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A monographic study of the genus *Sparganium* (Sparganiaceae). Part 2. Subgenus *Sparganium*

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Abstract

Cook, C. D. K. & Nicholls, M. S., 1987. A monographic study of the genus *Sparganium* (Sparganiaceae). Part 2. Subgenus *Sparganium*. Bot. Helv. 97: 1–44.

A taxonomic revision of *Sparganium* (Sparganiaceae) subgenus *Sparganium* is presented. Each species has a full description, short diagnosis, list of synonyms with typifications, distribution map with notes on ecology, variation and hybrids. Seven species and five subspecies are recognized. Two new names are used: ***Sparganium erectum*** subsp. ***stoloniferum*** (F. Hamilton ex Graebner) C. D. K. Cook & M. S. Nicholls ***comb. nova; S. eurycarpum*** subsp. ***coreanum*** (Léveillé) C. D. K. Cook & M. S. Nicholls ***comb. nova.*** An index to the complete genus *Sparganium* is given.

Introduction

Part 1 of this study is published in Botanica Helvetica, 96: 213–267 (1986) and includes introductory chapters for the entire genus: materials and methods, special terminology, family and generic description with typification, distribution, fossils, anatomy and morphology of vegetative and floral parts, chromosome numbers, floral biology, dispersal, ecology, parasites and animal feeders, applied aspects and a key to all species and subspecies. Individual accounts of the species and subspecies of subgenus *Xanthosparganium* are also included in Part 1.

This part of the study gives individual accounts of the seven species and five subspecies comprising subgenus *Sparganium*. An index to the genus is also provided on p. 30.

Acknowledgement

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Species of subgenus Sparganium

Perianth segments not translucent with a thickened dark-brown to black pad of tissue near the apex, apex emarginate to entire or nearly so.

Key to species in Botanica Helvetica 96: 228–230, 1986.

8. **Sparganium fallax** Graebner ex Graebner in Engler, Pflanzenreich 2 (IV. 10): 15. September 1900 – *S. fallax* Graebner, Allg. Bot. Zeitschr. 4: 32. February 1898, nomen sub-nudum. Type: "Asien: von Sikkim! Khasia! und Ostbengalen bis Japan" (holotype: Bangla Desh, "East Bengal, Herb. *Griffith 5618,* specimen with label in Graebner's handwriting dated 5 Jan. 1898, B; numerous syn- or isotypes in E, K)

= *S. yamatense* Matsumura ex Makino in Hara, J. Jap. Botany 12 (3): 171. March 1936 – *S. yamatense* Matsumura, Indig. Pl. Jap. (2) 1: 24. 1905, nomen nudum. Type: Japan, prov. Yamato, Nara, 15 July 1883, *J. Matsumura* (holotype: TI)

= *S. confertum* Y.-D. Chen, Acta Phytotaxonomica Sinica 19 (1): 53. 1981. Type: China, Yunnan, Gaoligong Shan, alt. 3100 m, 11 October 1940, *K. M. Feng 8379* (holotype: Acad. Sin., probably PE n.v.; paratype: 17 September 1938, *T. T. Yü 20343,* E).

= *S. yunnanense* Y.-D. Chen, Acta Phytotaxonomica Sinica 19 (1): 54. 1981. Type: China, Yunnan, Menghai Xian, alt. 1530 m, May 1936, 王 启 无 [*Z. W. Wang*] *73555* (holotype: Acad. Sin., probably PE n.v.).

Robust to slender plants with erect, emergent or occasionally floating leaves. Stolons up to 25 cm or more long, ca. 2–3.5 mm diameter.

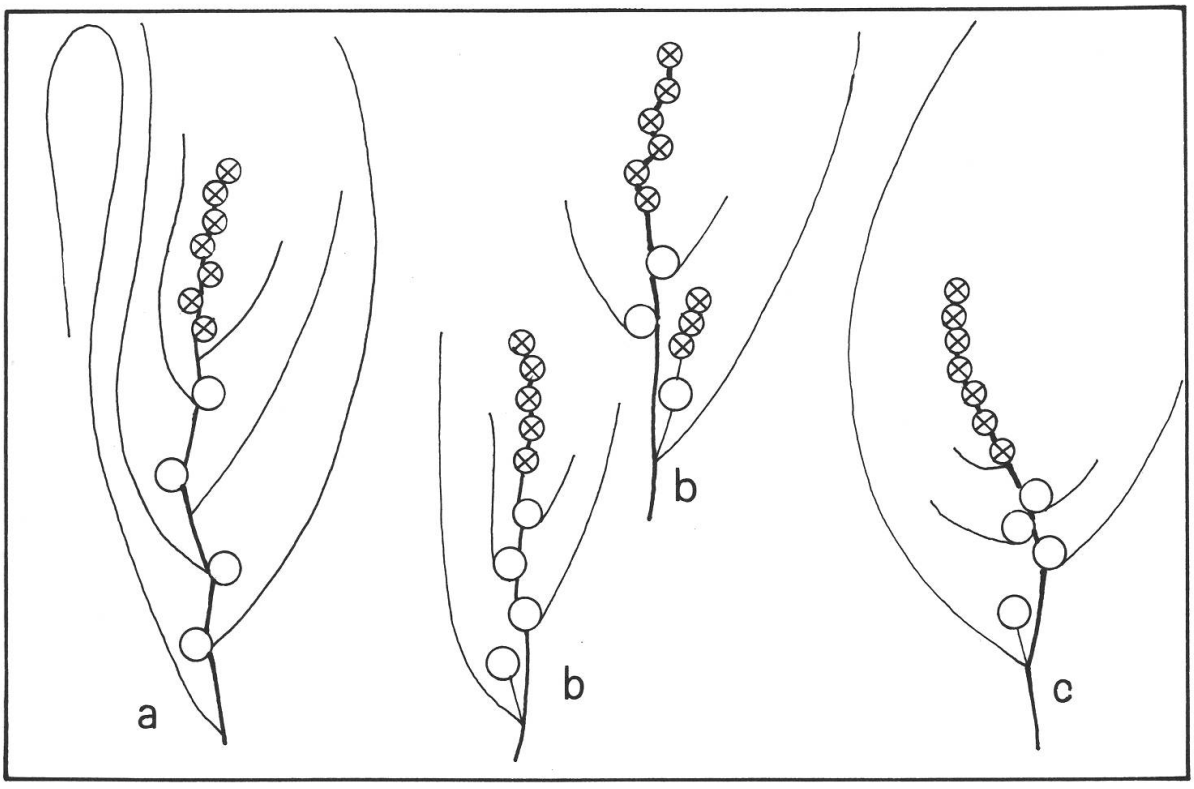


Fig. 13. Diagrammatic respresentation of the inflorescences of: a, *Sparganium fallax;* b, *S. subglobosum;* c, *S. japonicum.*

Basal leaves usually erect and partially emergent, 40–60(–80) cm long, usually exceeding the stem, (4–)5–10(–15) mm wide, sheathing but not inflated at base, carinate (usually to apex); apex rounded and dark-tipped.

Flowering stems 30–60 cm long, usually erect, simple, with 2–4, elongated, sterile nodes below the inflorescence.

Inflorescence bracts erect, diverging from the main axis at an acute angle, not or slightly inflated at base, sometimes with fine hyaline margins; lowermost bract up to ca. 20–35(–60) cm long, 1–2 or more times as long as the inflorescence (Fig. 13a).

Female heads 3–4(–6), usually supra-axillary, sometimes extending beyond the next internode (Fig. 14a), usually remote with zig-zag main axis, sessile above and usually pedunculate below; in fruit (10–)15–20(–34) mm diameter; penducle up to ca. 3 cm long.

Male heads 5–8 or more, 7–18 mm diameter, separated from the uppermost female head by a (8–)10–15(–50) mm long internode; the lower ones usually remote becoming overlapped above; the lowest sometimes supra-axillary and subtended by a leaf-like bract up to 6 cm long but usually less (the male inflorescence thus may appear to be stalked).

Female flowers with perianth segments oblong to spathulate, distinctly united below and sometimes partially united above (Fig. 14a) and then irregularly shaped, ca.

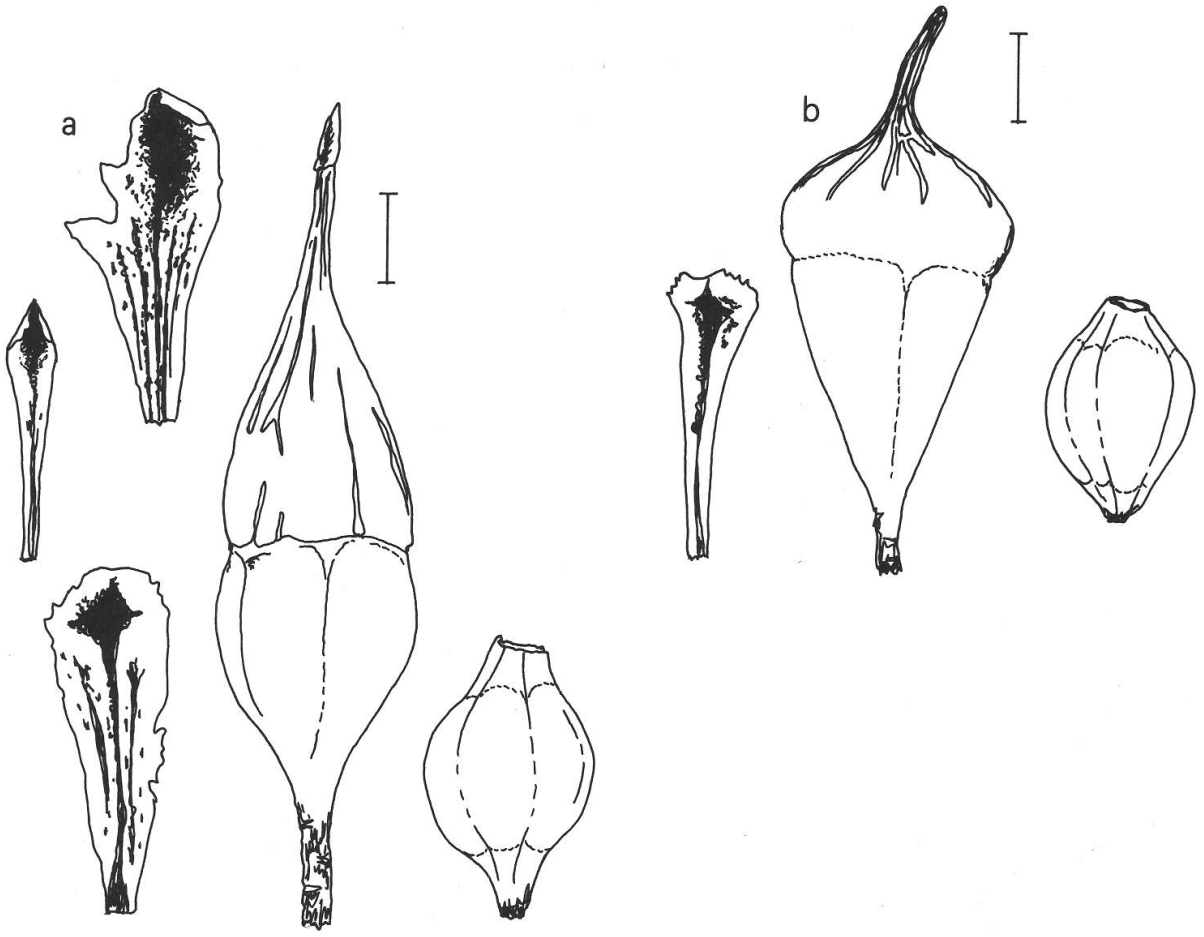


Fig. 14. Perianth segments, fruits and endocarps of: a, *Sparganium fallax;* b, *S. subglobosum* (scale bar: 1 mm).

3.5–5.5 mm long, more than half as long as the fruit, inserted at top half of pedicel, apex and midrib dark; pedicel ca.1–3 mm long; stigmas (0.4–)0.8–1.2(–1.6) mm long.

Male flowers with filaments up to 6 mm or more long; anthers (0.8–)1.0–2.0(–2.2) mm long.

Fruits fusiform, 5–6 mm long, sometimes constricted around the middle, ca. 2–2.5 mm wide, light brown, dull, tapering above to a 1.6–2.5(–3.0) mm long beak, tapering below into a 1.5–3 mm long pedicel; endocarp ovate ca. 3 mm long and 2 mm wide, truncate at micropyle, tapered below into an up to ca 3 mm long stalk (Fig. 14a).

Diagnostic features

Inflorescence simple; perianth segments with dark tips and midribs; female heads remote, mostly supra-axillary, some sometimes concaulescent beyond the next internode (Fig. 13a); leaves carinate to apex, usually more than 5 mm wide; lower bract 1–2 times as long as inflorescence; fruit beak more than 1.6 mm long; stigmas less than 1.6 mm long (see Table 4). It sometimes superficially resembles *S. emersum* but can be distinguished by the perianth segments with dark tips and shorter stigmas.

Distribution

S. fallax is an eastern Asian species extending from central Honshu, Japan, south to Kyushu, through southern China westwards through Yunnan and northern Burma to south eastern Tibet, Assam and Meghalaya, India, Map 14. It is also found in the highlands of New Guinea and reported in the mountains of central Sumatera (usually misidentified as *S. simplex*).

Ecology

We have no first-hand information. From herbarium specimens it appears to be an emergent aquatic growing in shallow water. In the north of its range it grows at sea level in the south at about 2000 m in New Guinea.

Variation

The variation observed on herbarium specimens is incorporated in the formal taxonomic description.

Hybrid

8×9. *S. fallax*×*S. subglobosum*

This hybrid has been reported but we doubt that it exists, see p. 8.

9. **Sparganium subglobosum** Morong, Bull. Torrey. Bot. Club 15 (3): 81. Pl. 79, Fig. 1. 2 March 1888. Type: New Zealand, Bay of Islands, U.S. Exploring Expedition under Command of *Capt. Wilkes* (holotype; GH n.v.)

= *S. stenophyllum* Maximovicz ex Meinshausen, Bull. Soc. Imp. Nat. Moscou N.S. 3(1889): 171. 1890. Type: USSR., Primorskiy Kray, Ussuriysk (Voroshilov), "S.O. Mandschurien, in einem kleinen Landsee beim Dorf Nikolsk (Goldenstädt), 28. Juli 1872", *Maximovicz* (holotype: LE not found).

= *S. antipodum* Graebner, Allg. Bot. Zeitschr. 4 (2): 33. Febr. 1899. Type: New Zealand or Australia, „Neu-Seeland: verbreitet. – Australien: Victoria, *F. v. Mueller*" "Fruc-

Table 4. Comparison of *Sparganium emersum* and the species of the *S. americanum* group

	emersum	*fallax*	*subglosum*	*japonicum*	*americanum*	*androcladum*
Perianth segment apex	translucent	dark	dark	dark	dark	dark
Leaves: width (mm)	(2–)4–12(–18)	(4–)5–10(–15)	2–4(–9)	(3–)5–10(–20)	(5–)7–12(–18)	5–12
Leaves: T.S. proximal	keeled	keeled	keeled	triangular-flat	keeled-triangular	keeled
Leaves: T.S. distal	triangular (–flat)	keeled-triangular	keeled-triangular	flat	flat	triangular-flat
Lowest bract: position	erect (floating)	erect	erect	asending-spreading	spreading	ascending
Lowest bract: relation to inflorescence	1–4 × longer	1–2 × longer	shorter-equal	1–2 × longer	1–2 × longer	longer
Inflorescence: lowest branch	no branch	no branch	♀ + ♂ or ♂ only	no branch	♀ + ♂ or simple	♂ only or simple
Female heads: remote or approximate	remote (approximate)	very remote	remote	upper approximate	remote	remote
Female heads: supra-axillary	usually	always	never	very rare	very rare	rare
Fruiting head: diameter (mm)	16–25(–35)	(10–)15–20(–34)	12–16(–23)	15–20	15–25	25–35
Fruit: texture	shiny	dull	shiny	dull	dull & pitted	shiny above dull pitted below
Fruit: body length (mm)	3.5–5.5	5–6	4–5(–6.5)	(–3)4–6	(3.5–)4–5(–5.5)	5–7
Fruit: body diameter (mm)	1.8–2.5	2–2.5	2–3	ca. 2	ca. 2	2.5–3
Fruit: beak length (mm)	2–4.5(–6)	1.6–2.5(–3)	1–2	1.5–3	(1.5–)3–4(–5)	4.5–7
Fruit: pedicel length (mm)	1–4	1.5–3	0–1	2–5	1–2(–3)	2.4–4
Stigma length (mm)	(1–)1.5–2(–2.5)	(0.4)0.8–1.2 (–1.6)	0.6–1.0(–1.2)	1–1.5	(0.9–)1–2(–3)	2–4
Endocarp length (mm)	2.5–3.5	ca. 3	2.5–3	ca. 3.5	3.5–4	ca. 4.5
Anther length (mm)	1–1.5(–2)	(0.8–)1–2(2.2)	0.5–0.9(–1)	0.7–1.0	0.8–1.3	1–1.6

tus mihi ignoti" (lectotype: chosen here, New Zealand, "Nov. Zeland", s.d., *J. D. Hooker s.n.* det. Graebner 5 Jan. 1898 in B; isolectotype K; paratype K).

= *S. nipponicum* Makino ex Makino. J. Jap. Bot. 3 (6): 21. 1926. – *S. nipponicum* Makino, Bot. Nat. Fr. Auth. Priv. Cabinet Fl. Jap. 2: 40. 1898, nomen seminudum. Type: Japan, Honshu, "prov. Shimousa, Junsai-numa, prope Ichikawa, September 1893." *T. Makino* (holotype: MAK n.v., there is material in MAK collected at this locality by Makino in 1894 but none has been found collected in September 1893; material in TI collected by Makino from this locality in September 1893 is the holotype of *S. macrocarpum*, see p. 28.

= *S. limosum* Y.-D. Chen, Acta Phytotax. Sinica 19 (1): 52. February 1981. Type: China, Yunnan, Goaligong Shan, alt. 1750 m, 26 June 1938, *T. T. Yü 19197* (holotype: Acad. Sin. probably PE n.v.)

Robust to slender plants with erect and emergent or rarely floating leaves. Stolons slender up to 20 cm or more long, 2–3 mm diameter.

Basal leaves usually erect and partially emergent or rarely floating, (25–)30–60(–120) cm long, usually exceeding the inflorescence, (1–)2–4(–9) mm wide, sheathing but not inflated at base, carinate (usually to apex), glossy, with a rounded blackish apex.

Flowering stems (16–)30–50(–130) cm long, usually erect, emergent, simple or with 1 or 2 branches at base of inflorescence, lateral branches axillary with (0–)1–2 female heads below and 3–4 male heads above (in Australasia some specimens lack female heads on branches); main inflorescence axis with (1–)2–3(–4) female and (3–)6–9(–11) male heads (Fig. 13 b).

Inflorescence bracts more or less erect, not or very slightly inflated at base, sometimes with very fine hyaline margins; lowermost bract up to ca. 15 cm long, about half as long as or equalling but very rarely exceeding the inflorescence.

Female heads axillary, sessile or very rarely with a peduncle less than 5 mm long, remote (each distinct and not touching), in fruit 12–16(–23) mm diameter.

Male heads 9–13 mm diameter, separated from the uppermost female head by a (5–)10–16(–22) mm long internode, usually distinct but not remote from each other at anthesis, usually ebracteate.

Female flowers with perianth segments oblong to spathulate, with a dark brown tip and midrib, not united below, at maturity one-third to half as long as the fruit; sessile or with an up to 1 mm long pedicel; stigmas 0.6–1.0(–1.2) mm long, lanceolate (Fig. 14 b).

Male flowers with filaments 2.5–3.2(–3.8) mm long; anthers 0.5–0.9(–1.0) mm long.

Fruits obovoid to almost globose, 4–5(–6.5) mm long, ca 2–3 mm wide, yellowish to pale brown, shiny-surfaced, tapering and angular in transverse section below, sessile or with up to 1 mm long pedicel, narrowed above to conic-based summit with a blackish, 1–2 mm long beak; endocarp ovoid to pyriform, 2.5–3 mm long and 1.6–1.8 mm wide, almost smooth with very faint longitudinal veins, stalk not persistent (Fig. 14 b).

Diagnostic features

Perianth segments with brown tips and midribs; leaves rarely more than 5 mm wide and keeled to the apex; lowest inflorescence bract not or rarely exceeding the inflorescence; inflorescence usually with 1 or 2 branches; all female heads axillary and remote; fruits obovoid to almost globose, shiny-surfaced, yellowish to pale-brown a with blackish beak; stigmas rarely exceeding 1 mm long (see Table 4).

Distribution

S. subglobosum is an eastern species with a somewhat disjunct distribution (Map 15). In the northern hemisphere it is found in Manchuria, north-west China and Japan extending from Hokkaido southwards to Okinawa. It reappears in south-west China in Yunnan (*Maire 896* in E, and see Chen Yao-Dong, 1981) and in Vietnam. There is a single gathering from Megalaya, India ("Khasia, c. 2000 m, 26 August 1850, *Hooker fil. & Thompson,* E, K and other herbaria). In the southern Hemisphere it occurs in New Zealand, Australia and the highlands of new Guinea. In New Zealand it is found in the North Island extending southwards into the South Island at about 42°S with isolated records from Canterbury. In Australia it is found along the eastern coast from S.E. Queensland to Victoria near Melbourne, in coastal to highland regions from sea-level to 1300 m altitude.

Ecology

S. subglobosum is a plant found in still or slowly-flowing water less than 1 m deep on the margins of creeks, rivers and lakes. In Australia it is characteristically in ditches, swamps and creek edges in dry sclerophyll forest and cleared grazing land. It is rather indifferent to soil, being found on sand, loam, peat and red soils overlying basalt, sandstone, granite and quartz porphyry. The following species are commonly associated with *S. subglobosum: Eleocharis sphacelata* R. Br., *Glyceria australis* C. E. Hubbard, *Myriophyllum propinquum* A. Cunn. s.l., *Philydrum lanuginosum* Blanks & Sol. In Australia it is often eaten by stock during the dry season and it is claimed to prevent the erosion of banks.

In Australia it flowers mostly from December to February and sets fruit by May or June. In Japan it flowers mostly from June to August and the fruit ripens by October.

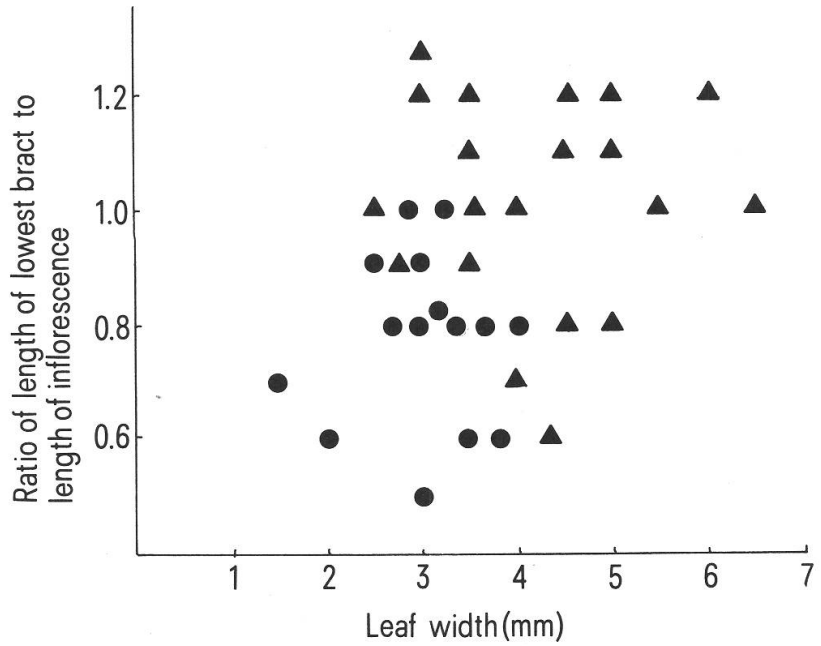


Fig. 15. *Sparganium subglobosum,* comparison of plants from New Zealand and Australia (▲) with plants from Japan (●). Vertical axis: ratio of the length of the lowest bract to the length of the inflorescence; horizontal axis: leaf-width.

Variation

S. subglobosum plants are typically slender and erect with leaves rarely more than 5 mm wide. Occasionally more robust specimens are encountered with wider leaves (reaching a maximum of 9 mm) but they do not differ in other respects. One specimen (Australia: NSW., Port Macquarie, November 1897, *J. H. Maiden 2404* – NSW) has floating leaves up to about 120 cm long; this specimen was seen by Rothert who suggested the plant had been growing in exceptionally deep water.

S. subglobosum has been little studied previously and there are areas of its range, particularly India, south-west China and New Guinea, where it remains poorly collected. Nevertheless, the degree of intraspecific variation observed in our study is far less than that of most other *Sparganium* species.

A comparison of plants from Japan with those from Australia and New Zealand revealed minor differences in leaf width and bract/inflorescence length ratio (see Fig. 15). Japanese plants have slightly narrower leaves (rarely exceeding 4 mm) and the lowermost bract tends to be shorter than the inflorescence while Australian plants mostly have wider leaves and slightly longer bracts. There is, however, considerable overlap in both characters and we have seen very little material outside Japan and Australia. We see no grounds for formally recognizing any intraspecific taxonomic categories.

Hybrid

8×9. *S. fallax* × *S. subglobosum*

On an herbarium sheet in Kew bearing speciments of both species from Khasia (Meghalaya, India), Rothert suggests one of the specimens is of hybrid origin. We contend that the specimen is in fact a slender plant of *S. fallax* and doubt that this hybrid exists.

10. **Sparganium japonicum** W. Rothert in Fedtschenko, Flora Aziatskoj Rossii 1: 26, Tab. 2. 1913. Type: USSR, Primorskiy Kray, "southern Ussuri Region, Village Grigor'evka, on the River Čichc, 1888, *Pal'čevskij*" (holotype: LE n.v.).

Slender to robust plants usually erect and emergent or floating in deeper water. Stolons up to ca. 15 cm long, 2.5–3.0 mm diameter.

Basal leaves erect or floating, up to 80 cm or more long usually exceeding the inflorescence, (3–)5–10(–20) cm wide, carinate or flattened below, usually flattened above, without keel; apex rounded and dark; midrib obscure towards apex.

Flowering stems ca. 40–80 cm long; inflorescence up to ca. 20 cm long, simple.

Inflorescence bracts spreading or spreading-ascending, not inflated at base, usually flattened and not keeled; lowermost bract ca. 12–40 cm long, 1–2 times as long as the inflorescence; upper bracts spreading to reflexed (Fig. 13 c).

Female heads (2–)3–6, axillary, the lower 1–3 often long-pedunculate, the upper heads usually approximate in fruit; in fruit ca. 15–20 mm diameter.

Male heads 5–9, the lower ones usually remote the upper ones usually approximate, ca. 10 mm diameter, separated from the uppermost female head by an internode up to 15 mm long.

Female flowers with perianth segments oblong to oblanceolate or spathulate, with a dark brown tip and midrib, 4–5 mm long, more than half as long as fruit, attached to top half of pedicel; pedicel 2–5 mm long; stigmas ca. 1–1.5 mm long.

Male flowers with dark tipped perianth segments; filaments ca. 4–5 mm long; anthers ca. 0.7–1.0 mm long.

Fruits fusiform (3–)4–6 mm long, ca. 2 mm wide, sometimes constricted around the middle, no obvious difference between upper and lower halves, brown to dark brown, dull-surfaced, tapering below into an obconic base with a 2–5 mm long pedicel; above gradually narrowed into a straight beak, ca. 1.5–3 mm long; endocarp ovoid, ca. 3.5 mm long, ca. 2.5 mm diameter,with an up to 3–5 mm long stalk, smooth or with very fine longitudinal veins (Fig. 16 a).

Diagnostic features

Perianth segments with dark brown tips and midribs. Like *S. americanum* (see p. 10) but inflorescence always simple; upper female heads approximate; fruit lacking dark brown glands, not pitted; beak not exceeding 3 mm; pedicel usually 3 mm or more long. Like *S. fallax* (p. 2) but usually all heads axillary; leaves flat at apex; upper bracts spreading to reflexed; upper female heads approximate; main axis not zig-zag; fruit dark-brown. Like *S. subglobosum* (p. 4) but fruits fusiform; inflorescence simple, fruits dark brown, dull; leaves usually more than 5 mm wide and distally flat; stigmas exceeding 1 mm long; pedicel usually exceeding 1 mm persistent in fruit; endocarp exceeding 3 mm long, stalked at maturity (see Table 4).

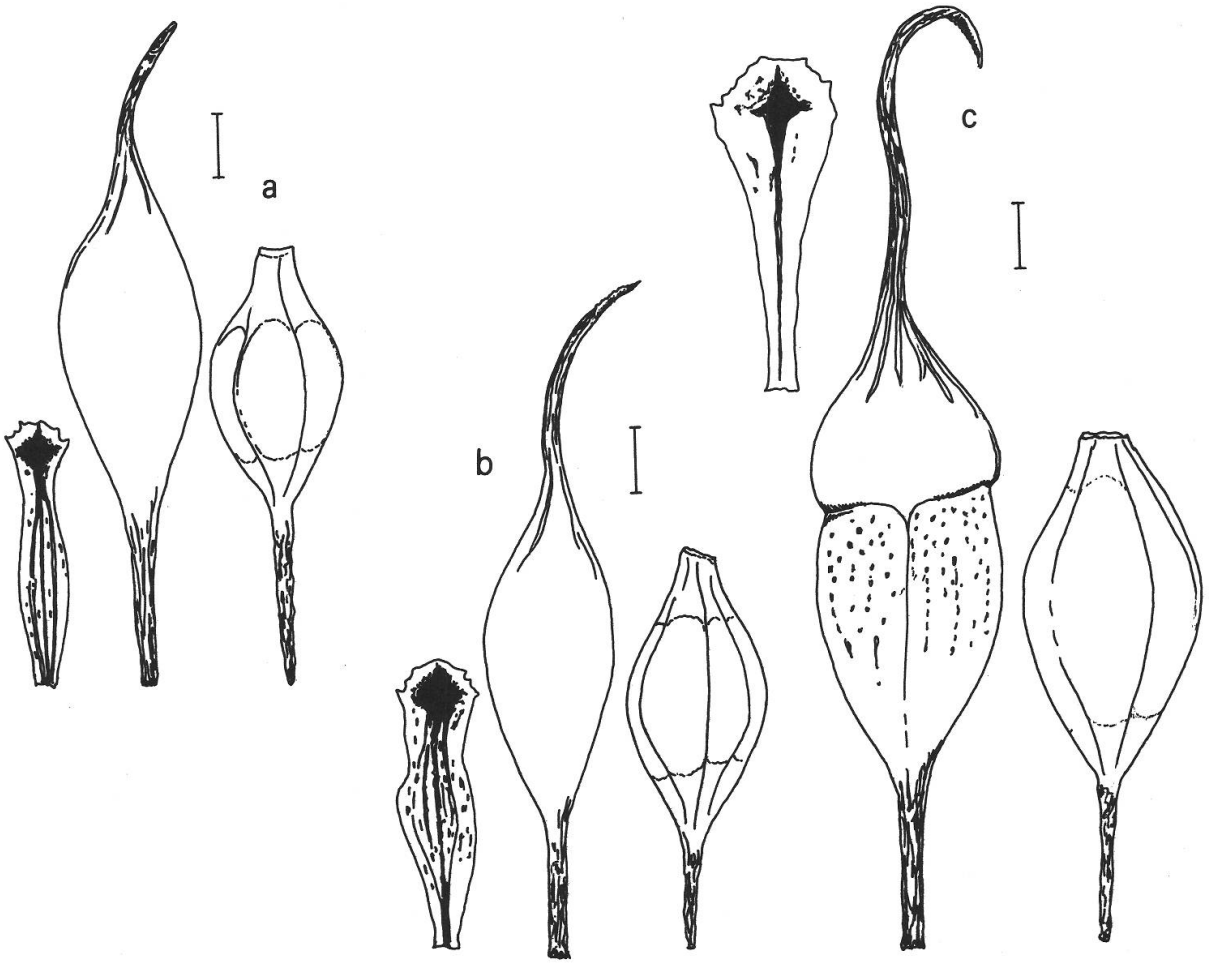


Fig. 16. Perianth segments, fruits and endocarps of: a, *Sparganium japonicum;* b, *S. americanum;* c, *S. androcladum* (scale bar: 1 mm).

Distribution

S. japonicum is from E. Asia and shows a compact distribution pattern. It is found in Japan from northern Honshu to southern Kyushu and in southern Primorskiy Kray (north of Vladivostok) and in Korea, see Map 16.

Ecology

We have no first-hand information. From herbarium material it appears to be a perennial, emergent aquatic growing in shallow water. On one herbarium sheet (Okinawa Island, 18 May 1955, *Hatusima 17886*, TI) it is reported to grow as an annual in a wet field – we consider this rather unlikely and suggest that the specimen might be incorrectly labelled. We have not included this locality on Map 16.

Variation

S. japonicum shows close affinities to *S. americanum* and could well be recognized at an infraspecific rank. Without more detailed work including field studies we prefer to keep them as separate species rather than to make a new nomenclatural combination. Its identity is clear.

11. **Sparganium americanum** Nuttall, Genera North American Plants 2: 203. 14 July 1818 ≡ *S. simplex* var. *americanum* (Nuttall) Engler in Engler & Prantl, Pflanzenfamilien 2 (1): 192. 1887. Type: USA, Pennsylvania, "vicinity of Philadelphia", *Nuttall* (holotype: PH n.v., ? BM).

= *S. americanum* var. *rigidum* Clausen, Rhodora 39: 189. May 1937. Type: USA, New Jersey, Ocean Co., Tuckerton Creek Pond, 22 September 1934, *Edwards & Clausen* (holotype: GH).

– *S. simplex* var. *nuttallii* Engelmann, in A. Gray. Manual Botany Northern U.S., ed. 5, 481. 1867 nomen illeg., based on *S. americanum* Nuttall.

Slender to robust plants, erect and emergent or floating in deeper water. Stolons 10–20 cm or more long, 3–4 mm diameter.

Basal leaves erect or floating, rarely exceeding the inflorescence, (30–)40–100 cm long, (5–)7–12 mm wide, flattened or carinate below, flat above; apex rounded and dark; midrib obscure.

Flowering stems up to ca. 100 cm long; inflorescence 10–25(–30) cm long, with up to 3 branches or occasionally simple (Fig. 17 a); branches axillary with 1–3 female and up to 7 male heads; main axis with 2–4 female and 4–10 male heads (Fig. 17 b).

Inflorescence bracts spreading or spreading-ascending, sometimes inflated at base, usually not keeled; lowermost bract (5–)10–35(–40) cm long, 1–2 times as long as the inflorescence.

Female heads axillary, usually sessile, all remote, in fruit ca. 15–25 mm diameter.

Male heads more or less distinct but not all remote at anthesis, 10–15(–18) mm diameter, separated from the uppermost female head by a (4–)10–20(–26) mm long internode.

Female flowers with perianth segments oblong to oblanceolate or spathulate, with dark brown tip and midrib often dotted with brown glands (Fig. 16 b), about half to three-quarters as long as the fruit, attached at top of pedicel; pedicel up to 3 mm long; stigmas (0.9–)1–2(–3) mm long.

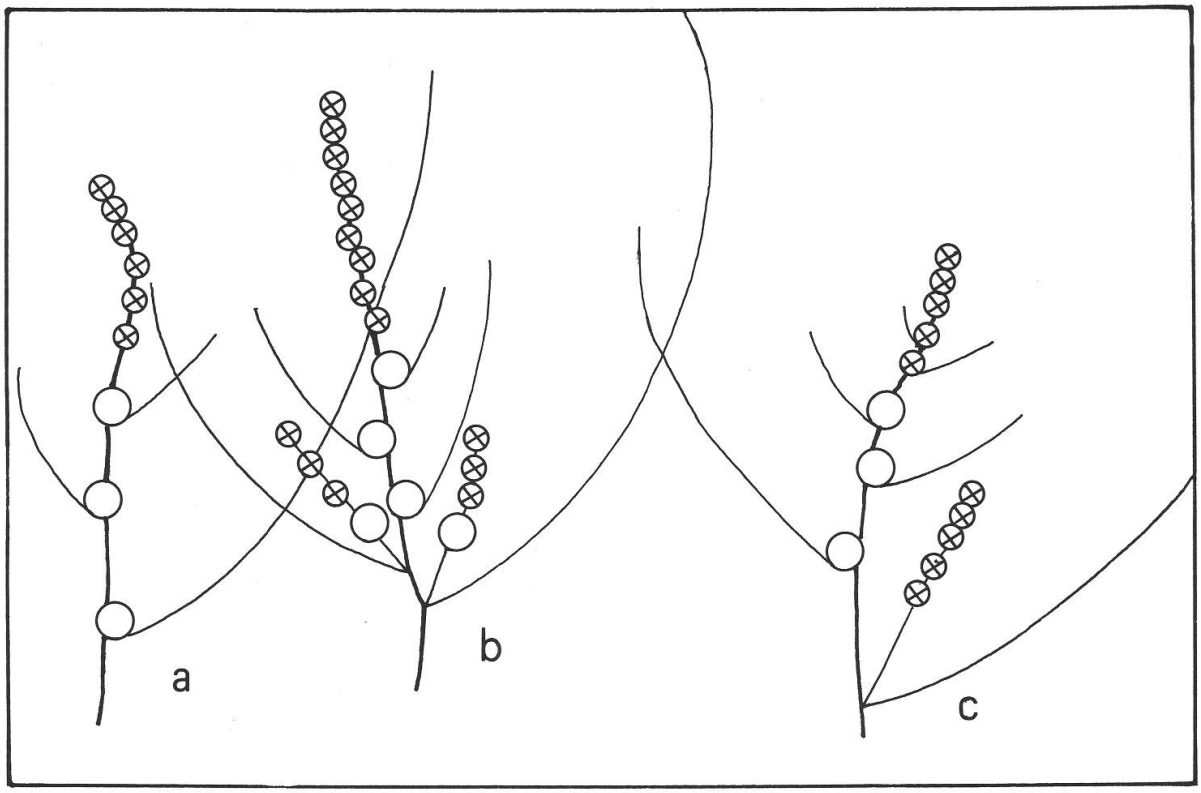


Fig. 17. Diagrammatic representation of inflorescences of: a, b, *Sparganium americanum* (a, unbranched; b, branched); c, *S. androcladum.*

Male flowers with dark-tipped perianth segments; filaments 4–5 mm long; anthers 0.8–1.3 mm long.

Fruits fusiform, (3.5–)4–5(–5.5) mm long, ca. 2 mm wide, sometimes slightly constricted around the middle, brown to dark brown, dull-surfaced and sometimes pitted, tapering below into an obconic base with a 1–2(–3) mm long pedicel; above rather abruptly narrowed into a straight or curved but not hooked beak, (1.5–)3–4(–5) mm long; endocarp ovoid, 3.5–4 mm long, ca. 2 mm diameter, smooth with fine longitudinal veins (Fig. 16 b), very difficult to remove from fruit.

Diagnostic features

Perianth segments with dark tips and midribs; inflorescence simple or lowest branch bearing both female and male heads; female heads axillary, in fruit not exceeding 25 mm diameter; fruits brown to dark-brown with surface dull and pitted, rarely more than 5 mm long and 2 mm diameter with a straight beak not more than 5 mm ling; stigmas rarely more than 2 mm long; leaves usually more than 5 mm wide, usually keeled or carinate below but flattened above; inflorescence bracts spreading, the lowest longer than the inflorescence; pedicel of female flowers or fruits rarely more than 2 mm long (see Table 4). *S. americanum* shows close affinities to *S. japonicum* (p. 8) and *S. androcladum* (p. 12).

Distribution

S. americanum is widespread in North America ranging from Newfoundland west to Ontario and North Dakota, extending south to northern Florida, southern Alabama,

Louisiana, Oklahoma and Texas, with an isolated record just north of 23°N. In the highlands of Mexico (Durango Prov., El Salto, 2600 m, 7 July 1956, *Dickerman 1005,* GH), see Map 17.

Ecology

S. americanum is found in shallow, still or flowing water in a variety of natural and artificial aquatic habitats. It is usually found near the shores and may build largish stands. In the Northeast it is a characteristic species of the bank vegetation along silted streams and is found in marshes.

Variation

S. americanum is a polymorphic species which has been studied in the southeastern USA by Beal (1960). Of particular interest to Beal was the correlation and distribution of the following characters: stem height, leaf width, thickness and texture, degree of branching of the inflorescence, position of the female heads, size of the fruit and length of style and stigma. On the basis of these characters Beal (1960) recognized three races: (1) the Coastal Race, with stigmas 1.5 mm or more long, relatively wide leaves and 2–5 inflorescence branches (see Fig. 17 b); (2) the Appalacian Race, with stigmas 0.9 mm or shorter, narrower leaves and simple or sparingly branched inflorescences (Fig. 17 a), and (3) the Ubiquitous Race, based on plants intermediate between the first two races. As the names suggest, the first two races are geographically somewat restricted while the third race is found throughout the range. Between all three races there is considerable overlapping and therefore Beal (1960) found it "inappropriate to dignify these races with formal names."

Beal (1960) made detailed morophological studies of 148 collections from the Carolinas. He attempted various correlations and designed an index. Despite all this playing around with numbers, the single and most frustrating fact to emerge about *S. americanum* is that, while undoubtedly polymorphic, it does not fit well into any of those patterns favoured by students of biosystematics and the like. Beal explored three explanations of the distribution patterns observed: environmental effects, introgressive hybridization and incipient race-formation. Having demolished the second of these he came to the sensible (if banal) conclusion that "a complex of interacting genetical and ecological factors have been involved." His subsequent call for further experimental work involving transplant and hybridization studies remains to be taken up.

Variation in *S. americanum* has produced an attendant nomenclatural confusion. In the original description of *S. americanum,* Nuttall (1818) referred only to plants of what Beal (1960) called the Appalacian Race. Unfortunately Morong (1888) followed by Mohr (1910), Fernald & Eames (1907) and Rydberg (1909) misinterpreted robust plants (Beal's Coastal Race) and failed to distinguish them from *S. androcladum* (see below). Fernald (1922) cleared up these problems, reinstating the species *S. androcladum.*

Clausen (1937) recognized a new variety *rigidum* for plants having narrow, stiff leaves and a supra-axillary lowest female head. Beal's (1960) and our own studies suggest these features are not correlated, are scattered throughout the range of *S. americanum* and are not worthy of taxonomic recognition.

12. **Sparganium androcladum** (Engelmann) Morong, Bull. Torrey Bot. Club 15 (3): 78. 2 March 1888 ≡ *S. simplex* var. *androcladum* Engelmann in A. Gray, Manual

Botany Northern U.S., ed. 5, 481. 1867 ≡ *S. americanum* Nuttall var. *androcladum* (Engelmann) Fernald & Eames, Rhodora 9: 87. May 1907. Type: USA, "New England" *Engelmann* (holotype: MO). Unfortunately Morong (op.cit.) misinterpreted robust plants of *S. americanum* and failed to distinguish them from Engelmann's var. *androcladum* (op.cit.). Morong's error was perpetuated by Mohr (Contr. U.S. Nat. Herb. 6:327. 1901) and Rydberg (N. Amer. Flora 17: 8. 1909). Fernald & Eames (op.cit.) proposed the new combination (*S. americanum* var. *androcladum*) and applied it to robust pants of *S. americanum*; the species now known to be *S. androcladum* they described as a new species, *S. lucidum*. Fernald (Rhodora 24: 26. February 1922) cleared up these problems, reinstating *S. androcladum* in the correct sense and reducing *S. lucidum* to synonymy.

= *S. lucidum* Fernald & Eames, Rhodora 9: 87. May 1907. Type: USA, Massachusetts, "small pond Medford, 29 July 1860, *Wm. Boott* (lectotype: GH).

– *S. simplex* Hudson var. *androgyna* Meinshausen, Bull. Acad. Imp. Sci. St. Pétersbourg N.S. 4 (36): 31. December 1893. This is probably a misprint for "*androcladum*".

Robust erect or rarely floating plants. Stolons up to 20 cm or more long, up to 4 mm diameter.

Basal leaves usually erect and emergent, up to ca. 100 cm or more long, 5–12 mm wide, exceeding the inflorescence, distinctly keeled from base to at least the middle; apex rounded and dark; midrib prominent and thickened at apex.

Flowering stems up to 100 cm or more long, rigid and erect; inflorescence normally branched or occasionally simple; main axis bearing (1–)2–4, sessile or at base shortly pedunculate, axillary female heads and up to 8 or more male heads; lateral branches axillary, the lowest with 1–6 male heads and nearly always without female heads or very rarely with 1 female head, the second or third lowest rarely bearing 1 female head otherwise with 1–6 male heads (Fig. 17c).

Inflorescence bracts ascending, not inflated below, distinctly triangular in transverse section, often keeled; the lowest ca. 25–40 cm long, exceeding the inflorescence; bracts subtending upper female and lower male heads usually green and more or less leaf-like.

Female heads axillary or rarely supra-axillary, sessile or sometimes the lowest shortly pedunculate, all remote, usually confined to main axis, rarely the second or third branch bearing solitary heads below the males, in fruit 25–35 mm diameter.

Male heads ca.10–15 mm diameter, distinctly separated from female ones by a (4–)10–20(–26) cm long internode, the lower ones remote and distinct from each other.

Female flowers with perianth segments oblong to oblanceolate or spathulate, with dark brown tip and midrib, attached to top of pedicel, half to two-thirds as long as the body of the fruit; pedicel 2.4–4 mm long; stigmas 2–4 mm long.

Male flowers with dark-tipped perianth segments; filaments up to ca. 6 mm long; anthers ca. 1–1.6 mm long.

Fruits ovoid to fusiform, 5–7 mm long, 2.5–3 mm diameter, often constricted around the middle; the lower part brown, almost terete and dotted with dark reddish-brown glands, with an obconic base and persistent pedicel; the upper part smooth, shiny, brown to olive-brown, gradually tapered above into 4.5–7 mm long beak often hooked at apex; pedicel 2.4–4 mm long, endocarp ovoid, ca. 4.5 mm long, ca. 2.5 mm diameter, smooth with the fine longitudinal veins (Fig. 16c), very difficult to remove from fruit.

Diagnostic features

Like *S. americanum* (p. 10) but inflorescence usually branched, the lowest or lower branches usually bearing male heads only or very rarely single female heads; fruiting heads more than 25 mm diameter, usually sessile and axillary or rarely one supra-axillary; leaves and bracts usually carinate to apex, usually more than 5 mm wide; fruits shiny above and dull, pitted and glandular below, 5–7 mm long, 2.5–3 mm diameter, with usually curved beak 4.5–7 mm long; pedicel of female flowers usually exceeding 2 mm long; endocarp usually more than 4 mm long; stigma 2–4 mm long; anthers 1–1.6 mm long.

Distribution

The distribution of *S. androcladum* has been studied in detail by Beal (1960). It is a species confined to northeastern North America. Its range extends from southern Ontario and Quebec southwards to southern Virginia, then westwards through northern Tennessee to Missouri (Map 18). Rather strangely, it seems to be absent in the middle of the range and is not known from Michigan, Indiana and Kentucky and is rare in Ohio and West Virginia.

Ecology

We have no first-hand knowledge of the ecology of *S. androcladum*. It appears to be a plant of shallow water growing in marshes or along the shores of lakes, rivers and streams.

Variation

S. androcladum is a remarkably constant species. It shows close affinities with *S. americanum* and it is sometimes difficult to distinguish the two when the plants are immature (see Table 4).

13. ***Sparganium erectum*** L. sensu lato
= *S. ramosum* forma *simplicior* Rothert, Acta Horti Botanici Univ. Imper. Jurevensis 11: 19. 1910. *Type:* no specimen cited; used for unbranched plants of *S. erectum*.
– *S. barrerae* Sennen, Bull. Soc. Bot. France 74: 404. 1927 nomen nudum

Robust erect, emergent or rarely floating or submerged herbs. Stolons up to 60 cm long, (3–)6–9 mm diameter. Corms 1.5–4.5 cm diameter, when mature hard and woody, each bearing up to 9 stolons.

Basal leaves obliquely erect and fan-like, usually emergent, often pink at base, (30–)50–150(–350) cm long, (6–)10–20(–28) mm wide, carinate from base to apex, with 3–8 layers of gas chambers.

Plants in very deep or swiftly flowing water may develop submerged or partly floating leaves but usually remain sterile.

Flowering stems erect, 20–100(–150) cm long, nearly always branched, with 1–2(–4) sterile nodes between the corm and the inflorescence; branches (0–)2–5(–9), with (0–)1–3(–6) female heads at the proximal end and (0–)6–9(–16) male heads at the distal end; the upper 1 or rarely 2 branches are often without female heads; the lowest branch often bears a solitary female head without any males, occasionally the solitary head is topped by some males or rarely the branch has male heads only; the terminal

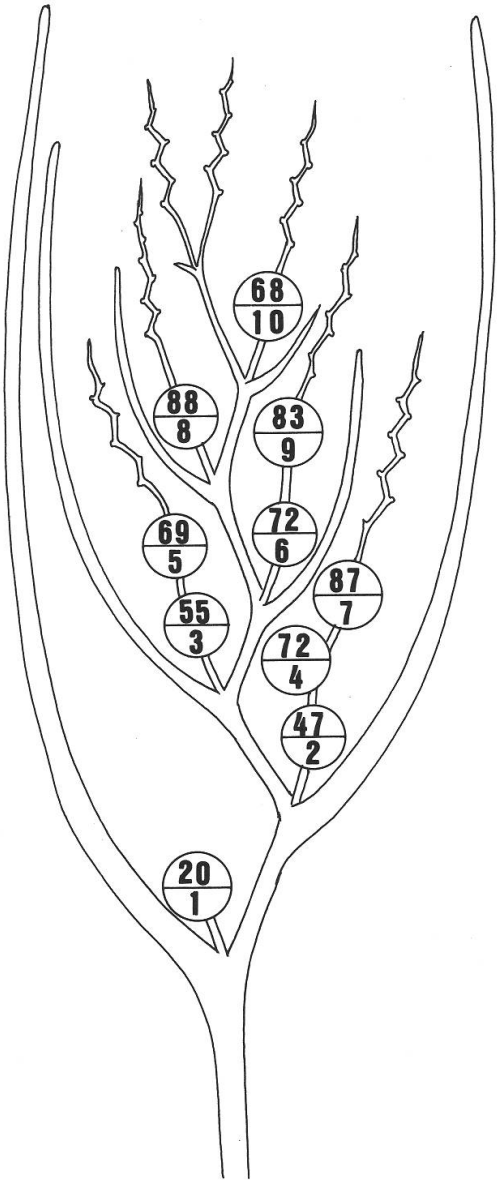


Fig. 18. Fruit set in *Sparganium erectum;* each circle represents a female head, the lower number shows the order of anthesis, the upper number shows the percentage of set fruits (calculated as an average from 85 robust plants growing in the Trent-Mersey Canal, near Derby, Great Britain).

part of the inflorescence (above the last branch) is without female heads and with (3–)5–15(–22) male heads (Fig. 18).

Inflorescence bracts leaf-like below, erect, carinate from base to apex; scale-like above; lowest bract usually exceeding the inflorescence.

Female heads borne on axillary branches, 12–20 mm diameter at anthesis, 15–32 mm diameter in fruit.

Male heads borne above female heads on branches or terminating the main axis, usually remote and distinct at anthesis; before anthesis green with black flecks and ca. 5 mm diameter; at anthesis 10–12 mm diameter.

Female flowers with perianth segments somewhat thickened and dark brown to black at the apex, not translucent, almost entire at apex (Fig. 2a); ovaries with 1, 2 or

rarely 3 carpels but at least half the ovaries are unicarpelate; more than half the styles are undivided; stigmas (1.5–)2–4 mm long, somewhat irregularly bent or coiled.

Male flowers with filaments ca. 5 mm long, anthers 1.2–1.5 mm long; perianth segments thickened and dark brown to black at the apex.

Fruits very variable in form (see subspecies), 4–12 mm long, 2–7.5 mm diameter; peduncle absent or up to 2 mm long, endocarp 3–6(–7) mm long, with sharp to blunt longitudinal ribs (Fig. 4c).

Diagnostic features

Perianth segments thickened and dark brown to black at apex, not translucent and almost entire; inflorescence usually branched; female heads born on axillary branches (very rarely sessile); anthers 1.2–1.5 mm long; less than half the styles are bifid.

Distribution

S. erectum sensu lato is found in Europe from the arctic circle southwards to North Africa extending through temperate Asia southwards to the western Himalaya and eastwards through Japan into northwestern North America (Maps 19–22). It is also in southeastern Australia where it is not certain if it is introduced or native see p. 22.

Ecology

Accounts of the ecology of *S. erectum,* written from different points of view, have been published by Loew in Kirchner et al. (1908), Cook (1962), and Haslam (1978). The autecology of *S. erectum* is very similar to that of *S. emersum* and when both grow together, which is often the case, *S. erectum* occupies the shallower water or it is confined to the banks.

S. erectum is a common species along waterways and in shallow water around ponds, pools and lakes. However, it rarely forms extensive and continuous stands like so many other reed-swamp plants (i.e. *Phragmites, Scirpus, Typha*); unlike these plants, it is very torerant to disturbance and can survive considerable battering. In Britain the optimum conditions for growth and flower production (Cook, 1962) are a loose, medium-grained, silty substrate in about 10–20 cm of unshaded, standing or slowly flowing water. In swiftly flowing water the leaves are bent over and there is poor vegetative growth and flowers rarely develop. It can grow in water up to about 2 m deep but again shows poor growth and rarely flowers. In plants stranded on land the immediate response is to remain small (less than 50 cm tall) and develop numerous stolons.

Solitary plants develop leaves which spread fan-like over the water surface. Plants growing in dense stands have almost vertical leaves. The leaves are triangular in transverse section with palisade parenchyma and stomata on all three sides. The spacial geometry of the leaves (see also Kaul, 1973, for *S. eurycarpum*) ensures a high assimilative area. Dykyjová & Ondok (1973) measured a total dry biomass, including below ground organs, exceeding 2500 g/m² in Czechoslovakia; an extremely high level for a componant of a natural community in the temperate zone. In spite of this *S. erectum* is a poor competitor and in relatively stable habitats may be overgrown by other erect, amphibious or marginal plants such as, *Glyceria, Typha,* or *Phragmites.* In standing water it can invade and replace smaller aquatic plants such as, *Berula erecta, Elodea canadensis, Ranunculus* spp. or *Rorippa nasturtium-aquaticum.*

S. erectum shows an enormous tolerance and is found in acid, almost oligotrophic waters to brackish or highly polluted water subjected to sewage effluents. In terms of growth and flower production the optimum is mesophytic to eutrophic water somewhat on the alkaline side (pH 7.5–8) in situations that are regularly disturbed (flooding, clearing, dredging, fluctuating water levels, etc). The loose substratum and frequently dirty eutrophic water that the adult plant thrives in are the worst conditions for the juvenite plant. Perhaps reproduction by seed is important in the colonization of newly dug pools and canals where the water is clear and there is no great algal growth. *S. erectum* is effectively spread by detached stolons.

In sluggish streams, canals and in slowly flowing rivers it accummulates silt which may lead to choking. It has been reported to be a serious weed at times in parts of England and the Netherlands. Importation, transportation, and cultivation of *S. erectum* is banned by the Federal Noxious Weed Act of the USA and by the State of Florida; nobody seems to have noticed that it is native in western North America, also it is most unlikely to be able to grow in Florida.

No ecological differences seem to exist between the various subspecies. Cook (1961 a) observed four subspecies growing together in the Trent and Mersey canal south of Derby, England. Despite their sympatric distribution, intermediate fruit-shapes were not found.

Notes

S. erectum shows considerable polymorphism in the form and size of the fruits. Polymorphic diaspores are found in several patristically unrelated aquatic plants such as, *Blyxa, Ceratophyllum, Eclipta, Ludwigia* and *Trapa,* see Cook (1987). These examples, like *S. erectum,* show a diaspore polymorphism that is not correlated with vegetative or other floral characteristics. The selective advantage of this polymorphism is difficult to interpret in terms of dispersal function. The taxonomic treatment of these polymorphisms also presents difficulties. In *S. erectum* there are five reasonably distinguishable units which have been variously recognised at ranks from form to species. We find it inpracticable to use the rank of species because plants can only be determined with ripe fruits. As each taxon shows a distinct distribution pattern with some allopatry we prefer to adopt the rank of subspecies, which at least allows determination to the rank of species without ripe fruit.

Despite differences in size between fruits of the subspecies of *S. erectum,* our studies show that size is strongly affected by external factors and that size alone may therefore be unreliable as a means of identifying the subspecies.

Plants of *S. erectum* subsp. *neglectum* which had been poorly pollinated (due to deliberate emasculation) were gathered at fruit-set from a pool at the University of Zurich. The number of set fruits in each head was counted and the width and weight of the fruits was measured. These results are presented in Fig. 19. They show a negative correlation between both size and weight of the fruits and the number of fruits per head. Similar size/number tradeoffs have been described, for example, by Galen & Weger (1986).

Ignoring the relative benefits of developing few but large or many but small fruits it was clear to us that *S. erectum* subsp. *neglectum* remained identifiable. From cultivation experiments and other studies we are convinced that the subspecies of *S. erectum* are genetically distinct units and not simply a manifestation of phenotypic plasticity. It is however impossible to distinguish the fruits using size alone; colour and form are the most important characteristics.

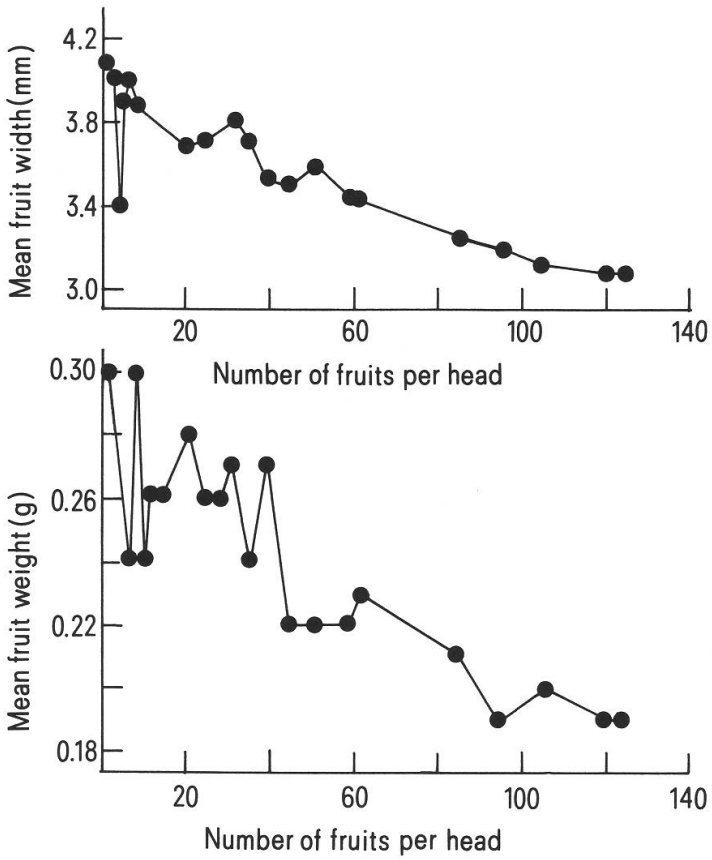


Fig. 19. Fruit size (above) and fruit weight (below) in *Sparganium erectum* subsp. *neglectum* from the University of Zürich campus plotted against the number of fruits in each head (the reduced fruit numbers were manipulated by selective pollination).

There are numerous reasons for reduced seed-set in *Sparganium*. Limitations in resources available for maternal function appear to play a role in the number of heads that develop but only influence the number of mature fruits in each head in conditions of stress. Another factor is pollination efficiency; the stigmas remain receptive for, at least, two to three days and pollen is shed over a period of weeks and effectively dispersed by wind. All plants tested were selfcompatible. Nevertheless, there are differences in fecundity between heads depending on their position, see Fig. 18. The lowest head is receptive before the pollen is shed and it is also partly covered by the base of the bract; it frequently shows low fecundicity. On all branches the lowest head is usually partially covered by the bract and shows consequently lower seed-set. The uppermost head of the total inflorescence often shows a lower fecundicity than its immediate neighbours; this is because it flowers late at a time when most male flowers have shed their pollen and those that are at anthesis are remote at the distal end of the inflorescence.

Some plants are partly sterile and show reduced seed-set on all female heads. The cause of this sterility is unknown but plants marked in nature and plants transferred to the botanic gardens have shown that semi-sterility persists from year to year. This sterility has little to do with pollination efficiency. We suspect it results from hybridization between different subspecies or races of *S. erectum*.

Čelakovský (1896) and his son (Čelakovský, 1899) were convinced that it is possible to distinguish the subspecies of *S. erectum* in Czechoslovakia on the basis of their leaf anatomy. Belavskaja (1984) made similar claims for plants in Russia. We have examined leaf sections of plants growing in different conditions. There is considerable plasticity and we are not convinced that it is possible to distinguish the subspecies on leaf or any other vegetative characteristics.

Hybrid

7 × 13. *S. emersum* × *S. erectum* sensu lato
= *S.* × *aschersonianum*, see p. 21
= *S. englerianum*, see p. 24

Experimental crosses have been attempted but the hybrid seems to be inviable. We have no evidence that this hybrid exists, see p. 21 and p. 24.

13. A. **Sparganium erectum L.** subsp. **erectum,** Species Plantarum 2: 971. 1753. Type: the illustration named *S. ramosum* in L'Obel, Plantarum Seu Stirpium Historia 41. 1576; see Cook (1985) for full discussion.

= *S. erectum* var. *angustifolium* Warnstorf, Verh. Bot. Verein Brandenburg 37: L [sic]. 2 April 1896 ≡ *S. ramosum* subsp. *polyedrum* subvar. *angustifolium* (Warnstorf) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 293. 15 June 1897 ≡ *S. ramosum* subsp. *polyedrum* var. *β angustifolium* (Warnstorf) Graebner in Engler, Pfanzenreich 2(IV.10): 14. Sept. 1900. *Type:* Germany, Neu-Ruppin, „im See bei der Wuthenower Fähre", 1985, *Warnstorf* (holotype: B, probably destroyed).

= *S. ramosum* forma *platycarpum* Čelakovský, Österr. Bot. Zeitschrift 46: 423. December 1896 ≡ *S. ramosum* subsp. *polyedrum* subvar. *platycarpum* (Čelakovský) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 284. 15 June 1897 ≡ *S. ramosum* subsp. *polyedrum* var. *ε platycarpum* (Čelakovský) Graebner in Engler, Pflanzenreich 2 (IV.10): 14. September 1900. Type: none cited, specimen probably in PR.

= *S. ramosum* forma *conocarpum* Čelakovský, Österr. Bot. Zeitschrift 46: 423. December 1896 ≡ *S. ramosum* subsp. *polyedrum* subvar. *conocarpum* (Čelakovský) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 284. 15 June 1897 ≡ *S. ramosum* subsp. *polyedrum* var. *δ conocarpum* (Čelakovský) Graebner in Engler, Pflanzenreich 2 (IV.10): 14. September 1900. Type: none cited, specimen probably in PR.

= *S. ramosum* subsp. *polyedrum* Graebner in Ascherson & Graebner, Syn. Mitteleurop. Flora 1: 283. 15 June 1897. ≡ *S. erectum* subsp. *polyedrum* (Graebner) Schinz & Thellung in Schinz & Keller, Flore Suisse, éd. Française, 1 Partie: Flore d'Excursion, 26. 1909. ≡ *S. ramosum* var. *polyedrum* (Graebner) Holmberg Skand. Flora 1: 79. 1922 ≡ *S. polyedrum* S. W. Juzepczuk, S. V. in Komarov, V. L., Flora USSR. 1: 219. 1934. Type: no specimen cited, based on *S. ramosum* sensu Curtis in W. Curtis, Flora Londinesis 2(fasc. 5): pl. 66 (according to index of fascicle), pl. 194 (according to index of volume 2), pl. 342 (as engraved on the plate, not visible in all copies). April 1787.

= *S. ramosum* subsp. *polyedrum* subvar. *dolichocarpum* Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 283. 15 June 1897 ≡ *S. ramosum* subsp. *polyedrum* var. *γ dolichocarpum* (Graebner) Graebner in Engler, Pflanzenreich 2 (IV.10): 14. September 1900. Type: Germany, „Westpreußen: Plehnendorf bei Danzig" (holotype: destroyed in B).

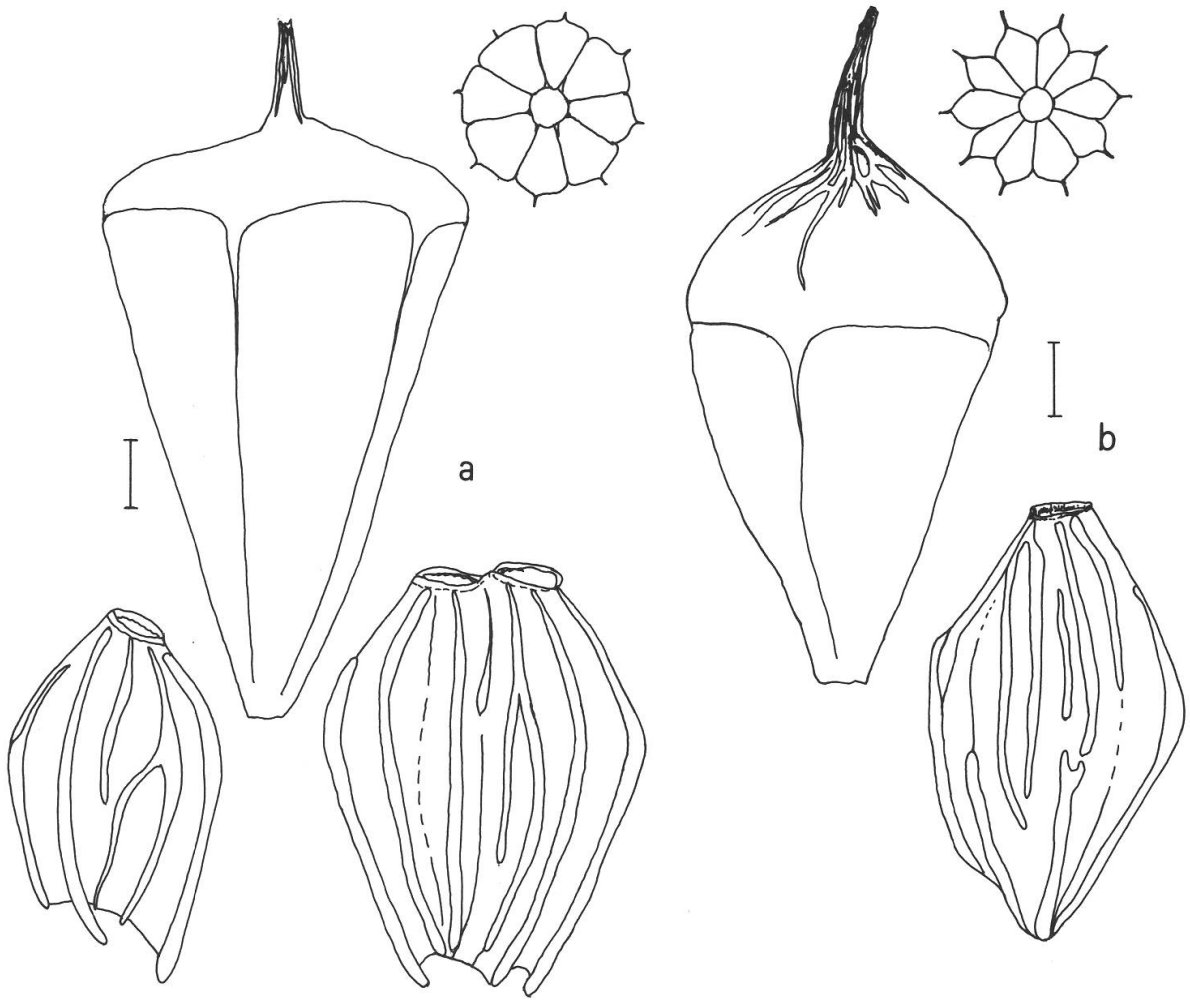


Fig. 20. Fruits, endocarps and diagrammatic sections of fruiting heads of *Sparganium erectum:* a, subsp. *erectum;* b, subsp. *stoloniferum* (scale bar: 1 mm).

= ?*S. draco* F. Hermann, Bull. Soc. Bot. Bulgarie 3: 43. 1929. Type: Bulgaria, "lacu prope Dragoman", specimen not located, not in SOM, perhaps destroyed in B.
– *S. ramosum* Hudson, Flora Anglica, ed. 2, 2: 401. 1778 ≡ *S. erectum* var. δ *ramosum* (Hudson) Laestadius, Wikström's Årsberättelse, 1950, Bihang: 2. 1853 or 1854, nom. illeg. based on *S. erectum* L.
– *S. reyesianum* Sennen, 24 August 1916, *Sennen,* nom. illeg., nom. in schaed.

Fruits cuneate-obpyramidal, (4–)6–10(–12) mm long, (3–)4–6(–7) mm wide, with a distinct shoulder between the upper and lower parts (Fig. 20a); lower part obpyramidal, (–4)5–8(–10) mm long, distinctly 3–6-angled in transverse section, light brown; upper part flattened light brown to dark brown or blackish, matt (not shiny), smooth (not creased when dry), very abruptly contracted into a beak; beaks not more than 2 mm long; bilocular ovaries frequent but less than half the total ovaries; endocarps (3.5–)5.5–6(–7) mm long, 4–5 mm wide (Fig. 20a), reaching the apex of the fruit; pedicels absent or very short; perianth segments not visible between the fruits on mature fruiting heads, 4.5–7.5 mm long.

Distribution

Common through much of central and southern Europe, but largely absent from Scandinavia. In Britain it is common only south of the Wash. It extends eastwards to the Causasus (Kaspiysk) and south to Turkey (Hakkari) (see Map 19, the map is based on recently seen herbarium specimens and reliable literature records we have not seen sufficient material from southern and western Europe).

Hybrid

7 × 13 A. *S. emersum* × *S. erectum* subsp. *erectum*

= *S.* × *aschersonianum* Haussknecht, Mitteilungen des Thüringischen Botanischen Vereins N.F, 1 (3–4): 84–86. 1893.

This hybrid is frequently cited in the literature. We very much doubt that it exists. Cook (1962) made some experimental crosses in the field in Derbyshire, England; this cross and the reciprocal cross have each been tried several times without success (the control crosses were fertile). *S. emersum* is often found in a zone occupying slightly deeper water than a parallel zone of *S. erectum* along the banks of canals, streams and small rivers. Pollen must frequently be transferred from one species to the other. We have never found plants in nature that could be referred to this hybrid. Herbarium material that has been determined as this hybrid is almost invariably depauperate and often unbranched *S. erectum.* Authentic material of S. × *aschersonianum* is referrable to *S. erectum* subsp. *microcarpum* (p. 22). Rothert (1910) was also of the opinion that this hybrid does not exist.

13 B. **Sparganium erectum** subsp. **stoloniferum** (F. Hamilton ex Graebner) C. D. K. Cook & M. S. Nicholls, **comb. nova** ≡ *S. ramosum* subsp. *stoloniferum* F. Hamilton ex Graebner in Engler, Pflanzenreich 2 (IV.10): 14. September 1900 ≡ *S. stoloniferum* F. Hamilton ex Juzepczuk in Komarov, Flora URSS 1: 219. 1934. *Type:* India, *Wallich 4990* (holotype: destroyed in B; isotype: K).

= *S. angustifolium* R. Brown, non Michaux, var. *latifolium* Bentham, Fl. Austral. 7: 161. 1878. Type: Australia, ?Queensland, Balfours Creek, *Leichhardt* (holotype: K?; isotype MEL).

= *S. greenei* Morong, Bull Torrey Bot. Club 15: 77, t. 79, fig. 3. 1888 ≡ *S. eurycarpum* var. *greenei* (Morong) Graebner in Engler, Pflanzenreich 2 (IV.10): 13. September 1900. Type: USA, California, Marin Co., Olema, September 1887, *E. L. Greene* (holotype: NY).

= *S. erectum* subsp. *mazanderanicum* Ponert, Fol. Geobot. Phytotax. (Praha) 7: 309. 1972. *Type:* Iran, prov. Mazanderan, "inter oppida Gorgan et Behshahr, 50 km ab Gorgan inter viam ferratam et sinum Gorganicum maris Caspici," 11 July 1970, *Jiri Ponert 37919/30,* (holotype: BATUMI n.v.; isotype, with male flowers, *37919/29:* BATUMI n.v.).

– *S. asiaticum* Graebner, Allg. Bot. Zeitschrift, 4 (2): 32. February 1898, nomen nudum, placed in synonymy of *S. ramosum* subsp. *stoloniferum* by Graebner in Engler, Pflanzenreich 2 (IV.10): 14. September 1900. "Type": specimen used as a basis for Fig. 3 c in Pflanzenreich, 2 (IV.10): 12. 1900; B.

– *S. carinatum* Falconer, Proc. Linn. Soc. (London) 1: 18. 1839, never published, nomen illeg., no type cited but hand written manuscript is in K.

Fruits obpyramidal below and domed to conical above, (5–)6–9(–10) mm long, 2.5–5 mm wide; lower part obpyramidal, 4–7 mm long, distinctly 3–6-angled, light

brown; upper part domed to conical with a slight constriction below the shoulder (Fig. 20b), light brown to straw-coloured, shiny, usually with irregular longitudinal creases, tapering rather abruptly into a beak; beak 2–3(–4) mm long; bilocular ovaries common but not more than half the total; endocarps 5–6 mm long, up to 4 mm wide (Fig. 20b), not reaching the apex of the fruit; pedicels absent or very short; perianth segments not visible between the fruits on mature fruiting heads, 4–6 mm long.

Distribution

From the Causasus and Afghanistan eastwards through north-eastern Pakistan to northern India and Lhasa, Tibet (Map 21). It is recorded from southern China and from west of Peking and occurs through much of Japan except for the extreme north (it is apparently absent from Hokkaido) and also occurs in S.E. Australia where it may have been introduced. It extends into western North America, from California to British Columbia (see Map 22).

Ecology

We have little first-hand knowledge on the ecology of subsp. *stoloniferum;* C.D.K.C. has seen it growing around Srinigar, Kashmir, India. It grows under conditions where one would expect to find other species of *S. erectum* in Europe such as ditches and at the edge of artificially maintained canals, where it is common but rarely builds large stands. In shady conditions, the leaves are often more than 2 m long.

Notes

S. erectum subsp. *stoloniferum* is the most widespread subspecies of *S. erectum.* In Australia it has usually been identified with European *S. erectum* and thus considered to be introduced. It is certainly to be included with the Asian/N. American subspecies *stoloniferum* and on this basis might be considered native in Australia. However, material from this region is abnormally uniform in fruit shape which may indicate that the Australian populations may have developed from a single introduction. In western North America it is also very uniform but is unlikely to be a recent introduction.

13. C. **Sparganium erectum** subsp. **microcarpum** (L. M. Neuman) Domin, Preslia 13: 53. 1935 ≡ *S. ramosum* forma *microcarpa* [sic] L. M. Neuman in Hartman, C. J. & Hartman, C., Handbok Skand. Flora, ed. 12, 122. October 1889 ≡ *S. microcarpum* (L. M. Neuman) L. J. Čelakovský, Österr. Bot. Zeitschrift 66: 378, 423, 1896 ≡ *S. ramosum* subsp. *neglectum* proles *microcarpum* (L. M. Neuman) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 281. 15 June 1897 ≡ *S. erectum* subsp. *neglectum* var. *microcarpum* (L. M. Neuman) A. Hayek, Prodr. Florae Pen. Balcan. Repert. Spec. Nov. Regni Veg. (Fedde), Beiheft, 30 (3): 426. 15 August 1932. Type: Sweden, Gotland, "Visby; Mpd. (Medelpad), *Klintehamn*"; Per Lassen (LD) could find no specimen collected by *Klintehamn,* it probably perished in the great fire of Sundsvall in 1888. However, there is a specimen from Medelpad collected by Neuman in 1888 (lectotype (designated here): LD – Medelpad: Tuna, Vattjom, 1888, *Neuman*)

Fruits acutely-obpyramidal below and domed above, (5.5–)6–7(–9) mm long, (2–)2.5–3.5(–4) mm wide; upper and lower parts different in form and texture with a distinct shoulder between them; lower part acutely-obpyramidal, 4–6 mm long, 3–6-

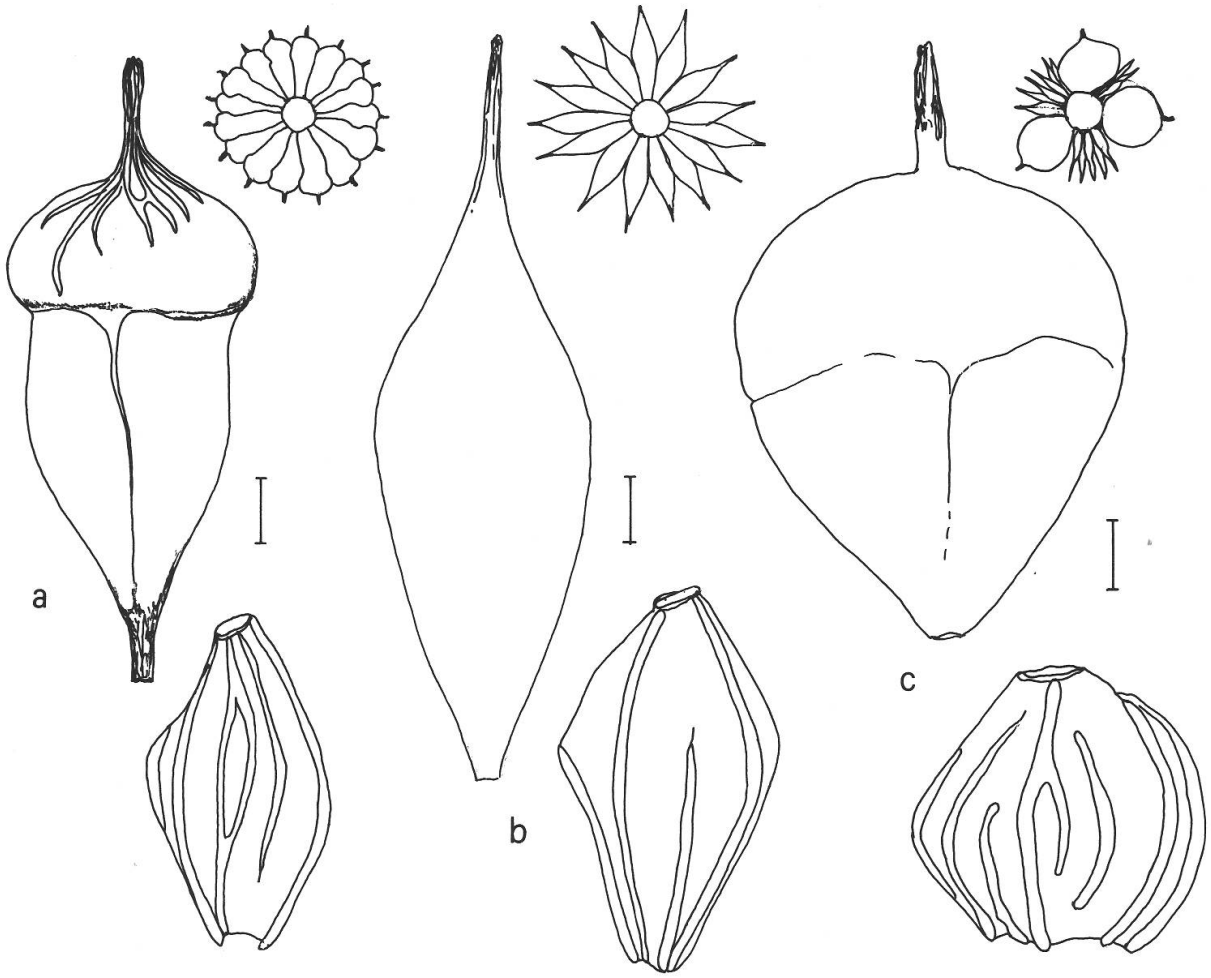


Fig. 21. Fruits, endocarps and diagrammatic sections of fruiting heads of *Sparganium erectum;* a, subsp. *microcarpum;* b, subsp. *neglectum;* c, subsp. *oocarpum* (scale bar: 1 mm).

angled in transverse section, the flattened faces sometimes bellied (endocarp pushes through the side); light brown to reddish brown; upper part domed and wider than the lower part (Fig. 21 a), with a slight constriction below the shoulder, brown to black, matt or somewhat shiny near the shoulder, with irregular longitudinal creases or wrinkles at base of beak, tapering rather abruptly into a beak; beak to 2 mm long, dark-brown to black; bilocular ovaries rare; endocarps (2.5–)4–5 mm long, 2.5–3 mm wide, not reaching the apex of the fruit (Fig. 21 a); pedicels to 1.5 mm long; perianth segments visible on mature fruiting heads, 4–6 mm long.

Distribution

Throughout Europe, particularly common in Scandinavia, extending eastwards to european Russia and south around the Sea of Azov and the Causasus (Tverksaya). Also from Turkey (Erzurum). See Map 20.

Hybrid

13 A × 13 C. *S. erectum* subsp. *erectum* × *S. erectum* subsp. *microcarpum*

This hybrid is recorded by Ostenfeld-Hansen (1897) and is perhaps the same as

S. ramosum var. ζ *substerile* Neuman, Bot. Not. 1897: 128. 1897 ≡ *S. ramosum* subsp. *polyedrum* var. ζ *substerile* (Neuman) Graebner in Engler, Pflanzenreich 2 (IV.10): 14. 1900. The fruit resembles subsp. *microcarpum* but the heads are usually highly sterile, see p. 17.

13 D. **Sparganium erectum** subsp. **neglectum** (W. H. Beeby) Schinz & Thellung in Schinz & Keller, Flore Suisse, éd. Française, 1 Partie: Flore d'Excursion, 26. 1909 ≡ *S. neglectum* W. H. Beeby, J. Bot. (London), 23: 193, 26, t. 258. 1885 (see also op. cit., 24: 142, 377. 1886) ≡ *S. ramosum* subsp. *neglectum* (W. H. Beeby) L. M. Neuman in Harman, C. J. & Hartman, C., Handbok Skand. Flora, ed. 12, 112. October 1889 or Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 281. 15 June 1897 ≡ *S. erectum* var. β *neglectum* (W. H. Beeby) Richter, Pl. Europ., 1: 10. 1890. Type: England, Surrey, "Albury ponds near Guildford", *W. H. Beeby* (lectotype: K; isolectotype E).

Fruits fusiform to ellipsoidal, (6–)7–9(–10) mm long, 2–3.5(–5) mm wide, upper and lower parts essentially alike in form, colour and texture, without a distinct shoulder, uniform light brown to straw coloured; lower part 3–5 mm long, about half the fruit length, hardly angled (almost circular in transverse section, Fig. 21 b); upper part smooth (without wrinkles) gradually tapering into a beak; beak (2–)2.5–3.5 mm long, sometimes dark-brown; bilocular ovaries extremely rare; endocarps (4–)5–6 mm long, up to 3.5 mm wide (Fig. 21 b), not reaching the apex of the fruit; pedicels absent or very short; perianth segments visible between the fruits on mature fruiting heads, 5–6 mm long.

Distribution

Throughout much of Europe extending northwards to about 58°N in Sweden and southwards to the northern coast of Africa (Morocco). Also recorded from european Russia and south into Greece and Turkey (Paphlagonia). See Map 19. The published records from Asia Minor are mostly referable to subspecies *stoloniferum.* We have not seen sufficient material from southern and western Europe.

Hybrids

7 × 13 D. *S. emersum* × *S. erectum* subsp. *neglectum*
= *S.* × *englerianum* Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 287. 15 June 1897. Type: Germany. "Pretzsch", "Berlin: Botanischer Garten" (lectotype: destroyed in B).

We are not convinced that this hybrid exists. Authentic herbarium material refers to depauperate *S. erectum* subsp. *neglectum.*

13 C × 13 D. *S. erectum* subsp. *microcarpum* × *S. erectum* subsp. *neglectum*

This hybrid is probably the same as *S. ramosum* var. ζ *substerile* Neuman, Bot. Not. 1897: 128. 1897 ≡ *S. ramosum* subsp. *polyedrum* var. ζ *substerile* (Neuman) Graebner in Engler, Pflanzenreich 2 (IV.10): 14. 1900. It resembles subsp. *microcarpum* but the fruits are somewhat larger and elongated and the heads are partly sterile. It is occasionally found growing with the parents.

13 A × 13 D. *S. erectum* subsp. *erectum* × *S. erectum* subsp. *neglectum*
= *S.* × *tardivum,* Ţopa in Săvulescu, T. Flora Republicii Socialiste România 11: 849 (see

also p. 106) 1966. Type: Romania, "Reg. Iaşi, Horleşti, propr. oppidum Iaşi, legit. *M. Răvărut*" (holotype: I or possibly IAGB, n.v.).

Several authors including Cook (in Stace, 1975)have suggested that *S. erectum* subsp. *oocarpum* is this hybrid, while others such as Čelakovský (1896) were convinced that it is not a hybrid. We note that subsp. *oocarpum* is not fully fertile, it well may be of hybrid origin but is most unlikely to be a simple cross between subsp. *erectum* and subsp. *neglectum* (for further discussion see p. 17).

13 E. **Sparganium erectum** subsp. **oocarpum** (L. J. Čelakovský) Domin, Preslia 13: 53. 1935 ≡ *S. neglectum* var. *oocarpum* L. J. Čelakovský, Österr. Bot. Zeitschrift 46: 425. December 1896 ≡ *S. ramosum* subsp. *neglectum* proles *oocarpum* (L. J. Čelakovský) Graebner in Ascherson & Graebner, Synopsis Mitteleurop. Flora 1: 282. 15 June 1897 ≡ *S. neglectum* subsp. *oocarpum* (L. J. Čelakovský) C. Ostenfeld-Hansen, Bot. Tidsskr. 21 (1): Meddelesler V. 6 July 1897 ≡ *S. oocarpum* (L. J. Čelakovský) Fritsch, Exkursionsflora Österr., ed. 2, 28. 1909 ≡ *S. erectum* subsp. *neglectum* var. *oocarpum* (L. J. Čelakovský) Hayek, Prodr. Florae Pen. Balcan. Repert. Spec. Nov. Regni Veg. (Fedde), Beiheft, 30 (3): 426. 15 August 1932. Type: Czechoslovakia, several localities given (lectotype: PR to be chosen).
= *S.* × *tardivum*, Ţopa in Săvulescu. T. Flora Republicii Socialiste România 11: 849 (see also p. 106) 1966. Type: Romania, "Reg. Iaşi, Horleşti, propr. oppidum Iaşi, legit. *M. Răvărut*" (holotype: I or possible IAGB, n.v.).

Fruits widely ovoid to almost spherical, 5–8 mm long, 4–7 mm wide, uniform light to medium brown and shiny, shoulder between upper and lower parts indistinct; lower part 2.5–5 mm long, almost circular in transverse section; upper part tapering into a beak and sometimes wrinkled or creased at base of beak but otherwise smooth (Fig. 21 c); beaks up to 2 mm long; bilocular ovaries very rare; endocarps 3.5–4 mm long, up to 4 mm wide; not reaching the apex of the fruit, pedicels absent or very short; perianth segments visible between the fruits on mature fruiting heads, 3–6 mm long (Fig. 21 c).

Distribution

Isolated records through much of Europe, Turkey (Istanbul, Vol Antalya) and Iraq (Map 20).

Notes

Specimens show very poor fertility which has led Cook (in Stace, 1975) and other to suggest that subsp. *oocarpum* is of hybrid origin. On morphological grounds, the suggested parents are subsp. *erectum* and subsp. *neglectum* but it is unlikely to be a simple cross between these two.

It has also been suggested that the big fat fruits of subsp. *oocarpum* are a consequence of resource allocation (caused, for example, by poor pollination). A plant with few fruits to mature per head might be expected to devote greater resources to the remaining fruits which will then grow fatter than fruits competing more strongly for resources. We have undertaken experiments with subsp. *neglectum* where pollination was artificially limited so that few ovules per head were fertilized. Under these conditions subsp. *neglectum* also produces "fat" fruits and both fruit-width and fruit-weight are strongly correlated with the number of fruits per head (see Fig. 19). Nevertheless, these

fruits are still distinguishable from true *oocarpum* leading us to discount this resource allocation hypothesis as a means of accounting for the origin of this subspecies.

14 A. **Sparganium eurycarpum** subsp. **eurycarpum** Engelmann in Gray, Manual Bot. Northern U.S., ed. 2, 430. 1856. Type: USA, "from New England and Pennsylvania northward and westward", *Engelmann* (lectotype to be chosen from material at MO; possible isotype: G).

= *S. californicum* Greene, Bull. Calif. Acad., 1 (3): 11. 1884. Type: USA, California, Calistoga, *E. L. Greene* (holotype: ND-G; isotype: ?NY).

Robust erect, emergent or rarely floating or submerged herbs. Stolons up to ca. 30 cm long, ca. 5 mm diameter. Corms up to 4.5 cm diameter, when mature hard and woody.

Basal leaves obliquely erect and fan-like, 50–100(–260) cm long, 6–20 mm wide, carinate at base but often becoming flattened towards the apex, with 3–6 layers of gas chambers.

Plants in very deep or swiftly flowing water may develop submerged or partly floating leaves but usually remain sterile.

Flowering stems erect, 50–150(–260) cm long, nearly alway branched with 1–4 sterile nodes between the corm and the inflorescence; branches (0–)2–5, axillary, with 1–2 or rarely more female heads at the proximal end and (0–)6–14 male heads at the distal end or upper branches with male heads only; the upper female head or heads are oc-

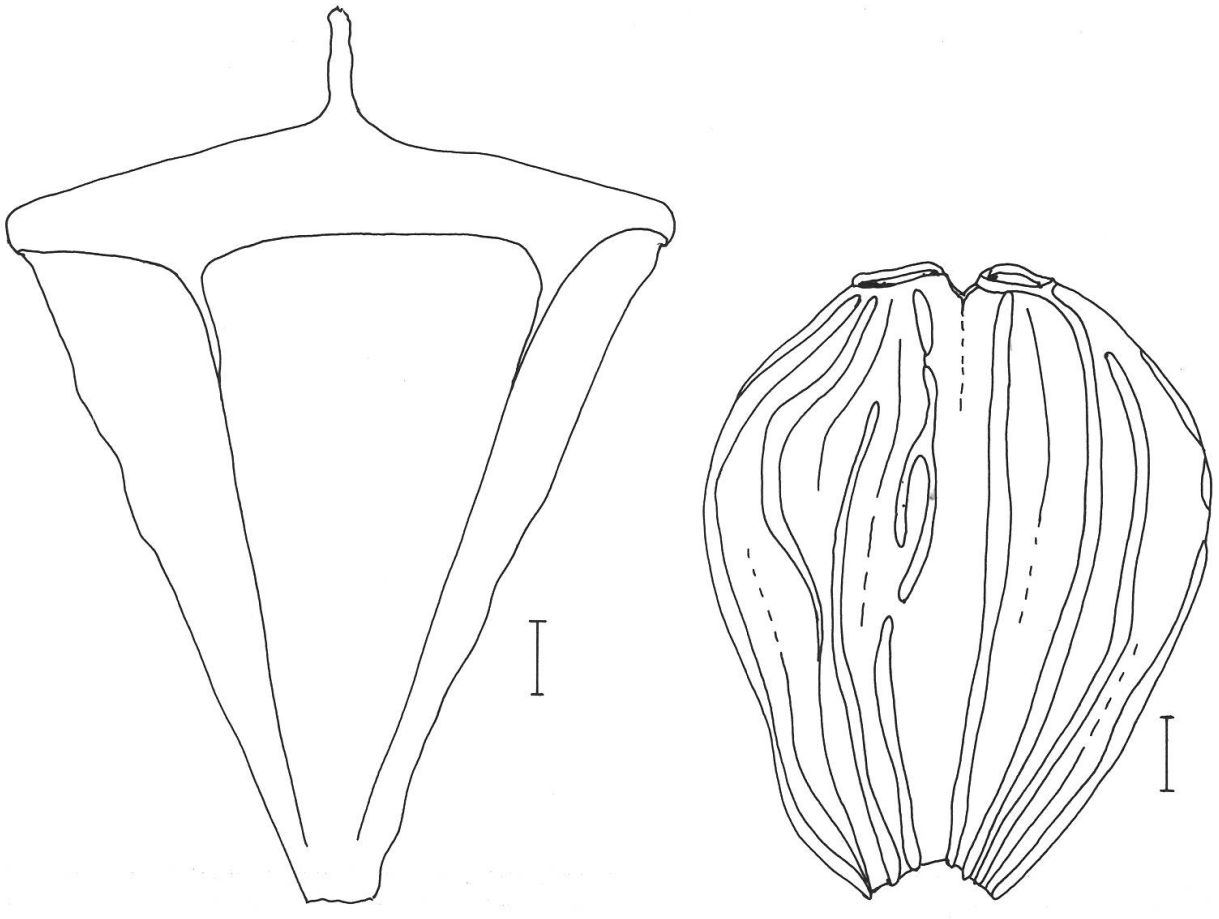


Fig. 22. Fruit and endocarp of *Sparganium eurycarpum* subsp. *eurycarpum* (scale bar: 1 mm).

casionally sessile on main axis; the lowest branch usually with both male and female heads.

Inflorescence bracts leaf-like below, erect, carinate at base; scale-like above; lowest bract usually not exceeding inflorescence at late anthesis.

Female heads borne on axillary branches, peduncles or sessile on main axis, 2–3.5 mm diameter in fruit (excluding beaks).

Male heads borne above female heads on branches or terminating the main axis, usually remote and distinct at anthesis; before anthesis green with black flecks and ca. 5 mm diameter; at anthesis ca. 12 mm diameter.

Female flowers with perianth segments somewhat thickened and dark brown to black at the apex, not translucent almost entire at apex; ovaries at least half with 2 carpels the majority of the rest with 1 carpel and some with 3 carpels; at least half the stigmas bifid; stigmas 2–3.5 mm long, usually curved.

Male flowers with filaments ca. 6 mm long; anthers 1–1.5 mm long, perianth segments somewhat thickened and dark-brown to black at apex.

Fruits cuneate-obpyramidal, 6–10 mm long, 6–8 mm wide with a distinct shoulder between upper and lower parts (Fig. 22); lower part obpyramidal, 5–9 mm long, distinctly 3–6 angled in transverse section, light brown; upper part flattened, straw-coloured to brown, sometimes sootyblack at base of beak, mostly smooth (not creased when dry), very abruptly contracted into a beak; beaks 2–4(–4) mm long; endocarps 7–10 mm long, up to 7 mm wide, usually 2-locular, distinctly ribbed with ribs projecting beyond the base (Fig. 22), reaching the apex of the fruit; pedicels absent; perianth segments not visible between the fruits on mature fruiting heads.

Diagnostic features

Like *S. erectum* but at least half the styles bifid (at least half the ovaries have two carpels); fruits sessile, cuneate-obpyramidal, 6–10 mm long, 6–8 mm wide, the top truncate depressed or very shallowly rounded, abruptly tipped with the style, straw coloured to somewhat sooty-black.

Distribution

It occurs across North America, from east to west between 60°N and 35°N, (Map 22).

Ecology

S. eurycarpum is essentially a north American vicariant of the eurasian species *S. erectum.* Both species are ecologically very similar and although we have no experience of *S. eurycarpum* in the field, most of the information presented on pp. 16–18 is probably relevant. It is reported to grow on damp shores and in still or slowly flowing water. It performs best in slightly alkaline conditions but tolerates acid substrates. It is often very abundant although not reported to be a serious weed. Rather suprisingly, it is on the rare and endangered plant list for New Hampshire.

Neely & Davis (1985 a) found that fertilization of *S. eurycarpum* with nitrogen and phosphorus increased the net annual above-ground production but the root-rhizome production was not altered. The litter is a poor nutrient sink and Neely & Davis (1985 b) noted that litter with an initially high nutrient content decomposed faster than litter with low initial nutrient content.

Cruden & Lyon (1985) showed that in *S. eurycarpum* the dry weight of both male and female heads increased with the number of inflorescence branches, and that dry weight is positively correlated with the number of seeds matured. They interpret these findings in the light of current theories regarding resource allocation patterns in plants.

Although Cruden & Lyon's findings are hardly surprising, we would question their assumption that *S. eurycarpum* is xenogamous, particularly in light of our own work on pollen-flow pattern in *S. erectum* (see p. 18).

14 B. **Sparganium eurycarpum** subsp. **coreanum** (Léveillé) C. D. K. Cook & M. S. Nicholls **comb. nova** ≡ *S. coreanum* Léveillé, Repert. Spec. Nov. Regni Veg. (Fedde) 10: 441. 1912 ≡ *S. stoloniferum* var. *coreanum* (Léveillé) Hara fide Ohwi, Flora Japan 119. 1965. Type: S. Korea, Cheju do, "Quelpaert, in stagno Terok", 14 September 1908. *Taquet 2150* (holotype: E; isotypes: G, K. TI).

– *S. macrocarpum* Makino in Matsumura. Indig. Pl. Jap. (2) 1: 24. 1905, nomen nudum ≡ *S. stoloniferum* var. *macrocarpum* (Makino) Hara fide Ohwi, Flora Japan 119. 1965. Type: Japan, Honshu, Chiba Pref., Junsai-numa, September 1893, *T. Makino s.n.* (holotype: TI).

Like subsp. *eurycarpum* but mature fruiting heads usually smaller, rarely exceeding 20 mm diameter (excluding beaks); individual fruits 5–9(–10) mm long, 5–8 mm wide; the top of the fruit less flat, shallowly rounded or widely pyramidal (Fig. 23) and light

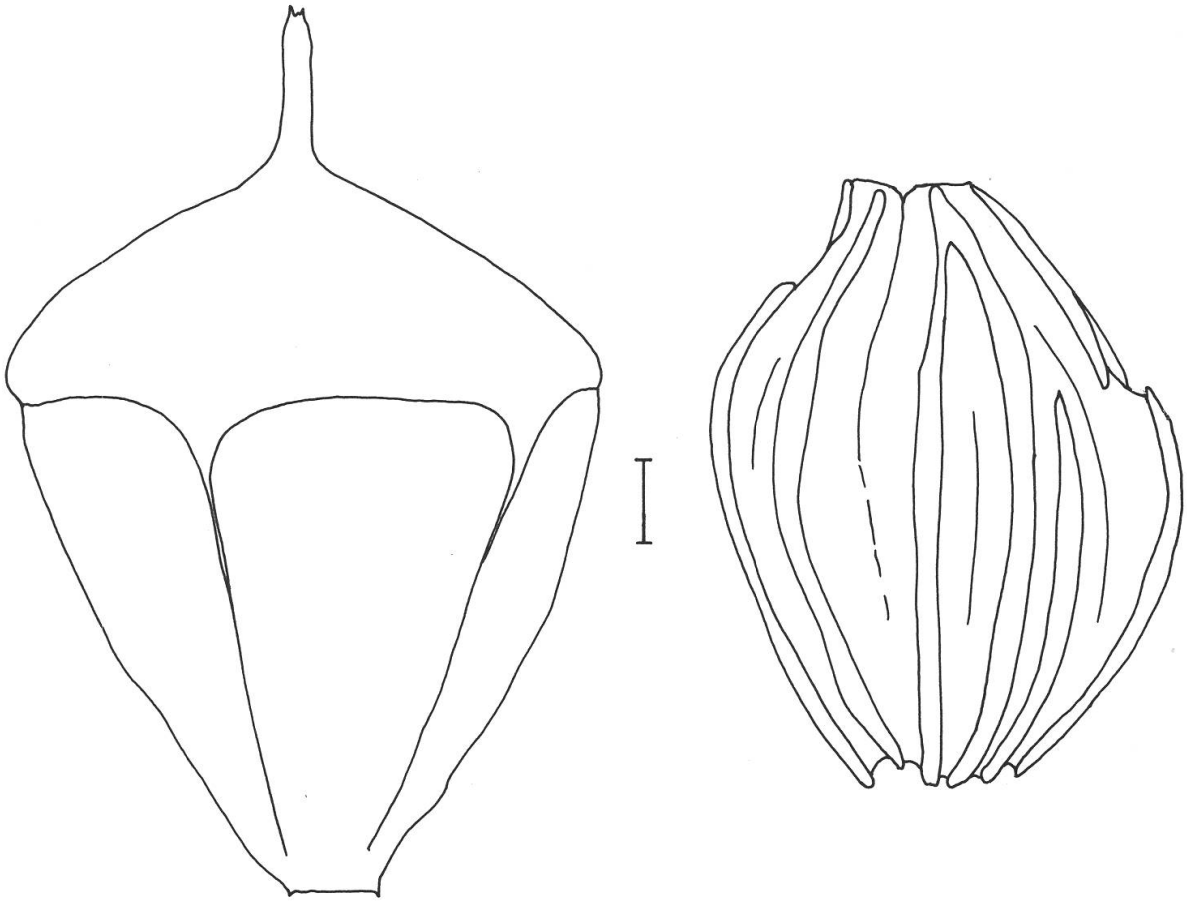


Fig. 23. Fruit and endocarp of *Sparganium eurycarpum* subsp. *correanum* (scale bar: 1 mm).

to dark brown, not shiny, abruptly contracted into a 2–4 mm long beak; endocarps 6–7 mm long, 4–5 mm wide with longitudinal ribs extending beyond the base (Fig. 23).

Distribution

Korea to northern and central Japan (Honshu). Also from Manchuria (see Map 21).

Notes

We have seen few adequate specimens but are, nonetheless, convinced that the affinities of this taxon lie with *S. eurycarpum* rather than *S. erectum*. The fruits are very large and more than half are bilocular with bifid styles.

Uncertain species

Sparganium affine forma *abbreviata* Meyerholz. Verh. Bot. Verein Brandenburg 34: 26. 1893, nomen nudum, no authentic specimens found.
Sparganium alpinum D. Don ex G. Don in Loudon, Hortus Britannicus, 375. 1830, nomen nudum, no authentic specimens found.
Sparganium androcladum var. *ζ microcarpum* Graebner in Engler, Pflanzenreich 2 (IV.10): 15. 1900, diagnosis inadequate, no authentic specimens found.
Sparganium axilare Rafinesque, Autikon Botanikon, 198. 1840, description inadequate, no authentic specimens found, see Cook (1985) for details.
Sparganium emersum forma *angustifolium* (Morong) [sic] Soó, Acta Bot. Acad. Sci. Hung. 17 (1–2): 124. 1971 publ. 1972, perhaps a misprint.
Sparganium ligulare Rafinesque, Autikon Botanikon, 198. 1840, description inadequate, no authentic specimens found, see Cook (1985) for details.
Sparganium simplex var. *subnatans* E. M. Fries, Bot. Not. 1868: 71. 1868, nomen nudum, no authentic specimens found.
Sparganium subspinosa Auct., Just's Bot. Jahresber. 21 (2): 670. 1893, name appears in index, probably a misprint or mistake.

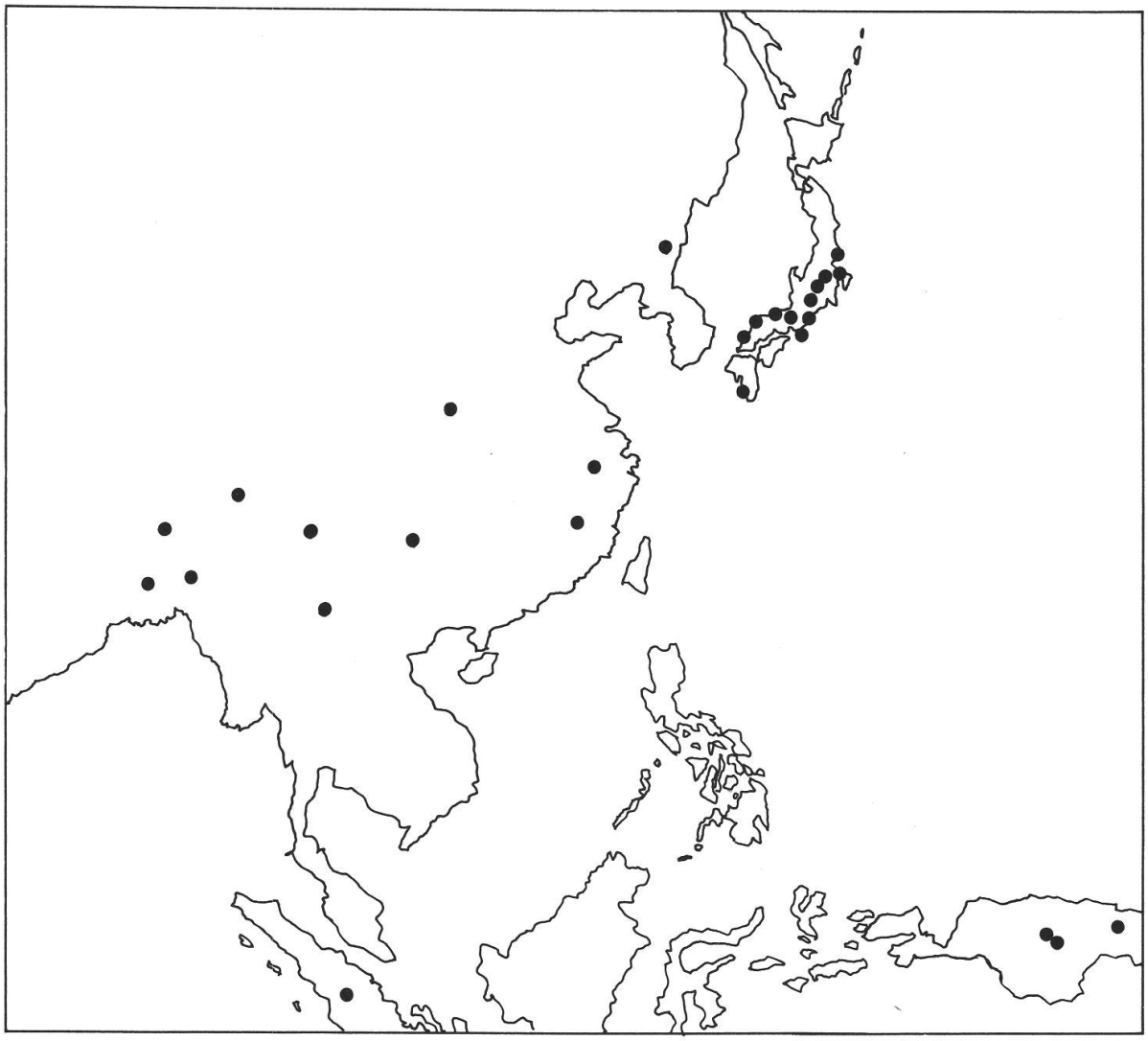
References

Beal E. O. 1960. *Sparganium* (Sparganiacae) in the southeastern United States. Brittonia 12: 176–181.
Belavskaja A. P. 1984. A contribution to the morphology of fruits of the genus *Sparganium* (Typhaceae) in the flora of the USSR. Botaničeskij Žurnal Akad. Nauk. SSSR (Leningrad) 69 (12): 1662–1668.
Čelakovský L. J. 1896. Über die ramosen Sparganien Böhmens. Österreich. Bot. Zeitschr. 46: 377–381, 46: 421–433.
Čelakovský L. 1899. Anatomický rozdíly v Pistech ramoních sparganií. Věstn. Král. Čes. Společ. Nauk, Cl. Math.-Natur. (Praha) 1899 (5): 1–11.
Chen Yao-Dong 1981. A study on Chinese *Sparganium* (in Chinese). Acta Phytotaxonomica Sinica 19 (1): 41–57.
Clausen R. T. 1937. A new variety of *Sparganium americanum*. Rhodora 39: 188–190.
Cook C. D. K. 1961. *Sparganium* in Britain. Watsonia 5: 1–10.
Cook C. D. K. 1962. Biological Flora of the British Isles, No. 82. *Sparganium erectum* L. J. Ecology 50: 247–255.

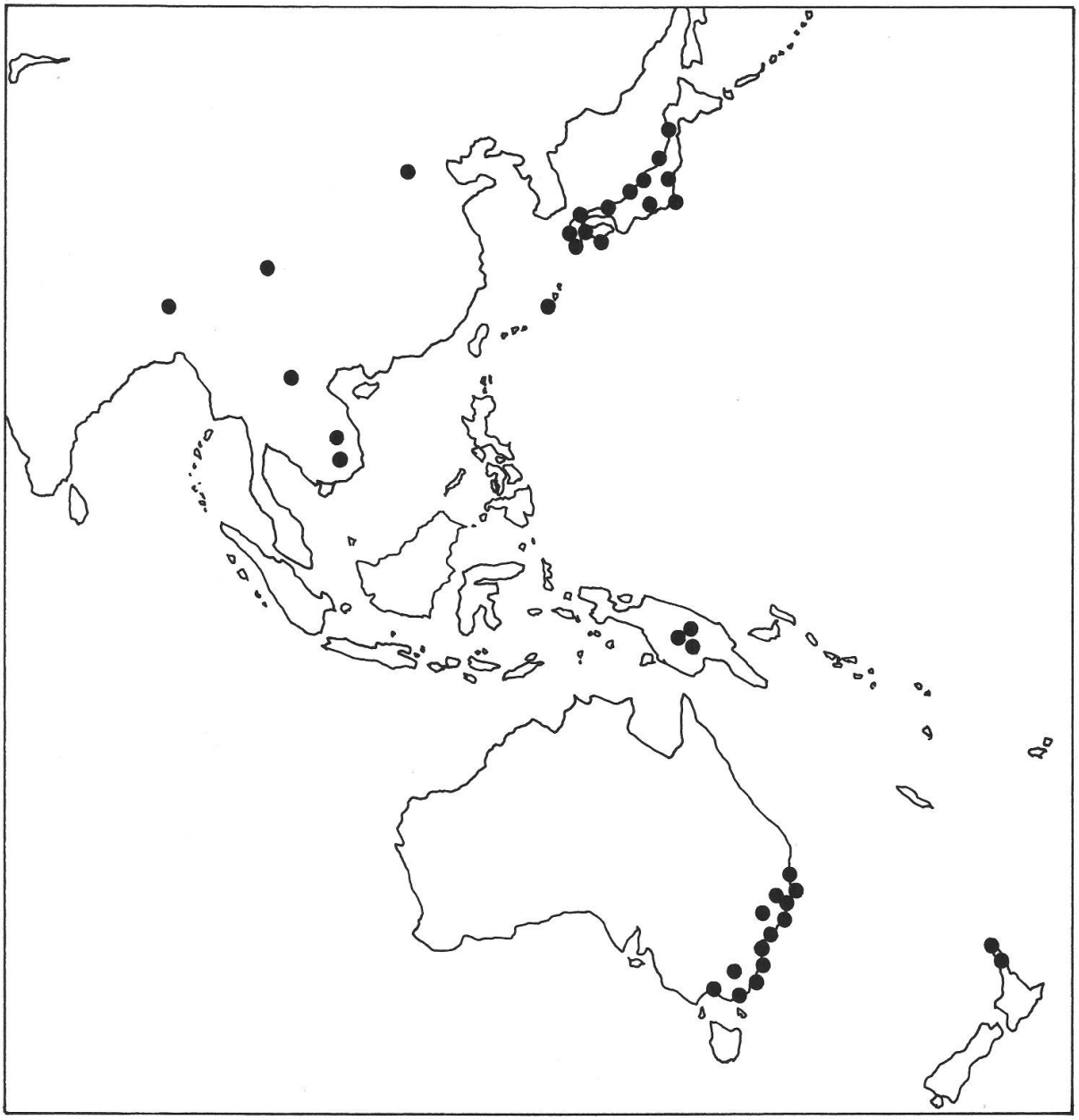
Cook C. D. K. 1985. *Sparganium:* some old names and their types. Bot. Jahrb. Syst. 107: 269–276.
Cook C. D. K. 1987. Dispersion in aquatic and amphibious vascular plants. In Crawford (Ed.) Plant Life in Aquatic and Amphibious Habitats. British Ecological Society Special Symposium Blackwell, Oxford (in press).
Cruden R. W. & Lyon D. L. 1985. Pattern of biomass allocation to male and female functions in plants with different mating systems. Oecologia (Berlin) 66: 299–306.
Dykyjová D. & Ondok J. P. 1973. Biometry and the productive stand structure of coenoses of *Sparganium erectum.* L. Preslia (Praha) 45: 19–30.
Fernald M. L. 1922. Notes on *Sparganium.* Rhodora 24(277): 26–34.
Fernald M. L. & Eames A. J. 1907. Preliminary lists of New England Plants, XX. Sparganiceae. Rhodora 8 (85): 86–90.
Galen C. & Weger H. G. 1986. Re-evaluing the significance of the correlations between seed number and size: evidence from a natural population of the lily, *Clintonia borealis.* Amer. J. Bot. 73: 346–352.
Haslam S. M. 1978. River plants. Cambridge University Press, Cambridge. pp. 1–396.
Kaul R. B. 1973. Development of foliar diaphragms in *Sparganium eurycarpum.* Amer. J. Bot. 60: 944–949.
Kirchner O., Loew E. & Schroeter C. 1908. Lebensgeschichte der Blütenpflanzen Mitteleuropas 1 (1): 374–394. Eugen Ulmer, Stuttgart.
Mohr C. 1901. Plant life of Alabama. Contrib. US. Nat. Herbarium 6: 327.
Morong T. 1888. Studies in the Typhaceae. II. *Sparganium.* Bull. Torrey Bot. Club 15: 73–81.
Neely R. K. & Davis C. B. 1985a. Nitrogen and phosphorous fertilization of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. I. Emergent plant production. Aquatic Bot. 22: 347–361.
Neely R. K. & Davis C. B. 1985b. Nitrogen and phosphorous fertilization of *Sparganium eurycarpum* Engelm. and *Typha glauca* Godr. stands. II. Emergent plant decomposition. Aquatic Bot. 22: 363–375.
Nuttall T. 1818. The genera of North American plants. Facsimile ed.: 1971. Hafner Publ. Co. New York. Classica botanica americana vol. 7.
Ostenfeld-Hansen C. 1897. De i Danmark voxende ramøse *Sparganium*-Arten. Bot. Tidskrift Bot. For. Kjøbenhavn 21 (1): V–IX.
Rothert W. 1910. Übersicht der Sparganien des Russischen Reiches (zugleich Europa's). Acta Horti Bot. Univ. Imper. Jurjevensis 11: 11–32.
Rydberg P. A. 1909. Sparganiaceae in North American Flora (New York Botanical Gardens) 17: 5–10.
Stace C. A. 1975. Hybridization and the Flora of the British Isles. Academic Press, London, New York, San Francisco. pp. 1–626.

Index

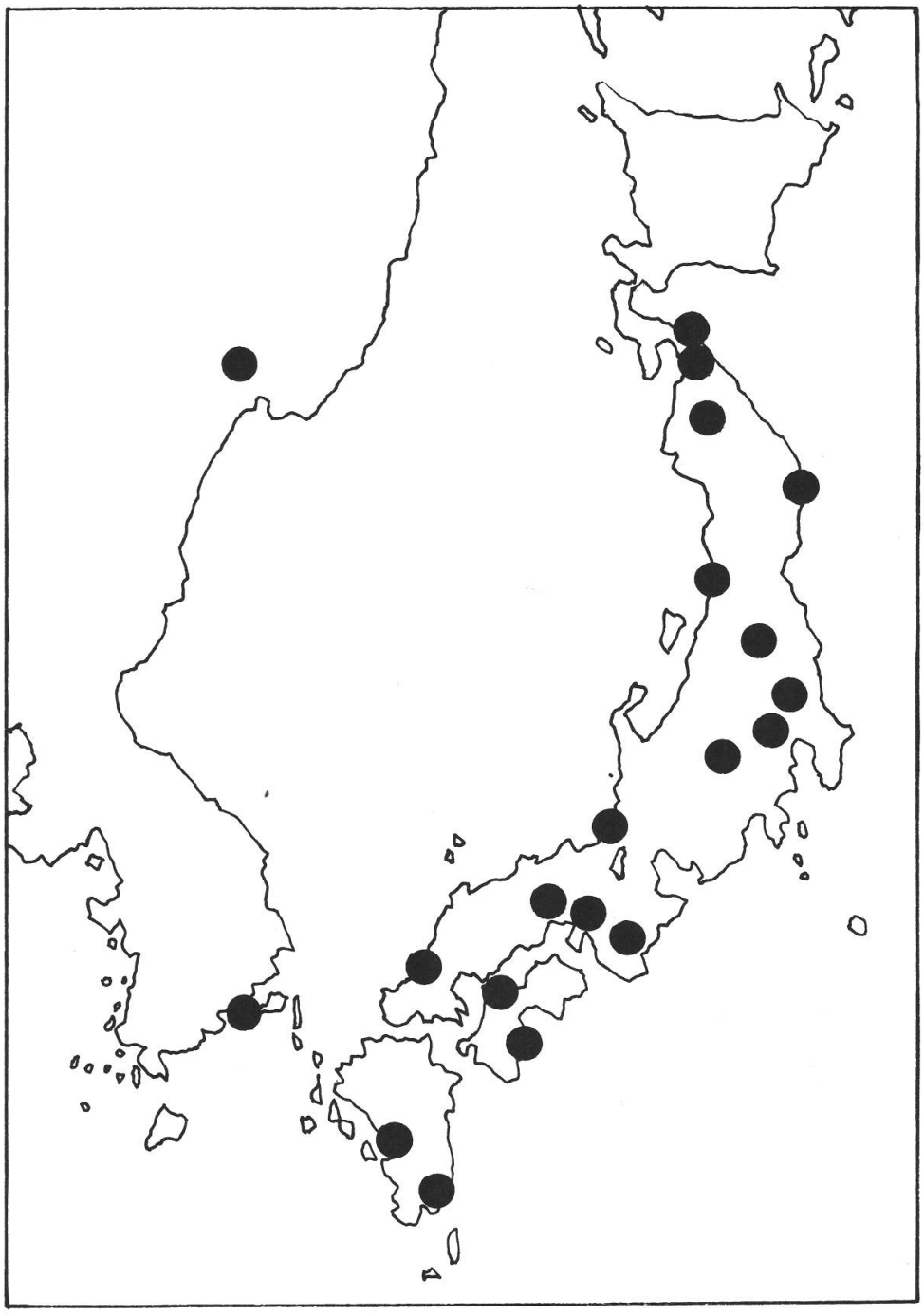
Index to names, combinations and synonyms used in this study. **Bold:** accepted names; *italic:* synonyms or illegitimate names. "1": indicates part 1, Bot. Helv. 96: 1–56 (1986); "2": in this part.



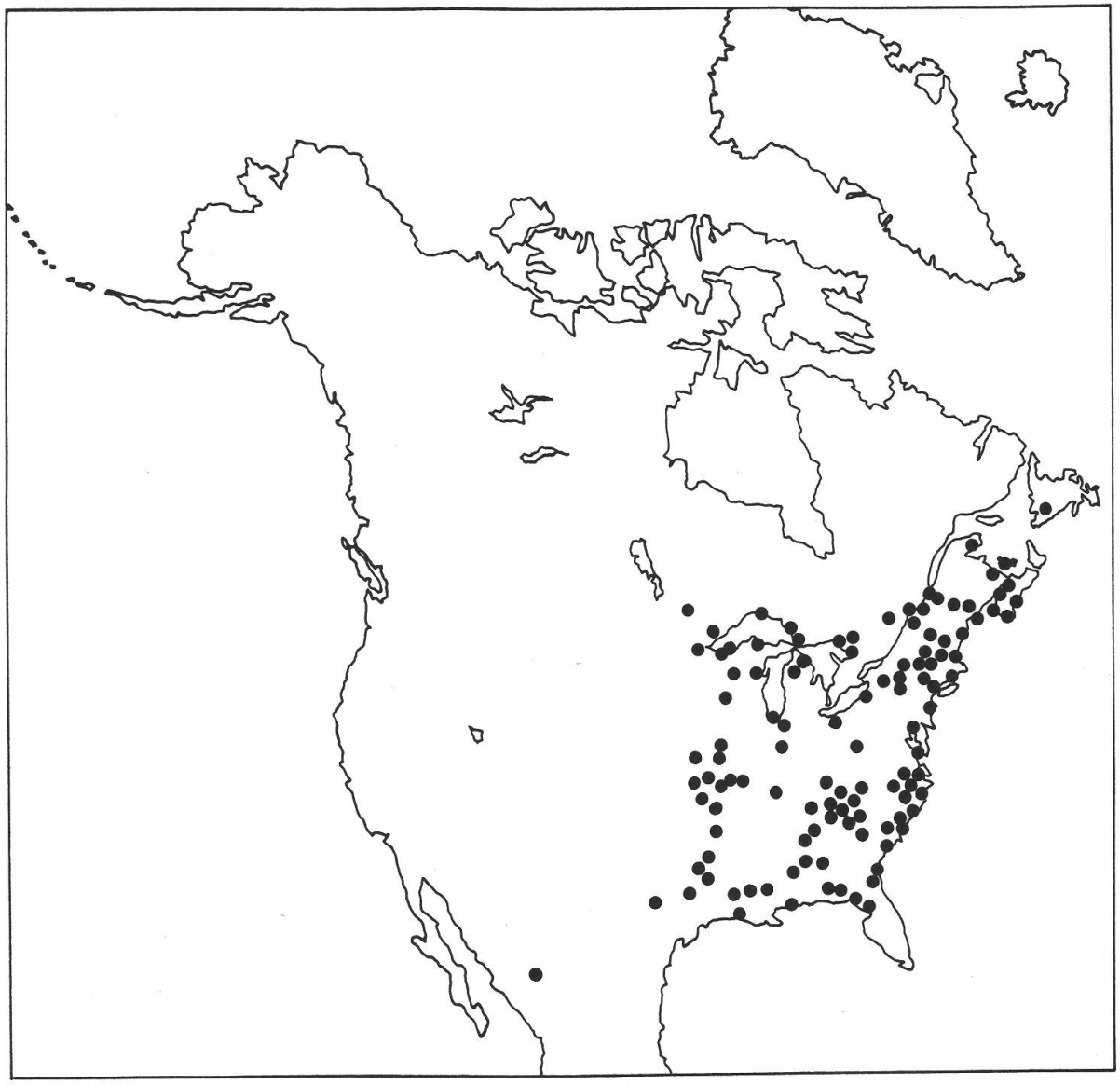
Map 14. *Sparganium fallax.*



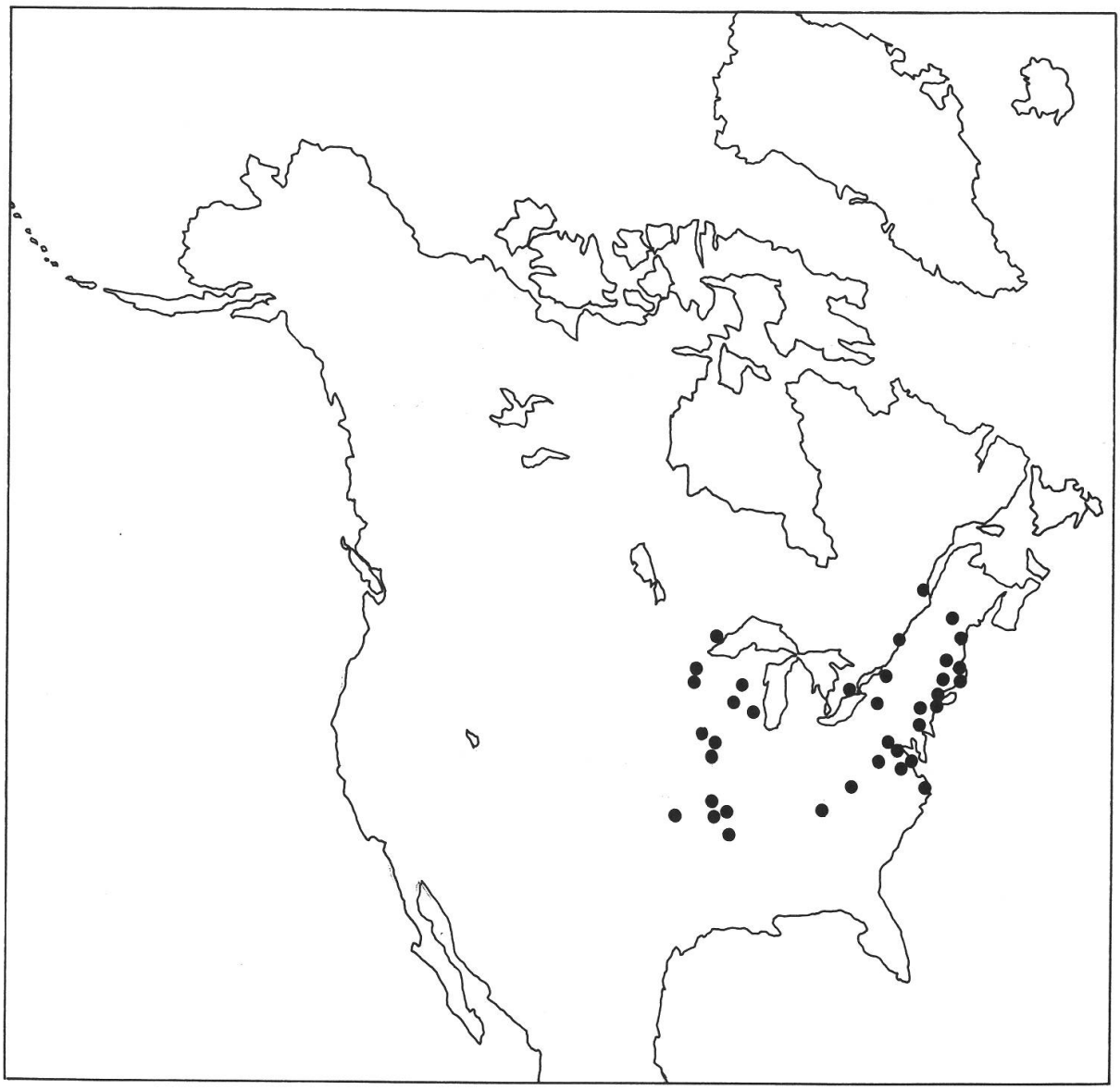
Map 15. *Sparganium subglobosum.*



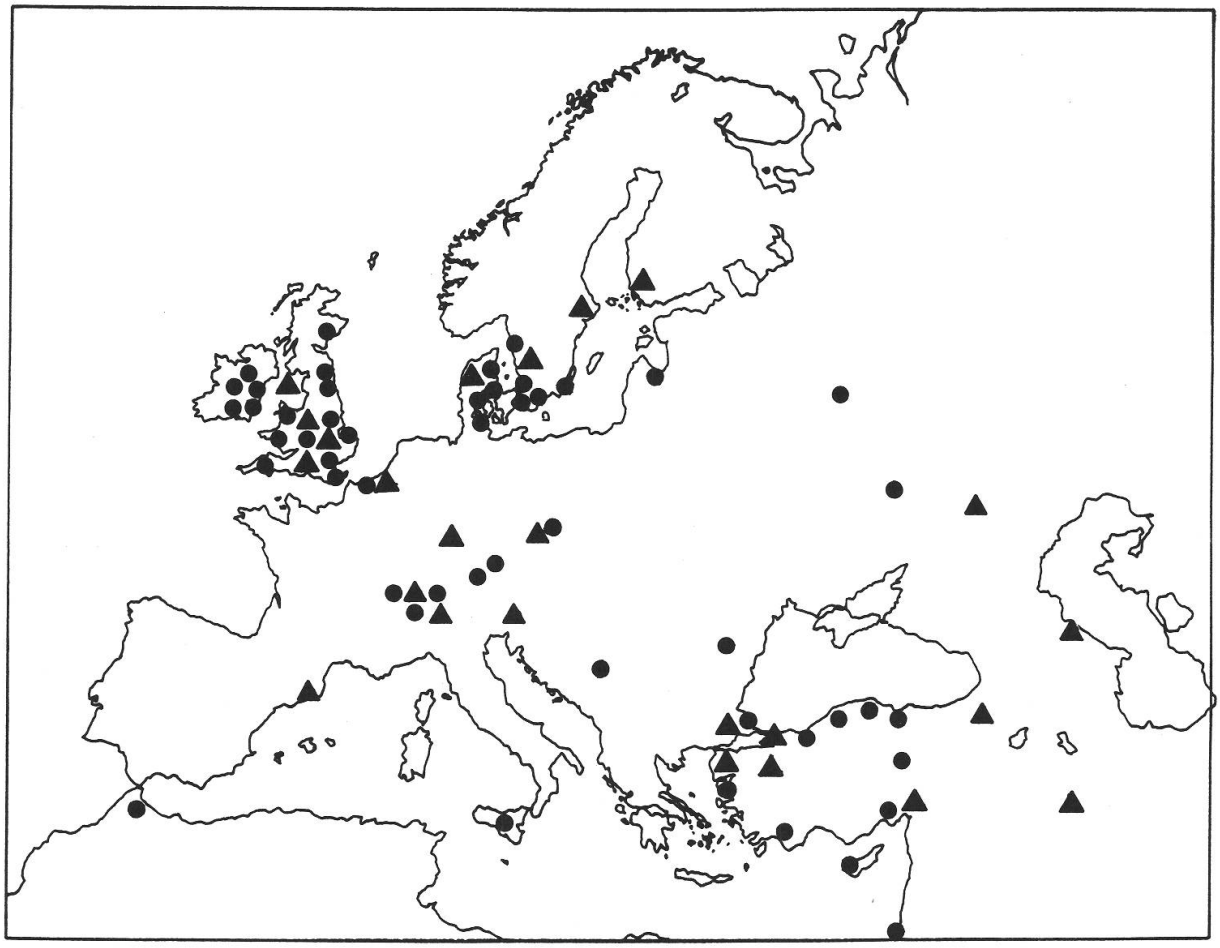
Map 16. *Sparganium japonicum.*



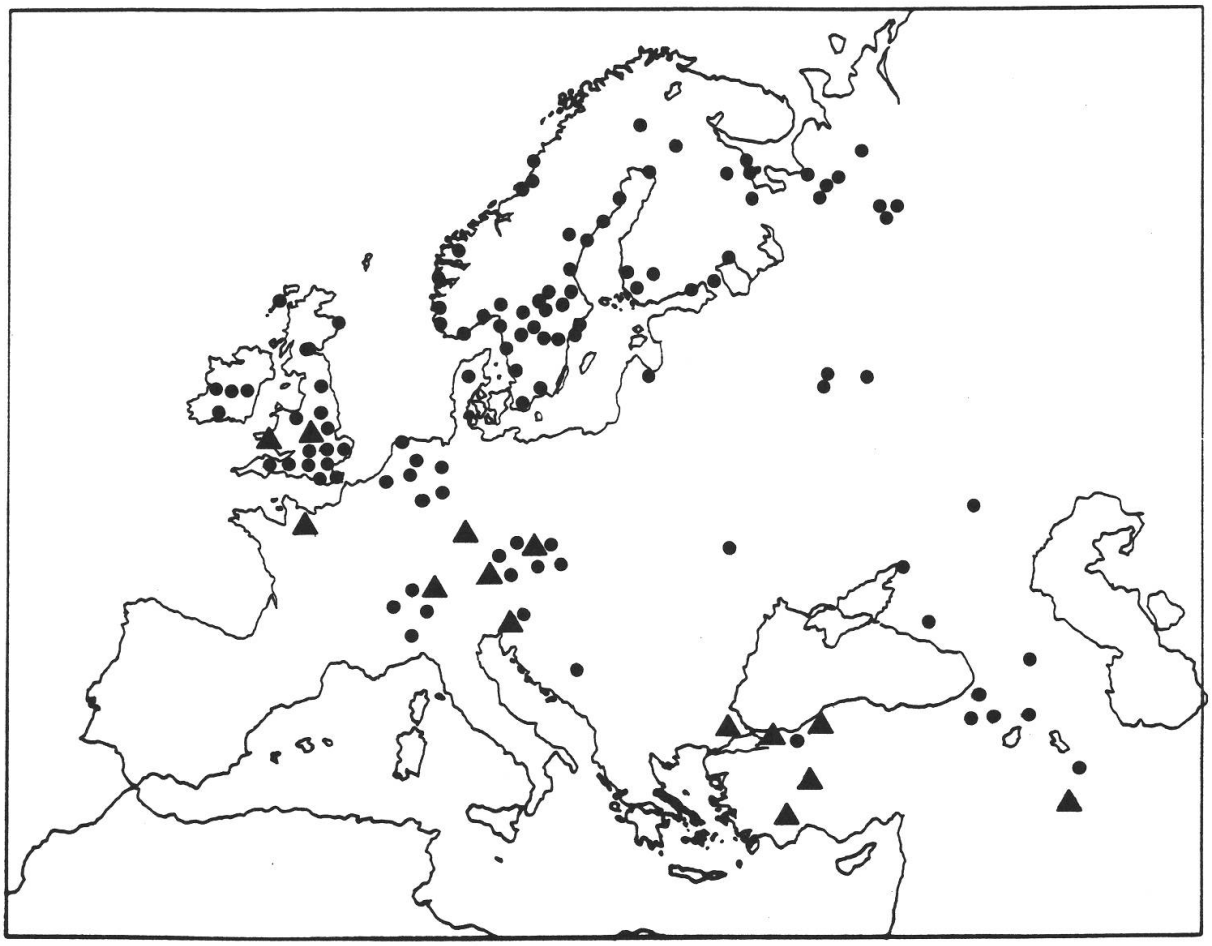
Map 17. *Sparganium americanum.*



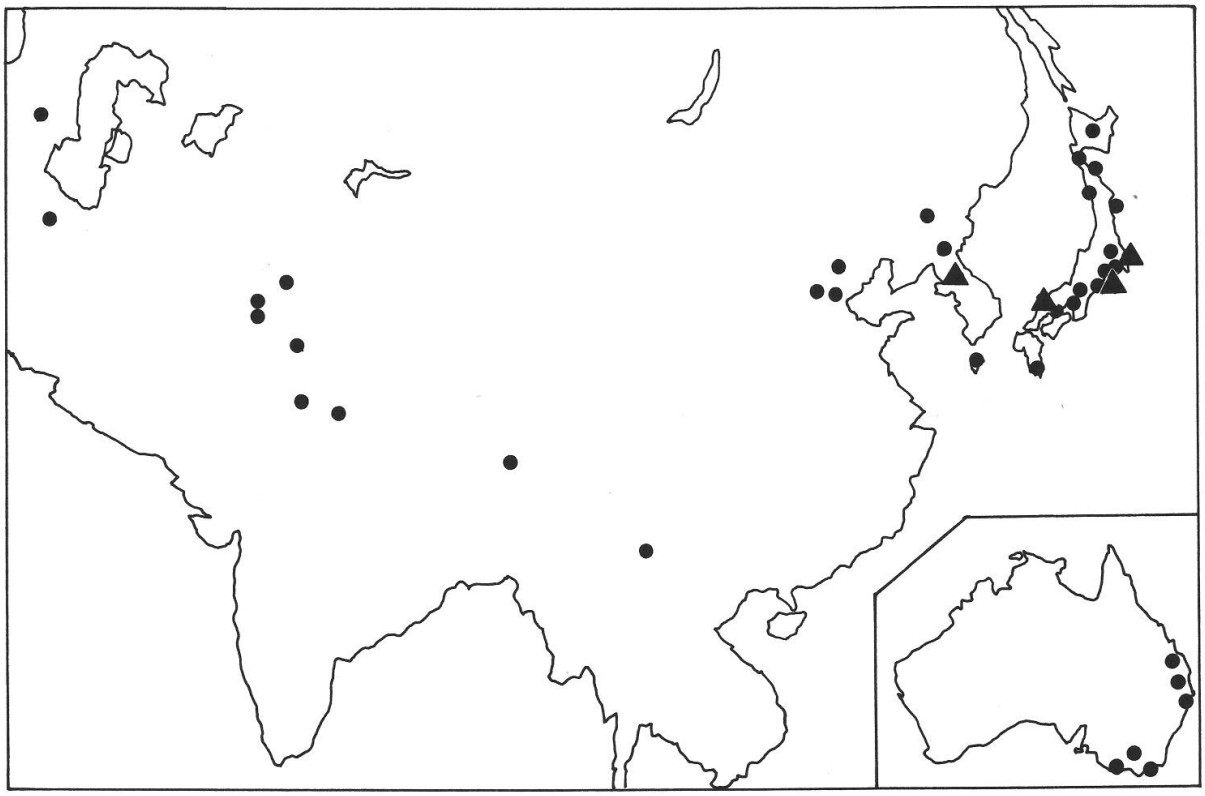
Map 18. *Sparganium androcladum.*



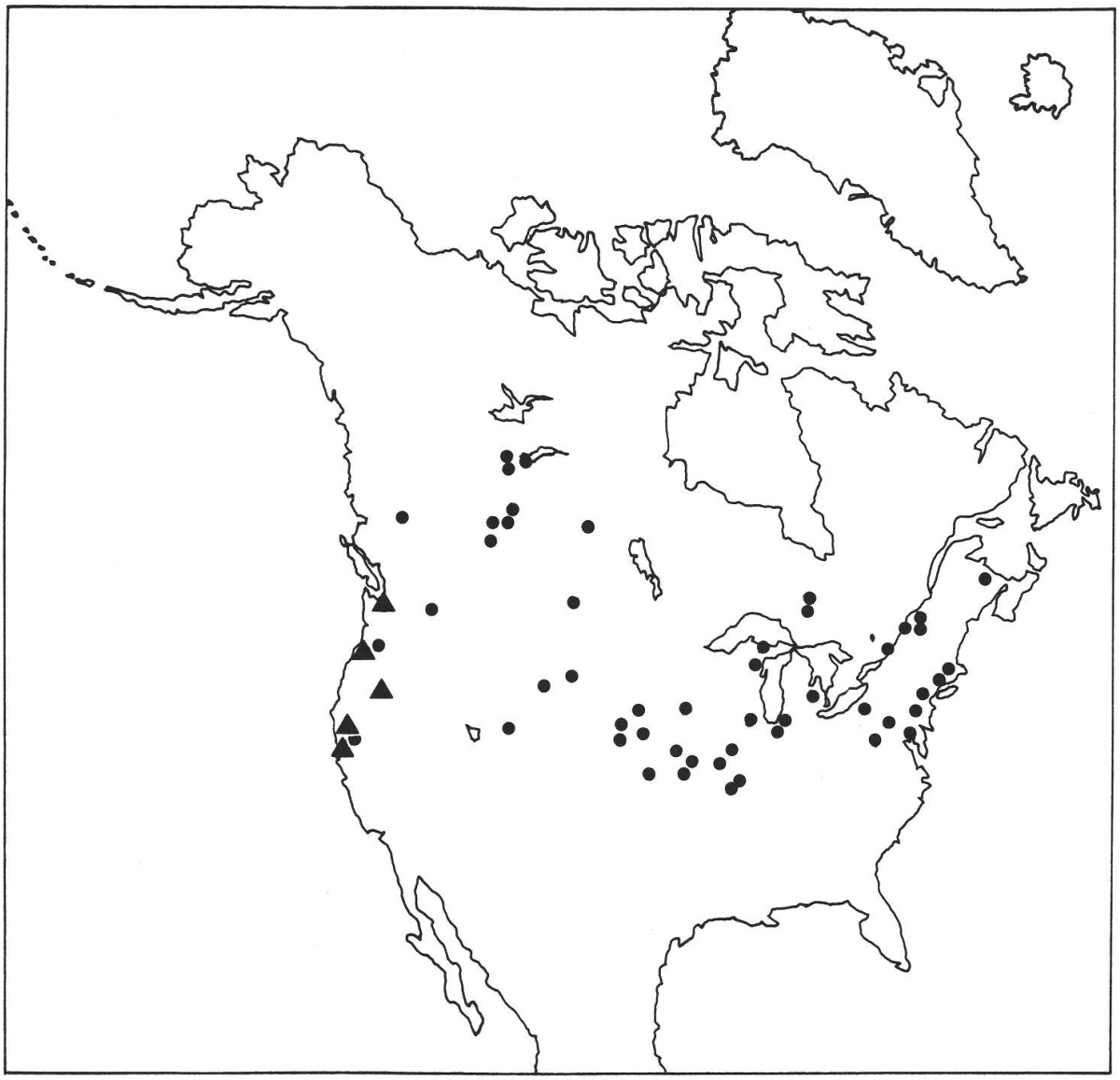
Map 19. *Sparganium erectum* subsp. *erectum* (▲), subsp. *neglectum* (●).



Map 20. *Sparganium erectum* subsp. *microcarpum* (●), subsp. *oocarpum* (▲).



Map 21. *Sparganium erectum* subsp. *stoloniferum* (●) and *S. eurycarpum* subsp. *coreanum* (▲) in Asia and Australia (inset).



Map 22. *Sparganium eurycarpum* subsp. *eurycarpum* (●) and *S. erectum* subsp. *stoloniferum* (▲) in N. America.