usually erect and carinate at base with hyaline margin and sometimes somewhat inflated; lowermost bract up to ca. 25 cm long, 1–2(–4) times as long as the inflorescence; bract of upper female head usually not exceeding the inflorescence (Fig. 10 a & b).

Female heads (1–)3–4(–6), the lower usually pedunculate and axillary (peduncles 0–4(–8) cm long), the upper sessile and some usually supra-axillary; in fruit 1.6–2.5(–3.5) cm diameter, appearing white to yellowish-green at anthesis.

Male heads (3–)4–7(–10), remote and distinct at anthesis, separated from the uppermost female head by a 3–20(–40) mm long internode; before anthesis pale yellowish-green.

Female flowers with perianth segments spathulate, translucent, with erose tips, scarcely clawed below (Fig. 2a), one-half to two-thirds as long as the fruit, united at base usually attached to pedicel (pedicel 1.0–2(–3) mm long); stigmas (1.0–)1.5–2(–2.5) mm long, obliquely attached to a 2–3 mm long style.

Male flowers with filaments 5–7 mm long; anthers 1–1.5(–2) mm long.

Fruits fusiform, sometimes slightly constricted around the middle, 3.5–5.5 mm long, ca. 1.8–2.5 mm wide, brown, shiny, tapering above to a 2.0–4.5(–6) mm long beak, tapering below to an obconic base with an up to 4 mm long (by shrinkage of the fruit)

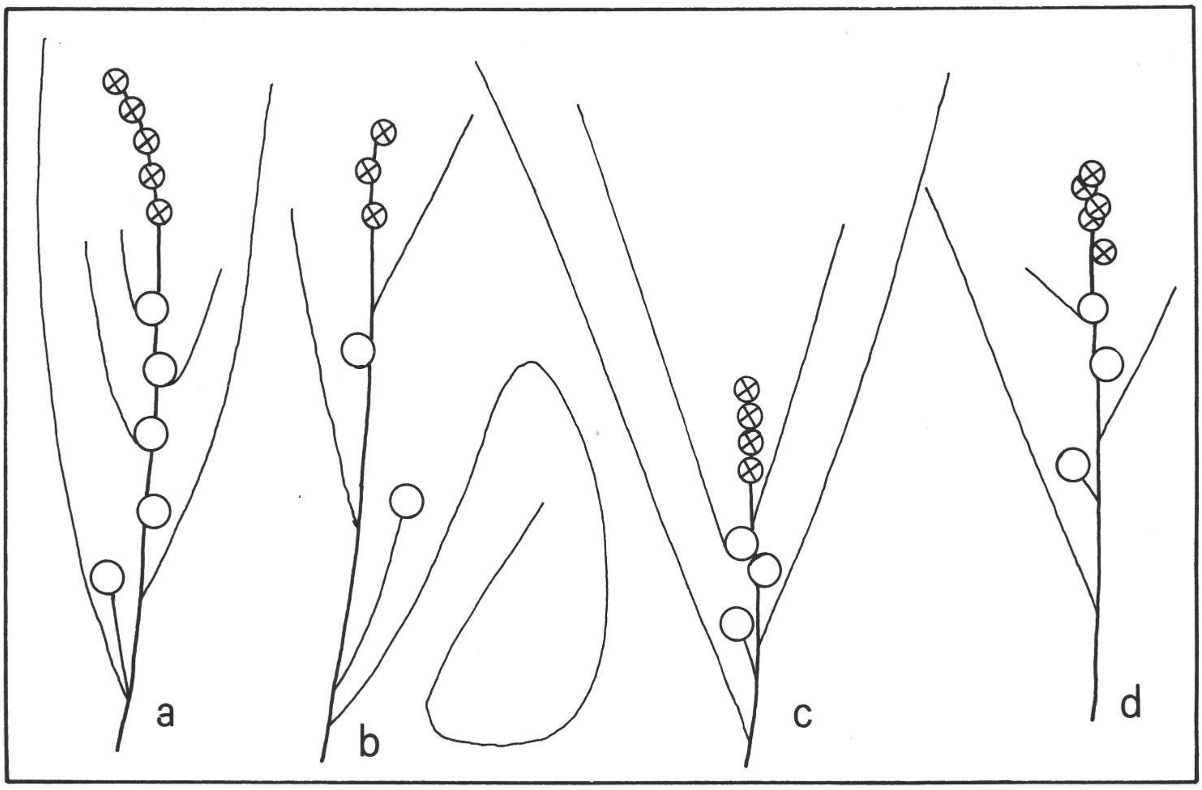


Fig. 10. Diagrammatic representation of inflorescences of: a, *Sparganium emersum* subsp. *emersum* (typical European inflorescence); b, *S. emersum* subsp. *emersum* (typical N. American inflorescence); c, *S. emersum* subsp. *acaule;* d, *S. angustifolium* × *S. emersum* subsp. *emersum.*

stalk; endocarp ovoid, 2.5–3.5 mm long, ca. 1.8–2.5 mm diameter, tapered below to a 1–4 mm long stalk, smooth with some fine longitudinal ridges (Fig. 8c).

Diagnostic features

Inflorescence simple; male heads 3 or more, remote and distinct at anthesis; stigmas more than 1 mm long; anthers 1–2 mm long; perianth segments translucent (heads appearing white to greenish-yellow at anthesis); upper female heads usually sessile and supra-axillary; leaves and lower bracts of flowering plants usually erect and distinctly carinate to apex. It may superficially resemble species of the *S. americanum* group; the presence of thin, translucent perianth segments is the distinguishing feature, see also Table 1 in part 2 (subgenus *Sparganium*).

Distribution

S. emersum has a holoarctic distribution with the main area in the temperate zone, Maps 12 and 13. It is found on lower ground throughout Europe from about the arctic circle to the submediterranean zone. In Asia it extends from the arctic circle south to about 40° N (growing between 1900 and 2300 m in Anatolia), eastward to Japan; there are isolated occurrences south of 40° N in high land in the Gilgit Wazerat district, around Nanga Parbat, Northern Area of Kashmir (3000 m) and Helan Shan (China).

In America it extends from east to west, from south of the arctic circle to about 40° N; in the southern parts of its range it is usually found at high levels, reaching 2900 m in Colorado and 2500 m in Wyoming.

The record from Sumatera is incorrect; it refers to *S. fallax*.

Ecology

We have experience of *S. emersum* in the field in central, west and southern Europe and have seen in growing in western N. America. It is found in a wide variety of aquatic habitats in still and flowing water but usually grows near the bank, particularly in somewhat disturbed or unstable places. Stolons are well-developed but *S. emersum* very rarely becomes dominant and is usually found in relatively small stands (up to about 12 m^2) or isolated clumps of shoots. Although it can tolerate periods of drought it is essentially an aquatic species that is partly or totally submerged most of the time.

S. emersum is relatively deep-rooted (15 cm or more deep) and is very tolerant to disturbance. For example, it is frequent in *Phragmites* or other reed-swamp communities in clearings or channels that are artificially maintained (for boating, fishing, swimming etc.); it also grows in ricefields in Europe without however, becoming a serious weed. It is mostly found in places where it is subjected to rapid changes in water level or irregular flooding.

Plants are not easily dislodged and it can stand severe spates. The leaves are somewhat frail and are frequently damaged following floods or disturbance but they seem to be quickly replaced. In a stream in Denmark, Waggers Neilson et al. (1985) found the lifetime of individual leaves was only 31–39 days and that the mortality rate constituted more than 50% of the production rate before maximum biomass was attained. These findings elegantly demonstrate that standing crop cannot be used as a measure for annual production.

It is usually found in shallow water (20–80 cm deep) but has been recorded in water up to 2.6 m deep in Finland. The leaves of *S. emersum* rarely grow more than 2 m long and they are usually much shorter so that plants in deep or in swiftly-flowing water remain submerged. Water quality does not seem to be very important; although it is most common in mesotrophic to semieutrophic conditions, it may occasionally be found in almost oligotrophic or strongly eutrophic water but is not tolerant to brackish water and is rarely found in salinities exceeding 0.2%. The substrate preferences are rather more restricted. It grows best in deep clay or fine, sandy soils. It is a characteristic species in the silted parts of small rivers and streams. In meandering rivers one tends to find it at almost each curve. It is also found along the banks of ponds, lakes, canals and drainage ditches. In Europe, it is ecologically rather like *Sagittaria sagittifolia* and both species frequently grow in an association named Sparganiieto-Sagittarietum.

Sparganium emersum shows a rather wide ecological spectrum but is a poor competitor which probably accounts for its inability to become dominant. Its performance is however not alike in all habitats and it is frequently found in a nonflowering state. For flowering it seems to need shallow water (less than 50 cm deep), a lot of light and little competition. Its poor ability to compete is compensated by its ability to withstand disturbance. Nevertheless, it does not possess the high growth rate that one expects from a ruderal (Grime 1979). As it grows in and is active in collecting and consolidating silt it is essentially a species in the middle of the aquatic hydrosere whereby aquatic habitats are converted into terrestrial ones.

Variation

S. emersum is a polymorphic species showing variation in the following characters: leaf-width, number and position of male and female heads, stigma length and anther length. In the past this has led to differing opinions regarding the taxonomic boundaries of the species and particularly in distinguishing it from *S. angustifolium.* The situation is complicated by the occurrence of hybrids (see p. 255).

Packer (1983) has reviewed these taxonomic failings. Comparing two recent keys to the species (Reveal, in Cronquist et al. 1977, and Cook, in Tutin et al. 1980) he found some suprising differences. Reveal describes *S. angustifolium* as having 2–5 male heads and in the accompanying illustration these are clearly depicted as being remote. The account also describes the leaves of both species as flat or rounded (but considers those of *S. emersum* as being weakly keeled underneath). Neither of these assertions are correct. It is unfortunate that Reveal's account should confuse these two attributes since they are of major importance in understanding the distinction between the species. The leaves of *S. angustifolium* are flat or abaxially convex but those of *S. emersum* are clearly triangular, at least, at the base. The most striking single attribute of *S. angustifolium* is that the male heads are less than four in number and contiguous (giving the appearance of a single elongated head); this is never the case in *S. emersum.* While Packer (1983) is correct in recognizing these difficulties, his decision to combine *S. emersum* (and *S. chlorocarpum*) under the single specific name *S. angustifolium* only makes matters worse.

The position of the female heads of *S. emersum* ranges from axillary and sessile to supra-axillary and pedunculate. There appears to be little geographic consistency in these attributes with the exception of subsp. *acaule* (see p. 257) which is confined to the northeast of North America; it has female heads that are typically crowded, supra-axillary and sessile. Generally, large and robust plants of *S. emersum* have the lower female heads pedunculate while small depauperate plants have fewer and sessile heads.

The position and number of the male heads also varies; while typically distinct at anthesis, the immature heads can be observed crowded at the distal end of the inflo-

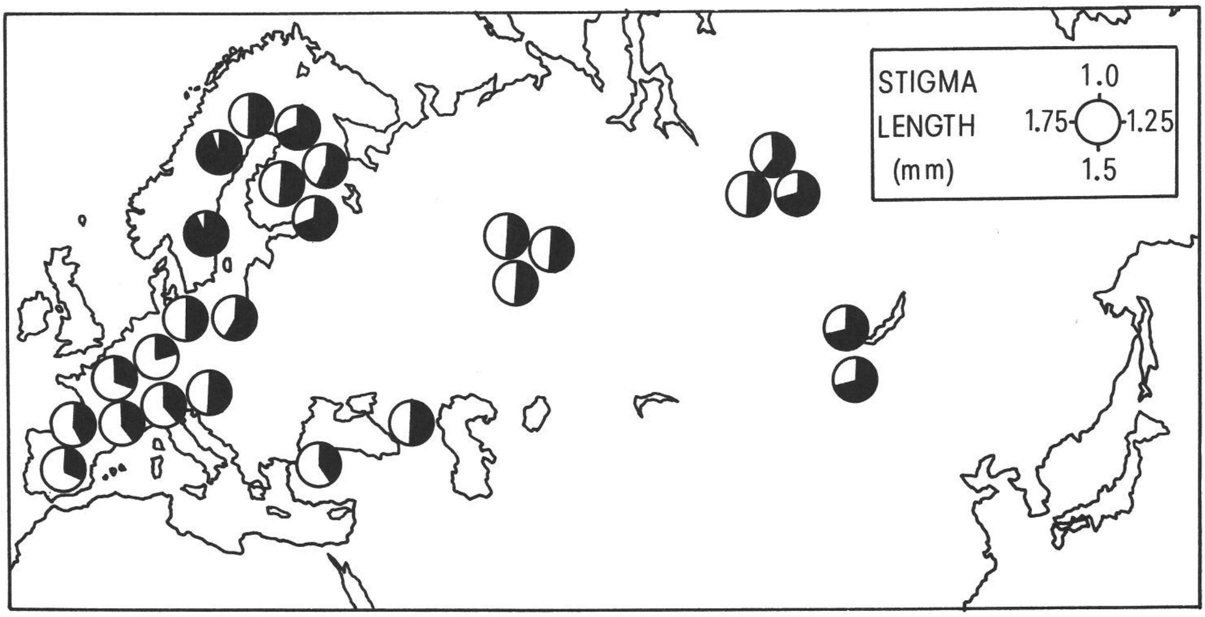


Fig. 11. Map representing the length of the stigmas of *Sparganium emersum* in Eurasia.

rescence. Variation in stigma length and anther length is strongly related to geography (see Fig. 11). Plants from west and central Europe possess relatively small stigmas (1.0–1.5 mm long) and anthers (1.0–1.3 mm long). Specimens from Scandinavia, eastern Europe, Turkey, Afghanistan and Siberia have longer stigmas (1.5–2.0 mm long) and anthers (1.3–1.6 mm long). The variation pattern is clinal from east to west.

Specimens of *S. emersum* from northwest North America often show characteristics of *S. angustifolium.* Particularly confusing is the number and arrangement of male heads; often there are three or four heads, the lowest is remote but often the upper are somewhat contiguous (Fig. 10b). Also the lowest bracts are often much longer than the inflorescence. The habit, arrangement of female heads and the dimensions of the flowers are all typically *S. emersum.* Populations appear to be constant in form and there is no evidence of segregation. It is possible that these plants are "stabilized" hybrids or backcrosses involving *S. angustifolium* but we agree with Rothert (determinations on herbarium sheets) that these plants are nevertheless assignable to *S. emersum.*

Several authors, including Casper & Krausch (1980) are convinced that the plants of deep or flowing water with long, band-like leaves are taxonomically distinct from the erect, partly emergent plants. Although the plants in extreme states do look very different, there is no convincing evidence to suggest that these states are genetically distinct. It is at times tempting to give formal taxonomic recognition to extreme phenotypes but is it not currently in accordance with taxonomic practice.

Hybrids

The following hybrids have been reported in nature (none have been raised after crossing experiments):

1×7. *Sparganium hyperboreum* × *S. emersum.* These species are largely allopatric. However, in Scandinavia they sometimes grow near together and Lid (1952) has recorded hybrids. From the available herbarium material we are not convinced that this hybrid exists.

2×7. *Sparganium natans* × *S. emersum* (often but incorrectly named *S. wirtgeniorum* (Graebner) Rouy). Many workers including Rothert (1910, 1913) are convinced that this hybrid exists. Both species often grow near together so one might expect hybrids where they are sympatric. We have seen no herbarium material that we consider to belong to this hybrid, also in the field we have never found hybrid plants in regions where both species grow together. We therefore doubt that this hybrid exists. In any case, on morphological grounds alone it may be difficult to distinguish it from some segregants of *S. emersum* × *S. angustifolium, S. emersum* × *S. glomeratum* or *S. emersum* × *S. gramineum.*

3×7. *Sparganium angustifolium* × *S. emersum.*

= *S. diversifolium* Graebner, pro parte, Schriften Naturforsch. Ges. Danzig, N.F., 9 (1): 335. 1896, pro parte. Type: Poland, "Lübtower See", "Bielawa-Bruch" (holotype: destroyed in B).

– *S. boreale* Beurling, Öfersigt Kongl. Vetenskaps-Akad. Förhandl. (Stockholm), 9 (8): 192, 13 October 1852, nomen nudum ≡ *S. erectum* var. *β boreale* (Beurling) Laestadius, Bihang till Wikström's Årberättelse, 1850: 1. ?1853, nomen illeg., based on *S. natans* L. (authentic material of *S. boreale* is in S; see Cook 1985).

– *S.* × *zetlandicum* G. C. Druce, British Plant List, ed. 2, 115. 1928, nomen nudum.

– (*S. borderi* [sic] W. O. Focke is often considered to be a hybrid but the type material is clearly terrestrially grown *S. angustifolium*).

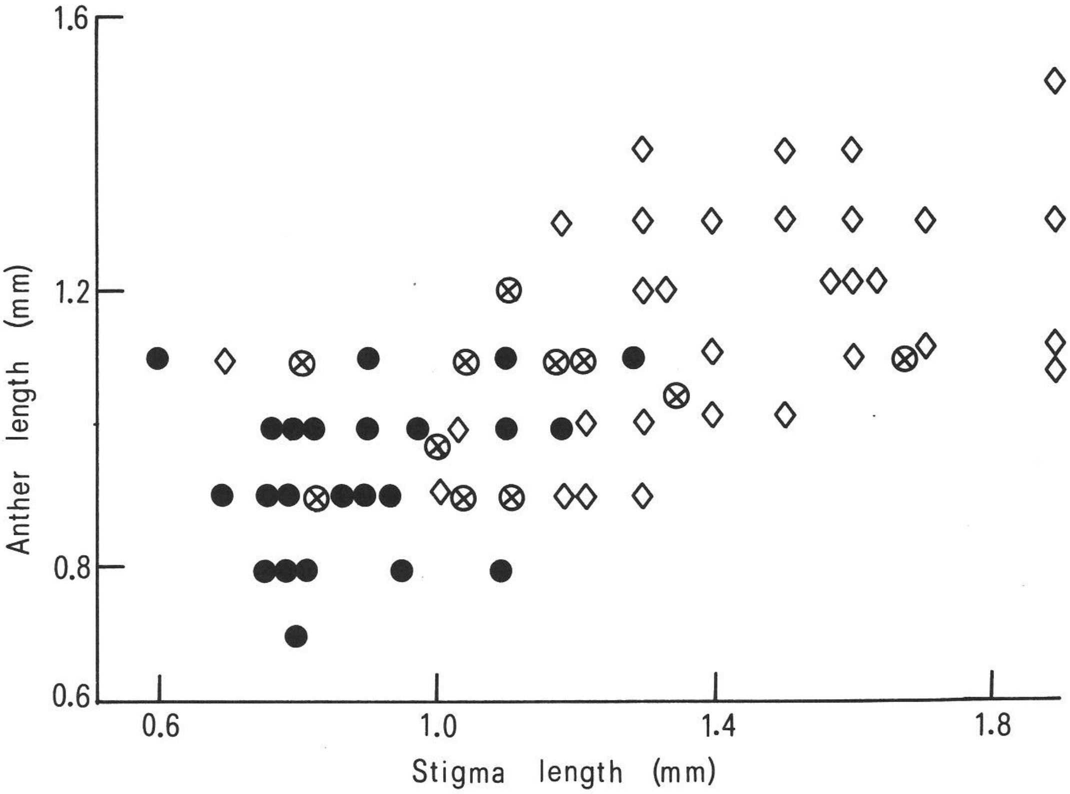


Fig. 12. A pictorialized scatter diagramme showing the relationship between anther length (vertical axis) and stigma length (horizontal axis) in *Sparganium angustifolium* (closed circle), *S. emersum* (diamond) and *S. angustifolium* × *S. emersum* (circle with cross).

Hybrids are intermediate between the parents in vegetative and floral characters. The F_1 is highly fertile. Segregants and backcrosses are frequent and an almost continuous variation pattern between the parents is found. The F_1 has the inflated leaf-bases of *S. angustifolium* (even when growing terrestrially) but the remote male heads of *S. emersum* (Fig. 10d). Stigma length and anther size are intermediate (Fig. 12).

S. emersum is mostly found in eutrophic conditions while *S. angustifolium* is confined to more or less oligotrophic waters. Most of the range of *S. angustifolium* lies within that of *S. emersum.* In northern Europe hybrids are common and usually grow with one or both parent species. In northwestern North America there is evidence that some *S. angustifolium* characters have become incorporated into *S. emersum* and that "pure" *S. emersum* (as it is realized in Europe) has been replaced by a relatively stable hybrid (Fig. 10b).

In western Scotland eutrophic and oligotrophic pools are often found near together; in Stoer, Wester Ross (now Highland) a hybrid population was seen (by C.D.K.C.) growing on a shingle beach, a habitat not exploited by either parent.

4×7. *Sparganium glomeratum* × *S. emersum.* In 1910 Rothert omitted this hybrid from his account of *Sparganium* hybrids but in 1916 he lists it without any description. Lid (1952) reports it from southern Scandinavia. We have seen no convincing material but feel that it may well exist but would be very difficult to distinguish from *S. angustifolim* × *S. emersum* (see above).

Table 3. Comparison of *S. emersum, S. gramineum* and their hybrid.

Character	*S. emersum*	Hybrid	*S. gramineum*
Inflorescence	Simple	Usually branched	Usually branched
Lowest ♀ bract/inflorescence ratio	1.0–4.0	1.3–3.4	1.0–2.0
Position of upper female heads	Supra-axillary	Supra-axillary	Axillary
Male head number	3–10	3–7	2–6
Male heads at anthesis	Distinct	Contiguous	Contiguous
Stigma length (mm)	More than 1.0	0.6–1.0	0.6–0.7
Beak	Straight	Straight or curved	Deflexed

5×7. *Sparganium gramineum* × *S. emersum.*

= *S. speirocephalum* L. M. Neuman in Hartman, C. J. & Hartman, C., Handbok Skand. Flora, ed. 12, 109. October 1889, pro parte. Type: Sweden (lectotype to be chosen from material in UPS; isotype B).

– *S. longifolium* Turczaninow Bull. Soc. Imp. Nat. Moscou, 1: 103. 1838. nomen illeg., nomen nudum. "Type": USSR, Buryatskaya, ASSR, Dahurica, "Ad fl. Angaram superiorum, 1834, *Turzmannoff*" (K).

This hybrid is common in regions where both parents grow together (Map 10). The hybrid is much more tolerant of eutrophic conditions than *S. gramineum* and may occupy areas where *S. gramineum* is absent or in habitats where *S. gramineum* has become extinct due to increasing eutrophication. The hybrid is fully fertile and while some segregation or back-crossing may be evident it is usually distinct (see Table 3 and Fig. 9c, d).

This hybrid is often difficult to distinguish from *S. gramineum* × *S. angustifolium* (Fig. 9a, b). The latter hybrid usually has 2–3 contiguous male heads, inflated bases to the inflorescence bracts, a simple inflorescence with some supra-axillary female heads and it grows in oligotrophic water.

7B. **Sparganium emersum** subsp. **acaule** (Beeby ex Macoun) C. D. K. Cook & M. S. Nicholls, comb nov. ≡ *S. simplex* var. *acaule* Beeby ex Macoun, Geological & Natural History Survey of Canada, Cat. Canadian Plants, Part 5 (Acrogens): 367. 1890 ≡ *S. diversifolium* var. *acaule* (Beeby ex Macoun) Fernald & Eames, Rhodora, 9: 88. May 1907 ≡ *S. acaule* (Beeby ex Macoun) Rydberg, North American Flora, 17: 8. 30 June 1909 ≡ *S. chlorocarpum* var. *acaule* (Beeby ex Macoun) Fernald, Rhodora, 24: 29. February 1922 ≡ *S. chlorocarpum* forma *acaule* (Beeby ex Macoun) E. G. Voss, Rhodora, 68: 436. October–December 1966. Type: Canada, "Quite common in ponds and wet spots by the road-side in many parts of Prince Edward Island, especially at Lake Verde, Brackley Point and Winter River", 1888, *Macoun* (lectotype to be chosen at CAN).

= *S. diversifolium* proles *γ nanum* Graebner in Engler, Pflanzenreich, 2 (IV. 70): 21. September 1900. Type: North America: "Neuengland: White Mountains (*Tuckerman jun.!*); Terra Nova (*Lapylaie!*)" holo- or lectotype destroyed in B.

Like *S. emersum* sensu stricto but usually smaller and less robust; leaves 3–7 mm wide; basal leaves and lower inflorescence bracts strongly erect and conspicuously longer than the flowering stems (Fig. 10c); female heads supra-axillary, sessile and crowded (the lowermost sometimes remote and pedunculate); anthers 0.8–1.0 mm long; stigmas 0.8–1.5(–1.7) mm long; fruits 3–4 mm long, ca. 1.5 mm wide, light brown, constricted around the middle; beak 3–4 mm long, about equal to the fruit body in length (Fig. 8 d).

Distribution

It is confined to eastern North America (Map 13), extending from Newfoundland southwards to Virginia and reaching westwards south of the Great Lakes to Minnesota and Iowa. It does not totally replace *S. emersum* subsp. *emersum* in this region although it is by far the most frequent of the two.

Notes

In its characteristic form, *S. emersum* subsp. *acaule* is easily distinguished on account of its erect habit and conjested female heads. Nevertheless, detailed studies suggest that a range of intermediates exist between it and subsp. *emersum* and that since the major differences are qualitative, it is often difficult to distinguish the two with confidence. In view of this and its limited distribution we have recognized it at the rank of subspecies. Its ecology is probably like *S. emersum* subsp. *emersum* but from examination of herbarium material it would seem to grow better in very shallow water.

Résumé

Révision taxonomique complète du genre *Sparganium* (Sparganiaceae) avec clé, et descriptions complètes de chaque espèce y compris les diagnoses, synonymes avec typifications, cartes de distribution, variabilité et illustrations qui elles-memes contiennent des informations sur les fossils, l'anatomie, la morphologie, les chromosomes, la biologie forale, la propogation, l'écologie, les parasites et animaux prédateurs, des aspects appliqués ainsi que les hybrides. Quatorze espèces et six sous-espèces sont reconnues. Dans la partie 1, sous-genre *Xanthosparganium,* 7 espèces sont présenteés, Un seul nouveau nom est employé: ***Sparganium emersum*** subsp. ***acaule*** (Beeby ex Macoun) C. D. K. Cook & M. S. Nicholls.

References

Abuziarova R. J. 1970. Spore-pollen complexes in the south of the Altai, locality Bukhtama (in Russian). Botaničeskij Žurnal Akad. Nauk SSSR. (Leningrad) 55: 1121–1126.

Arohonka S. 1982. Kromosomilukumääritysiä Nauvon Seilin saaren putkilokasveista Turun Yliopiston Biologian Laitoksen Julkaisuja, 3: 1–12; n.v. cited by Uotila P. & Pellinen K., 1985. Acta Bot. Fennica 130: 1–37.

Benum P. 1958. The Flora of Troms Fylke. Tromsø Museums Skrifter 6: 82–84.

Berry E. W. 1924. A. *Sparganium* from the Middle Eocene of Wyoming. Bot. Gaz. 78: 342–348.

Bijok K. & Młynek T. 1965. Badania cytologiczne nad trzema gatunkami rodzaju *Sparganium* L. Zesz. Nauk WSR. w Olsztynie 19: 205–211.

Bijok K. & Adamkiewicz E. 1971. Badania kariologiczne nad dwoma gatunkami rodzaju *Spanganium* [sic]. Acta Soc. Bot. Poloniae 40: 143–148.

Brayshaw T. C. 1985. Pondweeds and Bur-reeds, and their relatives, of British Columbia. Occasional Papers of the British Colombia Provincial Museum 26: 1–167.

Casper S. J. & Krausch H.-D. 1980. Pteridophyta und Anthophyta. 1. Teil: Lycopodiaceae bis Orchidaceae. Süßwasserflora von Mitteleuropa, ed. Ettl H., Gerloff J. & Heynig H., 23: 76–91. VEB Gustav Fischer Verlag, Jena.

Chen Yao-Dong 1981. A study on Chinese *Sparganium* (in Chinese). Acta Phytotaxonomica Sinica 19: 41–57.

Cook C. D. K. 1961 a. *Sparganium* in Britain. Watsonia 5: 1–10.

Cook C. D. K. 1961 b. Die bayerischen *Sparganium*-Arten Ber. Bayer. Bot. Ges. 34: 7–10.

Cook C. D. K. 1962. Biological Flora of the British Isles, No. 82: *Sparganium erectum* L. J. Ecology 50: 247–255.

Cook C. D. K. 1963. *Sparganium* nomenclature. Proc. Bot. Soc. British Isles 5: 124.

Cook C. D. K. 1985. *Sparganium:* some old names and their types. Bot. Jahrb. Syst. 107: 269–276.

Cronquist A., Holmgren N., Reveal J. & Holmgren P. 1977. Intermountain Flora 6: 465–468. Columbia Univ. Press, New York.

Crow G. E. & Hellquist C. B. 1981. Aquatic vascular plants of New England: Part 2. Typhaceae and Sparganiaceae. New Hampshire Agric. Exper. Station Bull. 517: 1–21.

Dietz S 1887. Über die Entwicklung der Blüte und Frucht von *Sparganium* Tourn. und *Typha* Tourn. Bibliotheca Botanica 5: 1–56.

Dorofeev P. I. 1979. On taxonomy of Tertiary *Sparganium* (in Russian). Sovietskaya palaeokarpologya. Publishing House Nauka, Moscow, 53–75.

Duke J. A. & Ayensu E. S. 1985. Medicinal plants of China. Vol. 2, p. 614. Reference Publishing Inc., Algonac, Michigan.

Feráková V., in Májovský J. 1974. Index of chromosome numbers of Slovakian flora. Acta Fac. Rerum Nat. Univ. Comenianae, Bot., 23: 1–23.

Fernald M. L. & Eames A. J. 1907. Preliminary lists of New England plants. – XX. Sparganiaceae. Rhodora 8 (85): 86–90.

Gadella T. W. J. & Kliphuis E. 1973. Chromosome numbers of flowering plants of the Netherlands. Proc. Koninkl. Nederl. Akad. Wetenschappen, ser. C, 76: 303–311. (repr.: Mededel. Bot. Mus. Herb. Rijksuniv. Utrecht, No. 392: 303–311).

Gervais C. 1981. Liste annotée de nombres chromosomiques de la flore vasculaire du nord-est de l'Amerique. II. Naturaliste Canad. 108: 143–152.

Glück H. 1938. Über das Vorkommen des arktischen *Sparganium hyperboreum* in der zentraleuropäischen Alpenkette. Bot. Jahrb. 69: 220–251.

Graebner P. O. P. P. 1900. Sparganiaceae, in Engler H. G. A., Das Pflanzenreich 2 (IV.10): 10–24.

Grime J. P. 1979. Plant strategies and vegetational processes. John Wiley & Sons, Chichester, New York, Brisbane, Toronto. pp. 1–222.

Guppy H. B. 1906. Observations of a naturalist in the pacific between 1896 and 1899. Vol. 2, Plant-Dispersal. Mac Millan, London. pp. 627.

Hagerup O. 1941. Nordiske Kromosom-Tal. I. Bot. Tidsskr. 45: 385–403.

Harada I. 1949. Chromosome numbers in *Pandanus, Sparganium* and *Typha.* Cytologia 14: 214–218.

Harms V. L. 1973. Taxonomic studies of North American *Sparganium,* I *Sparganium hyperboreum* and *S. minimum.* Canad. J. Bot. 51: 1629–1641.

Hegelmaier F. 1874. Zur Entwicklungsgeschichte monokotyledoner Keime nebst Bemerkungen über die Bildung der Samendeckel. Bot. Zeitung 32 (29): 631–640.

Hultén E. 1964. The circumpolar plants. Kungl. Svenska Vetenskapsakad. Handl. F.S. 8 (5): 1–280.

Jörgensen C. A., Sörensen T. H. & Westergaard M. 1958. The flowering plants of Greenland. A taxonomical and cytological survey. Kongl. Danske Videnskab. Selskab. Biol. Skrift. 9 (4): 1–172.

Kaul R. B. 1972. Adaptive architecture in emergent and floating *Sparganium.* Amer. J. Bot. 59: 270–278.

Kaul R. B. 1973. Development of foliar diaphragms in *Sparganium eurycarpum.* Amer. J. Bot. 60: 944–949.

Kaul R. B. 1976. Anatomical observations on floating leaves. Aquatic Bot. 2: 270–278.

Kirchner O., Löw E. & Schröter C. 1908. Lebensgeschichte der Blütenpflanzen Mitteleuropas 1 (1): 374–394. Eugen Ulmer, Stuttgart.

Kožuharov S. & Kuzmanov B. 1964. Chromosome numbers of four Bulgarian plants. Comptes Rendus Acad. Bulgare Sci. 17 (5): 491–494.

Lakela O. 1941. *Sparganium glomeratum* in Minnesota. Rhodora 43: 83–85.

Larsen K. 1965. IOPB Chromosome number reports. III. Taxon 14: 50–57.

Leereveld H. 1984. Anthecological relations between reputedly anemophilous flowers and syrphid flies. VI. Aspects of the anthecology of Cyperaceae and *Sparganium erectum* L. Acta Bot. Neerl. 33: 475–482.

Lid J. 1952. Norsk Flora. Det Norske Samlaget, Oslo. pp. 1–771.

Löve Á. & Löve D. 1942. Chromosome numbers of Scandinavian plant species. Bot. Not. 1942: 19–59.

Löve Á. & Löve D. 1948. Chromosome numbers of northern plant species. Atvinnudeild Háskólans Rit Landbúna ar-deilar, B-flokkur 3: 9–131.

Löve Á. & Löve D. 1956. Cytotaxonomical conspectus of the Icelandic flora. Acta Horti Gothoburgensis 20 (4): 65–291.

Löve Á. & Löve D. 1975. IOPB chromosome number reports XLVIII. Taxon 24: 367–372.

Löve Á. & Löve D. 1981. Chromosome number reports LXXII. Taxon 30: 694–708.

Löve Á. & Ritchie J. C. 1966. Chromosome numbers from central Canada. Canad. J. Bot. 44: 429–439.

Mai D. H. 1985. Entwicklung der Wasser- und Sumpfpflanzen-Gesellschaften Europas von der Kreide bis ins Quartär. Flora 176: 449–511.

Martin A. C. & Uhler F. M. 1939. Food of game ducks in the United States and Canada. Techn. Bull. US. Dep. Agric. 634: 1–157.

Mehra P. N. & Pandita T. K. 1979. IOPB chromosome number reports LXIV. Taxon 28: 391–408.

Muller J. 1984. Significance of fossil pollen for angiosperm history. Annals Missouri Bot. Garden 71: 419–443.

Müller-Doblies Ute 1969. Über den Blütenstand und Blüten sowie zur Embryologie von *Sparganium*. Bot. Jahrb. Syst. 89: 359–450.

Müller-Doblies Dietrich 1970. Über die Verwandtschaft von *Typha* und *Sparganium* im Infloreszenz- und Blütenbau. Bot. Jahrb. Syst. 89: 451–562.

Müller-Doblies Ute & Müller-Doblies Dietrich 1977. *Sparganium* in Hegi G., Illustr. Flora Mitteleuropa, ed. 3, II. 1 (4): 275–317.

Murin A. in Májovský J. 1978a. Index of chromosome numbers of Slovakian flora (Part 6) Acta Fac. Rerum Nat. Univ. Comenianae, Bot., 26: 1–42.

Murin A. in Májovský J. 1978b. IOPB chromosome number reports LXI. Taxon 27: 375–392.

Packer J. G. 1983. Flora of Alberta: *Sparganium angustifolium* and *Erigeron trifidus*. Canad. J. Bot. 61: 359–366.

Pinkess L. H. 1980. The possibility of pollination of *Sparganium erectum* by insects. Proc. Birmingham Nat. Hist. Soc. 24: 101–102.

Porsild A. E. 1951. Botany of Southeastern Yukon adjacent to the Canol road. Nat. Mus. Canad Bull. 121: 76.

Praeger R. L. 1913. On the buoyancy of the seeds of some Brittanic plants. Scient. Proc. Royal Dublin Soc. 14: 13–62.

Reveal J. L. 1970. *Sparganium simplex* Huds., a superfluous name. Taxon 19: 796–797.

Rothert W. 1910. Übersicht der Sparganien des Russischen Reiches (zugleich Europa's). Acta Horti Bot. Univ. Imper. Jurjevensis 11: 11–32.

Rothert W. 1913. In Fedtschenko B. A., Flora Aziatskoi Rossii 1: 17–37, St. Petersburg.

Saccardo F. 1895. Ricerche sull' anatoma della Typhaceae. Malpighia 9: 3–30.

Scheerer H. 1940. Chromosomenzahlen aus der schleswig-holsteinischen Flora. I. Planta 29: 636–642.

Sokolovskaya A. P. 1963. Geographic distribution of polyploid plants (observations from the Kamchatka Peninsula), in Russian. Vestnik Leningradskoza Universiteta 3 (15): 38–52.

Sokolovskaya A. P. 1972. Karyological characteristics of the flora of the Leningrad district (in Russian). Vestnik Leningradskoza Zbuversutetam 21: 60.

Solereder H. & Meyer F. J. 1933. Systematische Anatomie der Monokotyledonen, I, pt. 1: 50–67. Gebrüder Borntraeger, Berlin.

Stace C. A. 1975. Hybridization and the flora of the British Isles. Academic Press, London, New York, San Francisco. pp. 1–626.

Taylor R. L. & Mulligan G. A. 1968. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. Queen's Printer, Ottawa. pp. 148.

Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. 1980. Flora Europeae 5: 274–275. 1980. Cambridge Univ. Press, Cambridge.

Váchová M. in Májovský J. 1976. Index of chromosome numbers of Slovakian flora (Part 5). Acta Fac. Rerum Nat. Univ. Comenianae, Bot., 25: 1–18.

Velenovský J. & Viniklář L. 1926. Flora cretacea Bohemiae. I. Rozpr. Stat. Geol. Ust. ČSR. 1: 1–157.

Waggers Nielsen L., Nielsen K. & Sand-Jensen K. 1985. High rates of production and mortality of submerged *Sparganium emersum* Rehman [sic] during its short growth season in a [sic] eutrophic Danish stream. Aquatic Botany 22: 325–334.

Wulff H. D. 1938. Chromosomenstudien an der schleswig-holsteinischen Angiospermen-Flora. II. Ber. Deutsch. Bot. Ges. 56: 247–254.

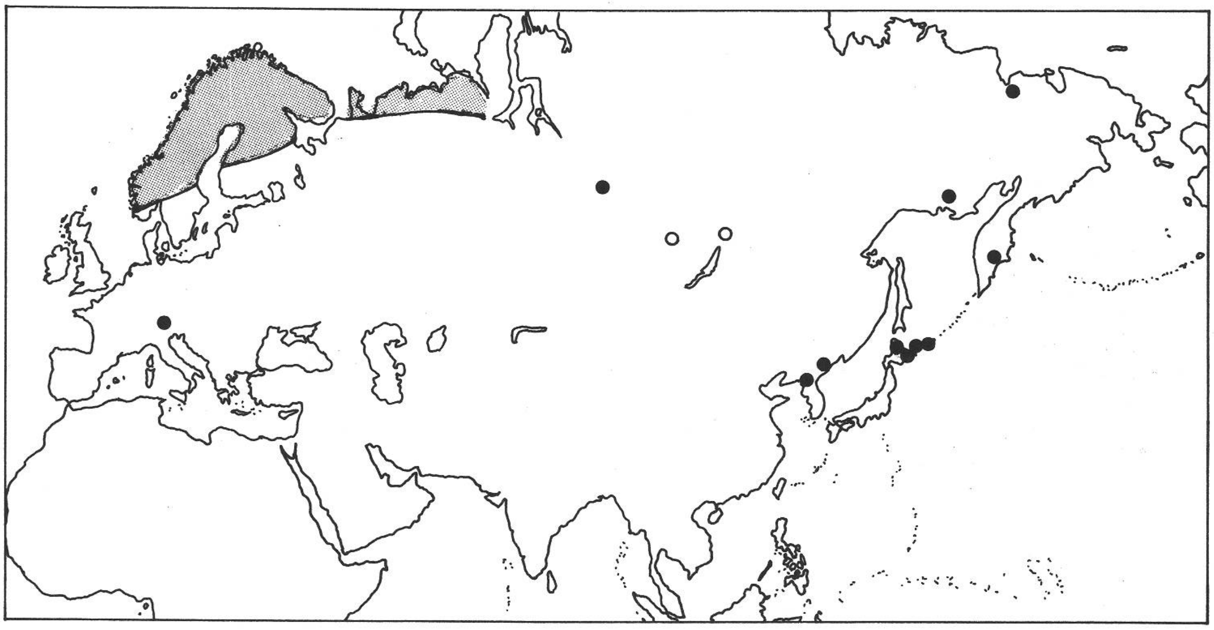
Yuzepchuk S. V. 1934. In Komarov V. L., Flora of the USSR. Izdatel'stvo Akademii Nauk SSSR. (Leningrad) 1: 216–229.

Zhukova P. G. 1980. Chromosome numbers of some Southern Chukotka plant species (in Russian). Botaničeskij Žurnal Akad. Nauk SSSR. (Leningrad) 65 (1): 51–59.

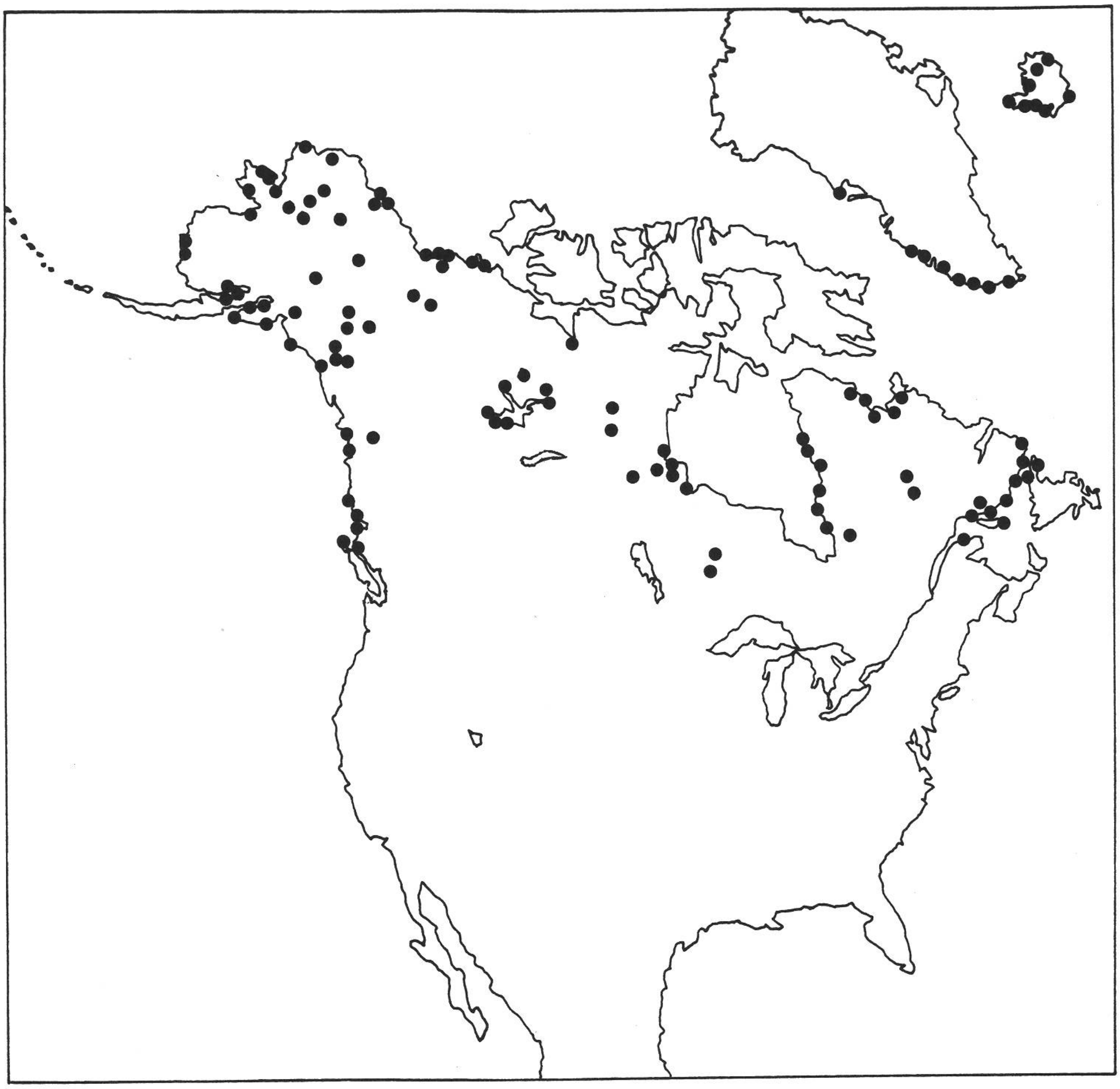
Zhukova P. G. & Petrovsky V. V. 1976. Chromosome numbers of some Western Chukotka plant species, II (in Russian). Botaničeskij Žurnal Akad. Nauk SSSR. (Leningrad) 61 (7): 963–969.

Zhukova P. G. & Tikhonova A. D. (1971). Chromosome numbers of certain plant species indigenous to the Chukotskiy province (in Russian). Botaničeskij Žurnal Akad. Nauk SSSR. (Leningrad) 56: 868–875.

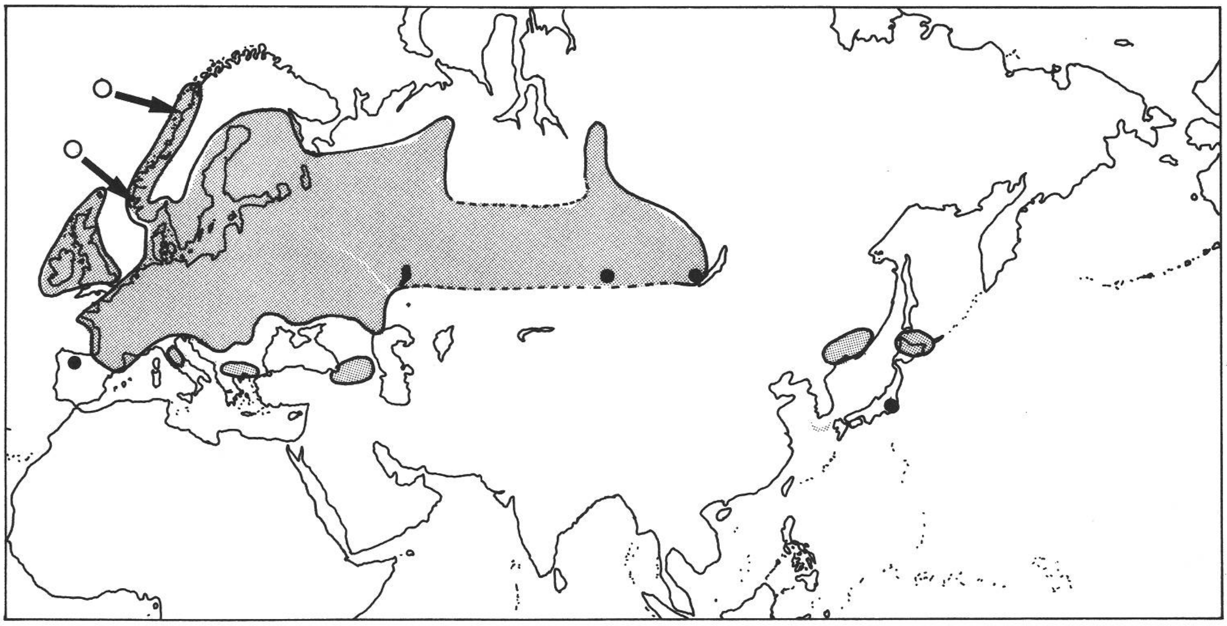
Maps



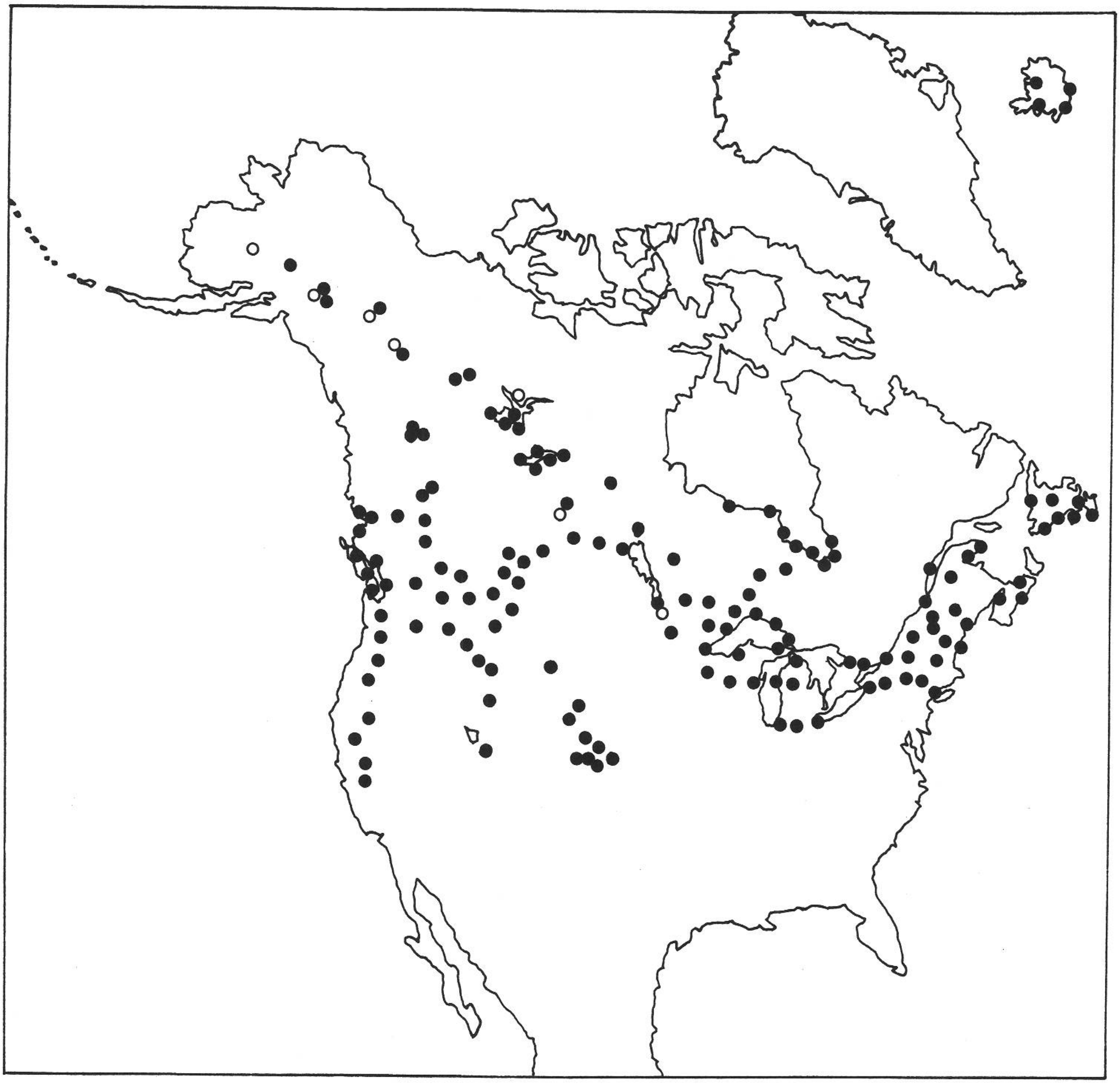
Map 1. *Sparganium hyperboreum* in Eurasia. Open circles denote unconfirmed literature records.



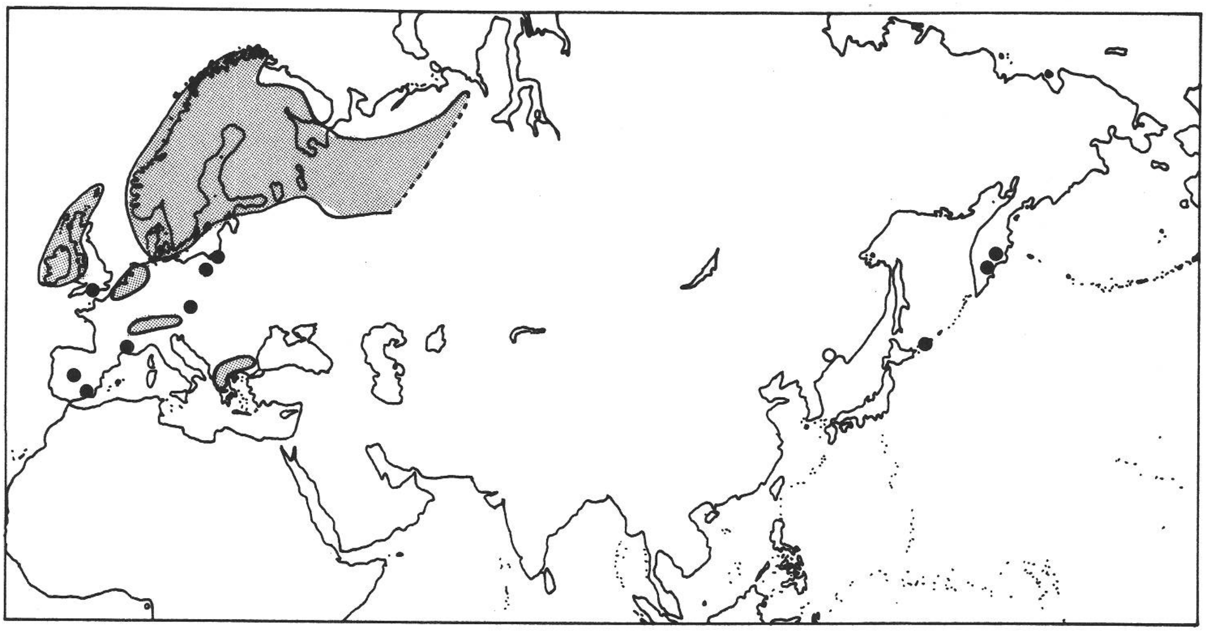
Map 2. *Sparganium hyperboreum* in N. America, including records published by Harms (1973).



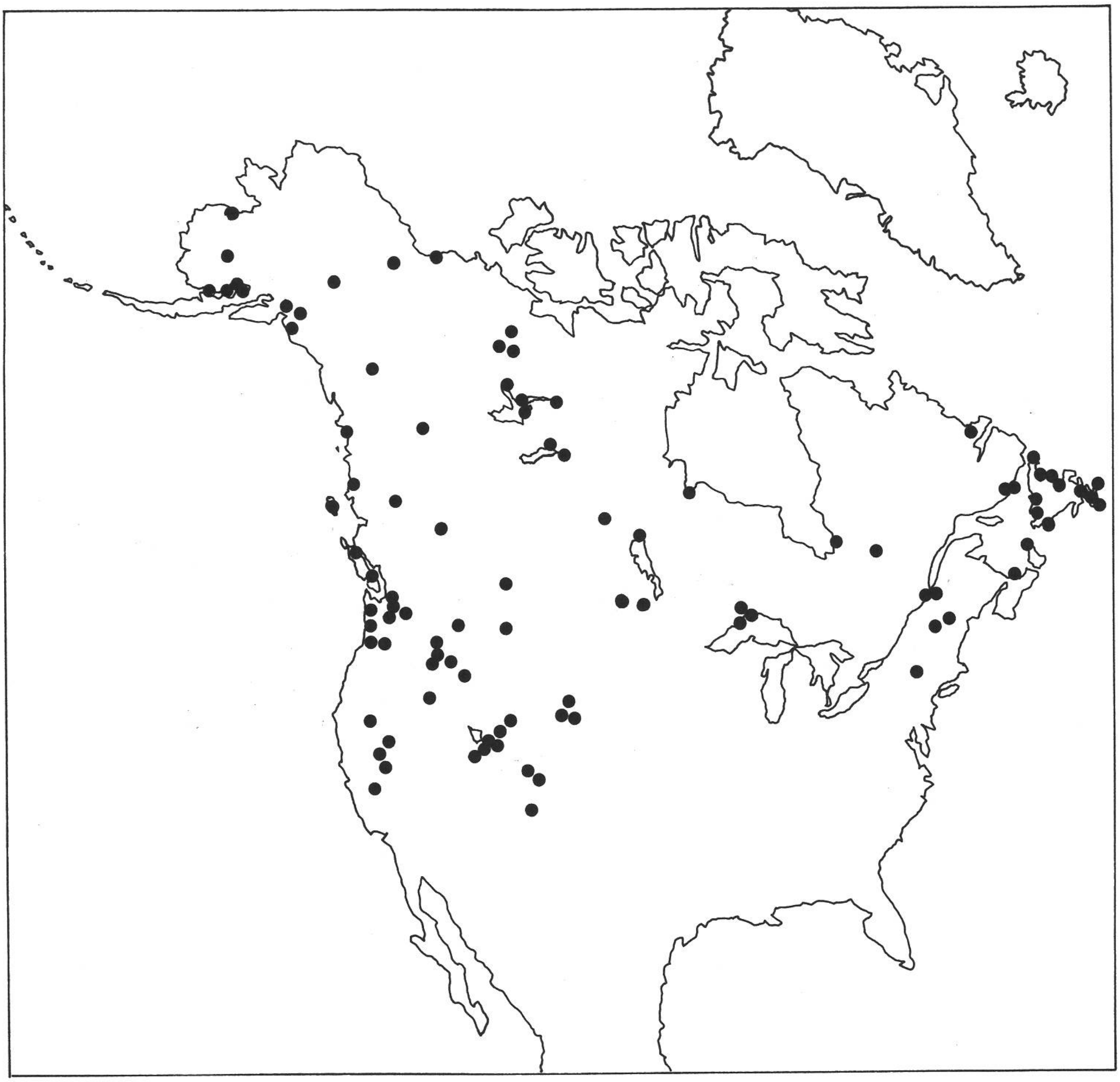
Map 3. *Sparganium natans* in Eurasia. Open circles denote hybrid *S. hyperboreum* × *S. natans.*



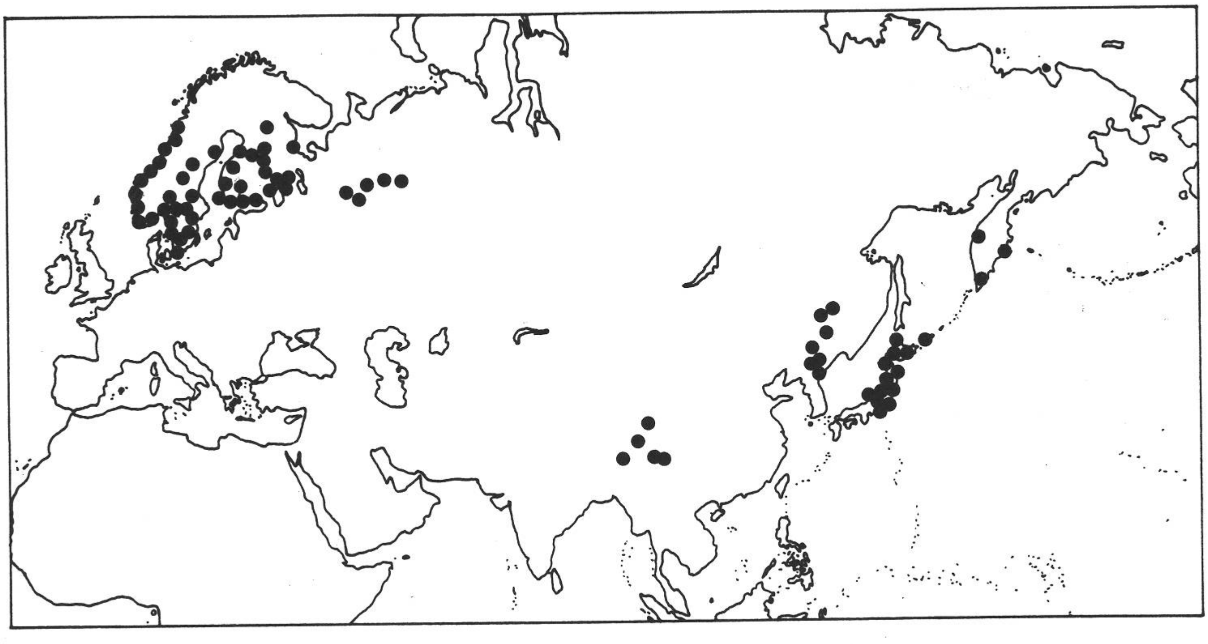
Map 4. *Sparganium natans* in N. America, including records published by Harms (1973). Open circles denote hybrid *S. hyperboreum* × *S. natans*.



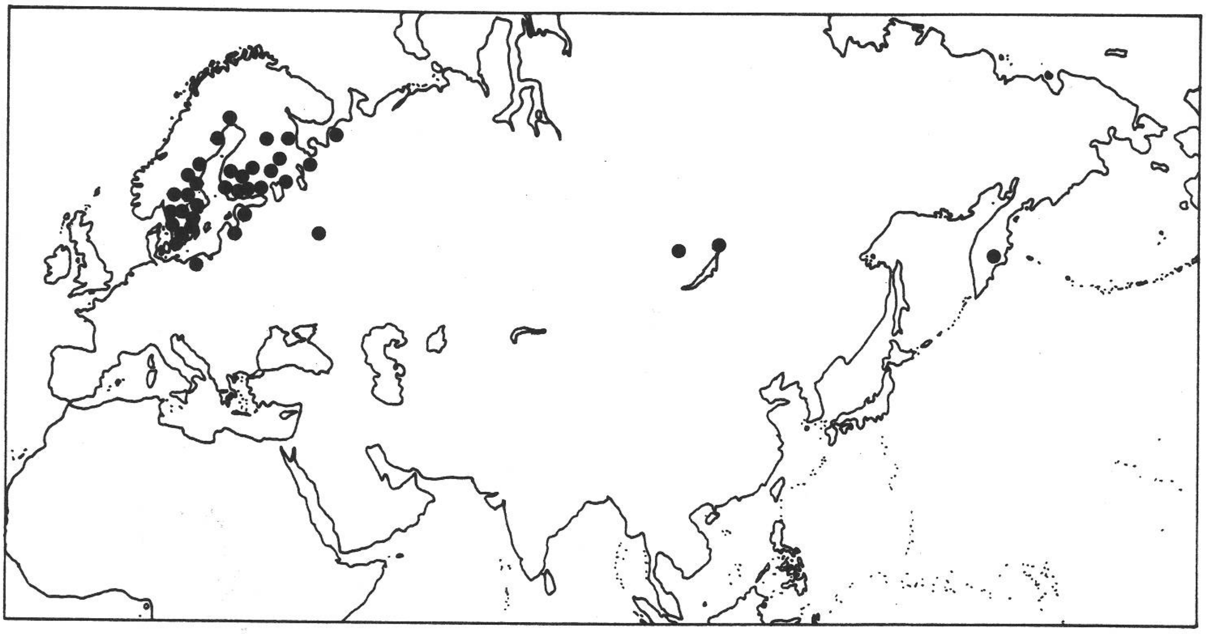
Map 5. *Sparganium angustifolium* in Eurasia. Open circle denotes unconfirmed literature record.



Map 6. *Sparganium angustifolium* in N. America.



Map 7. *Sparganium glomeratum* in Eurasia.



Map 8. *Sparganium gramineum.*

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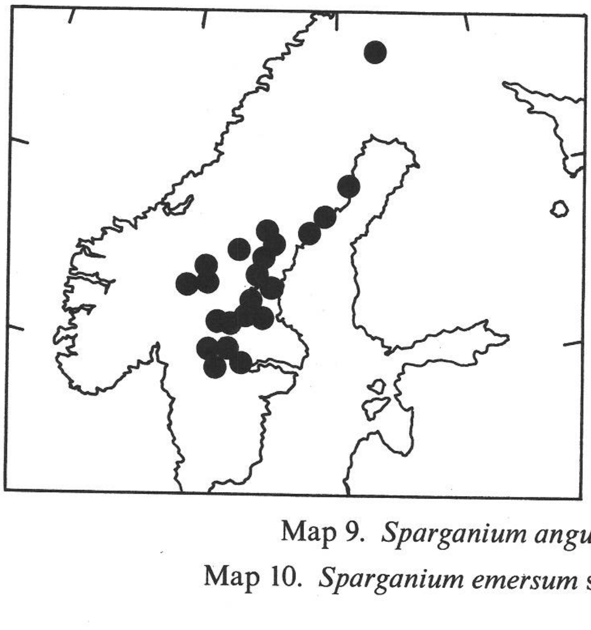

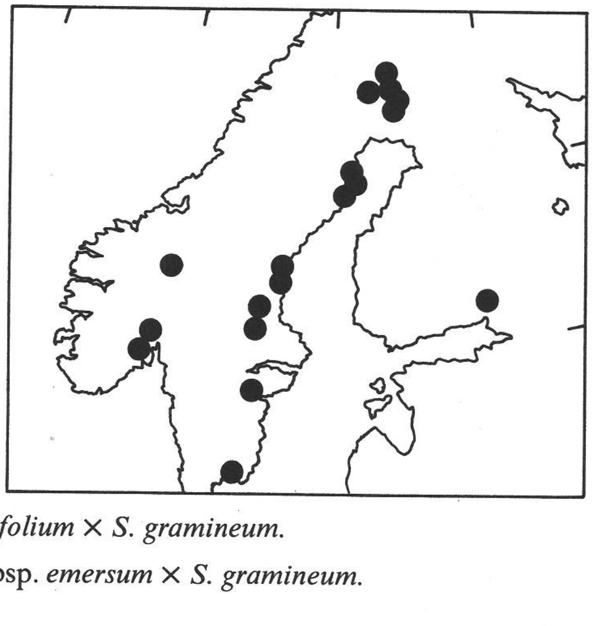

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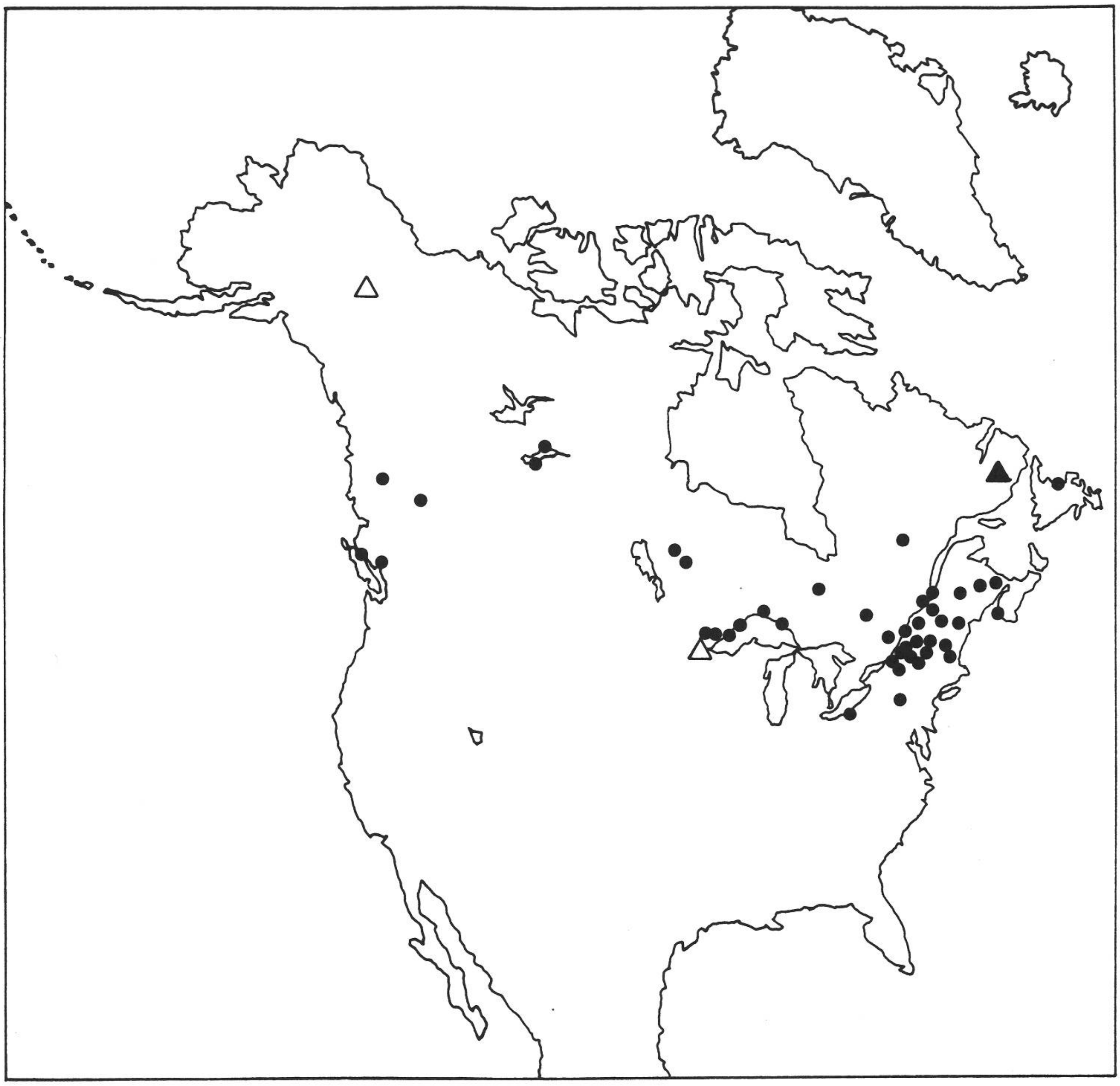
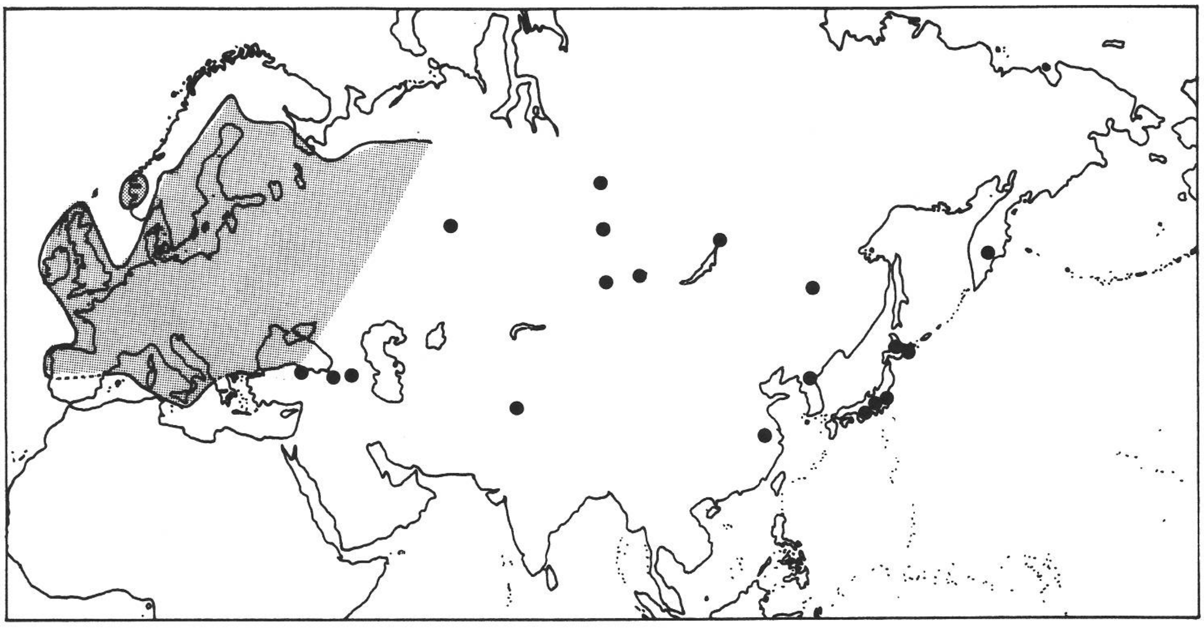
Map 9. *Sparganium angustifolium* × *S. gramineum.*

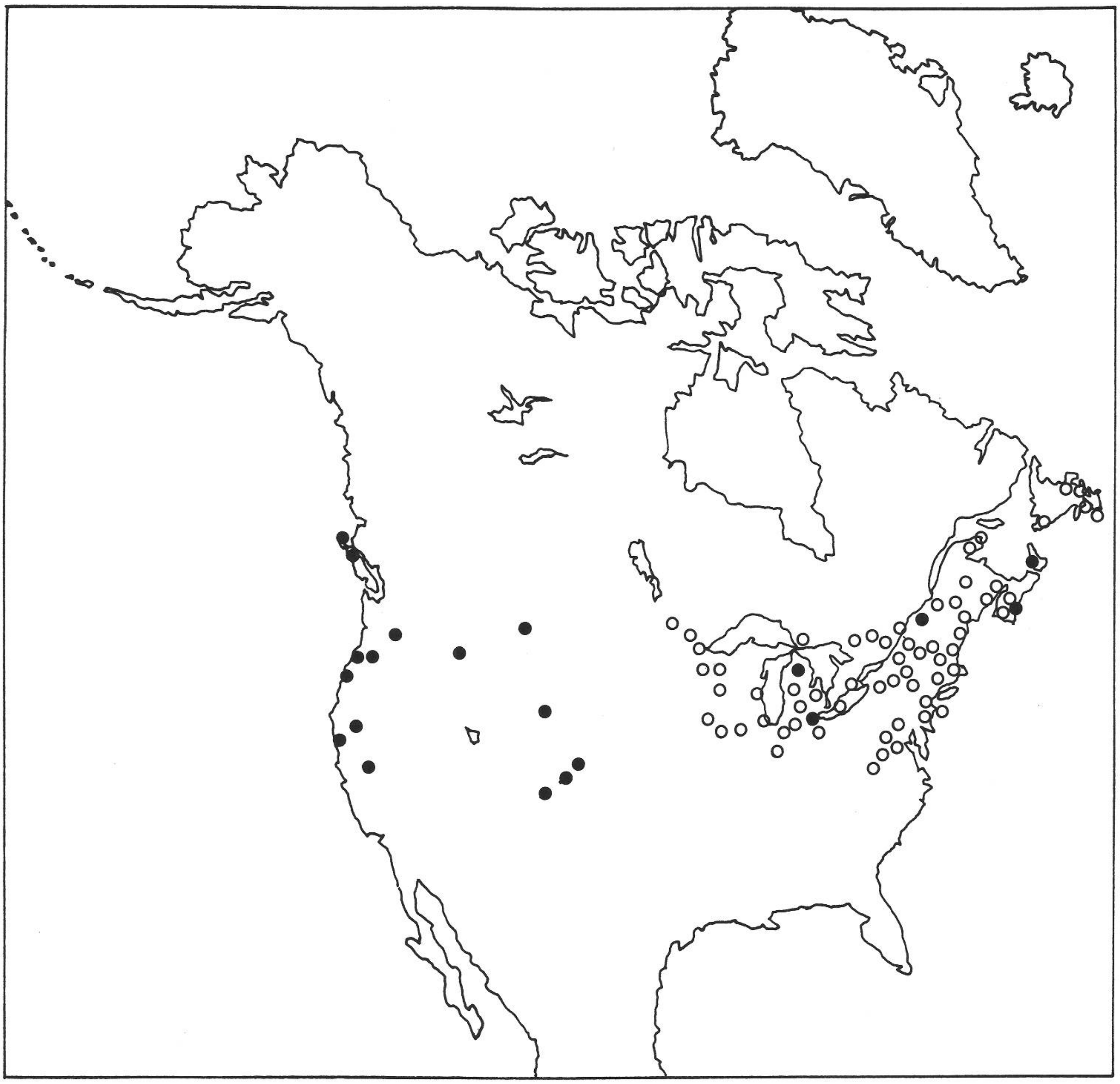
Map 10. *Sparganium emersum* subsp. *emersum* × *S. gramineum.*



Map 11. *Sparganium fluctuans,* closed circles; *S. glomeratum,* closed triangles confirmed record, open triangles unconfirmed literature records.



Map 12. *Sparganium emersum* subsp. *emersum* in Eurasia.



Map 13. *Sparganium emersum* in N. America: subsp. *emersum* closed circles; subsp. *acaule* open circles.