

SPARGANIUM IN BRITAIN

By C. D. K. COOK

Institut für systematische Botanik der Universität München

The Sparganiaceae were monographed by Graebner (1900) in *Das Pflanzenreich*. About seven years later Professor Wladislaw Rothert, formerly at the University of Odessa, started to prepare a more comprehensive monograph. Unfortunately Rothert suffered the tragic fate of so many elderly Polish and Russian scientists in the Russian Revolution and his work seems to have been lost. In 1911, however, he visited the herbaria at Kew and the British Museum and wrote notes on many of the herbarium sheets. I have used these notes as a guide to the taxonomy.

SPARGANIUM L., *Sp. Pl.*, 971 (1753).

Glabrous aquatic (occasionally semi-terrestrial) perennial herbs, reproducing vegetatively by long, thin, underground rhizomes. Stems simple or branched. Leaves linear, distichous, sheathing at the base, erect or floating. Flowers unisexual, crowded into separate globose capitula, the female capitula towards the base in each inflorescence; perianth of 3–6 radiate scales; male flowers of 3–8 stamens, the filaments sometimes partially united; female flowers of one, occasionally two, rarely three, fused carpels with a single style persisting in fruit, and as many stigmas as carpels. Fruit drupaceous with a dry, spongy exocarp, and a hard endocarp; seed albuminous, with a large embryo. Pollination mainly by wind.

There are about fifteen species in the North Temperate regions, extending from sub-arctic Scandinavia and North America to the Mediterranean and Mississippi Basin; the distributional belt stretches across North America, Europe, and Asia to Japan. Two species occur in South Australia and New Zealand. *S. erectum* has been collected at 12,000ft. in Tibet. The morphology and biology of the genus are dealt with by Glück (1911, 1924), Kirchner, Loew & Schröter (1908), Muenscher (1944), and Steinbauer & Neal (1948).

Most of the species have been investigated cytologically; so far, they have all been found to have the diploid chromosome number of $2n = 30$. (Wulff 1938, Hagerup 1941, Lohammer 1942, Löve & Löve 1948, 1956). In view of this uniformity, the cytology was not investigated further by the writer.

The genus was widely distributed in the Northern Hemisphere in late Tertiary times. The fossil forms are very much like the plants of to-day except in the larger number of loculi. *S. multiloculare*, described by Reid from Bembridge, showed two to five loculi, while Dr. Hartz recorded an inter-glacial form of *S. erectum* with two to four loculi. Only *S. erectum* to-day frequently shows plurilocular ovaries; the highest number seen is three.

Ascherson & Graebner, *Synopsis der mitteleuropäischen Flora* 1, 279, (1897), proposed three sections:—

- I. **ERECTA** : Large plants with distinctly keeled or triquetrous leaves, the floating ones (when present) keeled towards the apex. Style and stigma long, filiform.
- II. **NATANTIA** : Floating leaves rounded or flat on the back, never keeled, the midrib usually obsolete towards the apex. Erect leaves obtusely triquetrous or keeled towards the base.
- III. **MINIMA** : Small plants. Leaves all flat, not keeled. Stigma ovoid, often sessile.

Their section *Natantia* is ill-defined, and floating forms of *Erecta* or erect forms of *Minima* can easily be incorporated into it.

Holmberg (*Bot. Notis.* (1922), 203–209) suggested that the genus be subdivided into two subgenera. He based his classification on a single perianth character :—

I. MELANOSPARGANIUM : Tepala crassiora firmiora fusco-atra.

II. XANTHOSPARGANIUM : Tepala tenuia dilute colorata.

This classification is a great improvement on that of Ascherson & Graebner, as it splits the large erect forms from the smaller floating ones. In addition to the diagnostic characters cited by Holmberg, the seed of *Melanosparganium* (which must now be called *Sparganium*) has six to ten longitudinal ridges, whereas in *Xanthosparganium* the seed is smooth.

Hybrids between the subgenera have not been observed by the author.

KEY TO BRITISH SPARGANIA

-
- 1a. Perianth segments black-tipped; inflorescence branched, male capitula on lateral branches; seed with 6–10 longitudinal ridges : subgen. SPARGANIUM. 1. *S. erectum*
- 2a. Fruit with distinct shoulder, upper part dark brown to black.
- 3a. Fruit large, (5–) 6–8 (–10) mm. long (excluding style), (3–) 4–6 (–7) mm. wide (at shoulder); upper part of fruit flattened. subsp. *erectum*
- 3b. Fruit smaller, 6–7 (–8) mm. long, 2·5–4·5 mm. wide; upper part of fruit domed, wrinkled below style. subsp. *microcarpum*
- 2b. Fruit with indistinct shoulder, spherical to ellipsoidal, upper and lower parts uniform, shiny, light brown.
- 4a. Fruit ellipsoid, 7–9 mm. long, 2–3·5 mm. wide. subsp. *neglectum*
- 4b. Fruit ± spherical, 5–8 mm. long, 4–7 mm. wide. subsp. *oocarpum*
- 1b. Perianth segments translucent, not black-tipped; inflorescence unbranched, all male capitula on the main axis; seeds smooth : subgen. XANTHOSPARGANIUM.
- 5a. Male capitula remote, usually more than three; cauline leaves keeled but not inflated at the base, triangular in cross-section. 2. *S. emersum*
- 5b. Male capitula approximated, usually less than three; cauline leaves not keeled at the base, flat in cross-section.
- 6a. Leaf-like bract subtending lowest female capitulum 10–60 cm. long, at least twice as long as the whole inflorescence; male capitula usually two, elongated. 3. *S. angustifolium*
- 6b. Leaf-like bract subtending lowest female capitulum 1–5 (–8) cm. long, barely exceeding the inflorescence; male capitula usually solitary. 4. *S. minimum*
-

Sub-genus SPARGANIUM (*Melanosparganium* Holmberg, 1922). Perianth segments thick, with dark brown to black tips. Seeds with 6–10 longitudinal ridges.

SPARGANIUM ERECTUM L., *Sp. Pl.*, 971 (1753). *S. ramosum* Huds., *Fl. Angl.*, 2, 401 (1778).

The following description covers all the segregates discussed later :

Plant large, erect, semi-terrestrial, (30–) 50–150 (–200) cm. tall. Leaves triangular in cross-section, usually erect (may be floating in young plants or in deep water); apex broadly rounded, truncate or apiculate. Inflorescence branched (rarely simple) with male capitula borne above the female capitula on lateral branches.

On banks of ponds and slow flowing rivers, in ditches and on ungrazed marshland.

Within *S. erectum* L. there are about five forms with distinct fruit-shapes. In Europe, Asia and North America these fruit-shapes have been recognised and given taxonomic ranks varying from species to variety.

In Britain four forms have been found, but so far only *S. neglectum* Beeby has received any attention. During the past two years a critical search for characters correlated with fruit-shape has been undertaken, but with little success. The only difference found was a slight variation in geographical range. Ecological differences have been reported, but these could not be confirmed. In fact, the opposite seemed to be the case ! Along the Trent and Mersey canal south of Derby, for example, all four forms were found growing within

a quarter of a mile of each other, and all under what appeared to be similar conditions. Despite their sympatric distribution, intermediate fruit-shapes were not found.

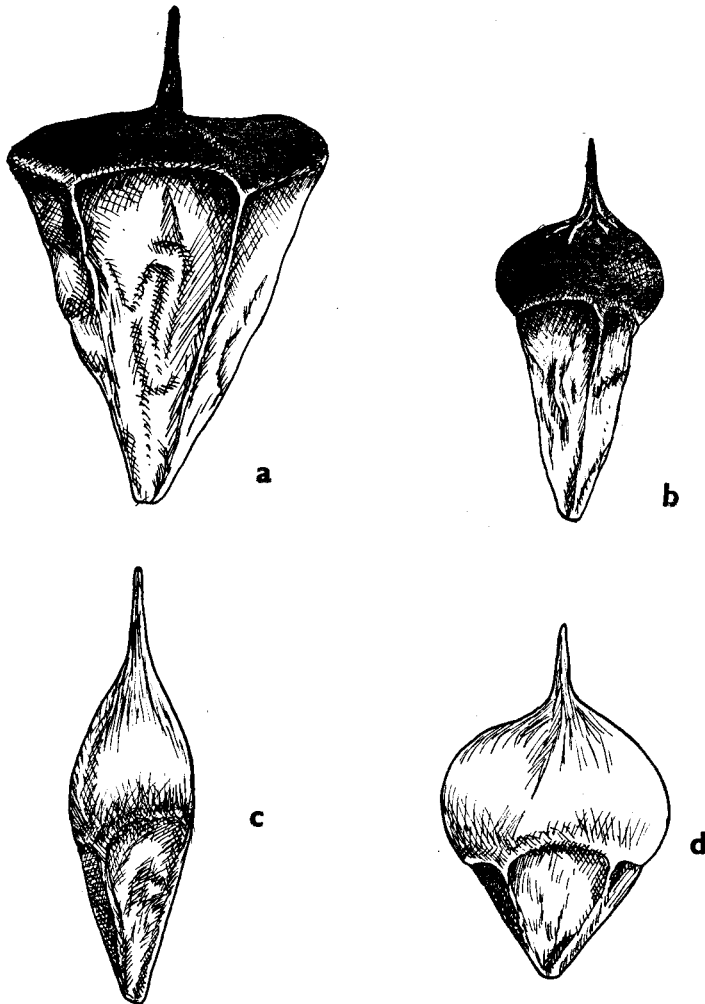


Fig. 1. Fruits of the subspecies of *Sparganium erectum* L., $\times c.7$. (a) subsp. *erectum*, (b) subsp. *microcarpum* (Neuman) Hylander, (c) subsp. *neglectum* (Beeby) Schinz & Thell., (d) subsp. *oocarpum* (Čelak.) C. D. K. Cook.

I am adopting the classification used by Hylander (1953) in his *Nordisk Kärleväxtflora*. In this work subspecific rank is assigned to three of the forms which I have recognised as occurring in Britain; the fourth (*S. oocarpum* Čelak) is here given subspecific rank in conformity with Hylander's treatment.

S. ERECTUM L., *Sp. Pl.*, 971 (1753) subsp. *ERECTUM*. *S. ramosum* Huds. *emend.* Beeby, *J. Bot. Lond.*, 23, 26, 193 (1885); *S. ramosum* subsp. *polyedrum* Asch. & Graeb., *Syn. mittl-europ. Fl.*, 1, 283 (1897); *S. erectum* subsp. *polyedrum* Schinz & Thell., *Fl. Schweiz.* ed. 3, 2, 14 (1914); *S. ramosum* var. *polyedrum* Holmberg, *Skan. Fl.*, 1, 79 (1922); *S. polyedrum* Juz. in Komarov, *Fl. U.R.S.S.*, 1, 219 (1934).

Fruit cuneate-obpyramidal, (5 –) 6 – 8 (– 10) mm. long, (3 –) 4 – 6 (– 7) mm. wide, with a distinct shoulder between upper and lower part; lower part pyramidal, (4 –) 5 – 7 (– 8) mm. long, light brown in colour; upper part flattened, dark brown to black in colour; in cross-section sharply 3 – 5-angled. Style less than 2 mm. long, persistent. Ovary usually bilocular, but occasionally uni- to trilocular (Fig. 1a).

From herbarium material and descriptions it appears that the North American *S. eurycarpum* Engelm. is the same as *S. erectum* subsp. *polyedrum* (Asch. & Graeb.) Schinz. & Thell. from Europe and Asia. If this can be established then the following should be included in the synonymy: *S. eurycarpum* Engelm., *Gray. Man. Bot.* 5, 48 (1864); *S. californicum* Greene, *Bull. Calif. Acad.*, 3, 11 (1884).

South Sweden and Finland to South Mediterranean, extending eastwards to Central Siberia. In Britain occurs south of the Wash only.

S. eurycarpum in North America extends from coast to coast, the southern limit being in Florida; its northern limits are unknown.

S. ERECTUM subsp. *MICROCARPUM* (Neuman) Hylander, *Nordisk Kärlväxtflora*, 1, 83 (1953). *S. ramosum* forma *microcarpum* Neuman, *Krok. Hartm. Handbk.*, 12, 112 (1889); *S. microcarpum* Čelak., *Österr. Bot. Zeitschr.*, 66, 281 (1896); *S. ramosum* var. *microcarpum* Asch. & Graeb., *Syn. mitteleurop. Fl.*, 1, 281 (1897).

Type, collected from central Czechoslovakia by Neuman, ? in Prague (*n.v.*).

Fruit obpyramidal with a rounded apex, 6–7 (–8) mm. long, 2.5–4.5 mm. wide, with a distinct shoulder between the upper and lower parts; lower part pyramidal, 4–6 mm. long, light brown with a slight constriction below the shoulder. The upper part domed with longitudinal ridges below the style, dark brown in colour. Below the shoulder fruit 3–5 angled in cross-section. Style persistent, less than 2 mm. long. Ovary usually unilocular, rarely bilocular (Fig. 1b).

Extends from the Arctic circle southwards to north Africa and east to Siberia. Occurs throughout the British Isles.

S. ERECTUM subsp. *NEGLECTUM* (Beeby) Schinz & Thell. *Fl. Schweiz.*, ed 3, 2, 14 (1914). *S. neglectum* Beeby, *J. Bot. Lond.*, 23, 26, 193 (1885); *S. ramosum* subsp. *neglectum* Neuman, *Krok. Hartm. Handbk.*, 12, 112 (1889); *S. erectum* var. *neglectum* Fiori & Paoletti, *Fl. Anal. Ital.*, 1, 146 (1896–98).

Type collected at Albury ponds near Guildford, Surrey; lectotype in Herb. Kew ! Isotype in Herb. Edin.!

Fruit ellipsoidal, 7–9 mm. long, 2–3.5 mm. wide, shoulder between upper and lower parts indistinct. Upper and lower parts conical, uniform light brown, shiny. Lower part 4–6 mm. long. In cross-section fruit barely angled. Style persistent, usually more than 2 mm. long. Ovary unilocular. (Fig. 1c.)

From South Sweden to North Africa, extending eastwards to the Caucasus. In Britain most common south of the Wash, but northern limit in Westmorland.

S. erectum subsp. *oocarpum* (Čelak.) *comb. nov.* *S. neglectum* var. *oocarpum* Čelak., *Österr. Bot. Zeitschr.*, 21, 5 (1896); *S. oocarpum* Ostenf. & Hansen, *Bot. Tidsskr.*, 21, 5 (1897).

Described from specimens collected from Bohemia ? now in Herb. Berlin *n.v.*

Fruit ovoid to spherical, 5–8 mm. long, 4–7 mm. wide, uniform light brown in colour, shoulder between upper and lower parts indistinct, upper part hemispherical, lower part broadly pyramidal, 2.5–5 mm. long, almost circular in cross-section. Style persistent, usually less than 2 mm. long. Ovary unilocular, rarely bilocular (Fig. 1d).

Distribution imperfectly known in Europe; specimens have been seen from Turkey and North Africa. Not found north of the Wash in Britain.

Very poor fertility is shown in all the specimens that have been examined. This may be due to hybrid origin, although this has not been tested; on morphological grounds, the suggested parents are subsp. *erectum* and subsp. *neglectum*.

Sub-genus *XANTHOSPARGANIUM* Holmberg 1922. Perianth scales thin, lightly coloured. Seeds without longitudinal ridges.

SPARGANIUM EMERSUM Rehman, *Verh. Nat. Ver. Brünn*, 10, 80 (1871). *S. erectum* L., *Sp. Pl.*, 971, p.p. (*saltem quoad [partim?]*) (1753); *emend.* Wahlenberg, *Fl. Suec.*, 2, 582 (1826);

S. simplex Huds. *sensu* Curtis, *Fl. Lond.*, 5, 66 (c. 1788); *S. multipedunculatum* Morong., *Bull. Torr. Bot. Club*, 15, 79 (1888); *S. glehnii* Meinsh., *Mel. Biol. Acad. St. Petersb.*, 13, 388-390 (1893); *S. simile* Meinsh., *loc. cit.* (1893). *S. splendens* Meinsh., *loc. cit.* (1893). *S. subvaginatum* Meinsh., *loc. cit.* (1893); *S. diversifolium* var. *acaule* Fernald & Eames, *Rhodora*, 9, 88 (1907); *S. chlorocarpum* Rydberg, *N. Amer. Fl.*, 17, 8 (1909).

Type collected in the River Rov at Bar in the Ukraine, syntype in Herb. Kew !

Erect or floating aquatic, 20-60 cm. tall. Leaves triangular in cross-section, sheathing at the base but not inflated. Inflorescence simple, unbranched; male capitula 3-10, distinct, remote and all borne on the main axis; anthers when mature 6-8 times as long as broad; female capitula 3-6 with lower ones frequently stalked. Fruit pedunculate, ellipsoidal, frequently with a constriction around the centre; peduncle 2-3 mm. long; style persistent, 3-4 mm. long.



Fig. 2. Flowering shoots and fruiting capitula (\times c. 3) of (a) *Sparganium angustifolium* Michx., and (b) *S. minimum* Wallr.

In shallow rivers and canals and by the edge of ponds and lakes, on wet mud or in water to a depth of 100 cms. Throughout North Temperate regions from the Arctic Circle south to lat. 40°N. Occurs throughout the British Isles, but not found on very high ground.

S. ANGUSTIFOLIUM Michx., *Fl. Bor. Am.*, 2, 189 (1803). *S. natans* L., *Sp. Pl.*, 971, p.p. (1753); *S. simplex* Huds., *Fl. Angl.*, 2, 401, p.p. (1778); *S. alpinum* D. Don ex G. Don, in Loud. *Hort. Brit.*, 375, *nomen nudum* (1830); *S. affine* Schnizlein, *Typhac.*, 27 (1845); *S. boreale* Laestadius ex Beurl, *Oefeurs. Vet. Akad. Faerhaud.*, 9, 192 (1852); *S. vaginatum* Larsson, *Fl. Verml.*, 259 (1859); *S. borderi* Focke, *Bremen Abh.*, 5, 409 (1877).

Described from specimens collected from Lake Mistassini in Canada. Type specimen ? at Herb. Mus. d'Hist. Nat. Paris *n.v.*

Floating (rarely erect) aquatic. Leaves flat in cross-section, sheathing and inflated at the base. Inflorescence simple, unbranched; male capitula 1–2 (–3), clustered together, appearing as an elongated capitulum on the main axis; anthers 3–4 times as long as broad; female capitula 2–4, lower capitula stalked; leaf-like bract subtending lowest female capitulum 10–60 cm. long and at least twice as long as the whole inflorescence. Fruit shortly pedunculate, ellipsoidal and light brown in colour (Fig. 2a).

In highland or northern acidic peat lochs, in water from 10 to 150 cm. deep.

An arctic-alpine species found in suitable habitats in Europe from Iceland to the Pyrenees and Alps, extending eastwards across Asia to Japan. Distribution limits for North America unknown. In Britain found in north Scotland, Pennines, north Wales and northern and western Ireland. There is also a single location near Beaulieu, Hampshire.

S. MINIMUM Wallr., *Erster Beitrag Fl. Hercyn.*, 2, 297 (1840). *S. natans* L., *Sp. Pl.*, 971, *nom. ambig.* (1753); *S. simplex* Huds., *Fl. Angl.*, 2, 401 *nom. illegit., quoad. var.* (1778); *S. natans* var. *minimum* Hartm., *Handb. Skand. Fl.*, 43 (1820); *S. gramineum* Wallr., *loc. cit., ined. in syn.* (1840); *S. minimum* Fries, *Summa. Veg. Skand.*, 2, 560 (1849); *Bot. Notiser*, 154 (1849); *S. rostratum* Larsson, *Fl. Verml.*, 260 (1859); *S. septentrionale* Meinsh., *Bull. Soc. Nat. Moscow, N.S.*, 3, 174 (1889); *S. ratis* Meinsh., *loc. cit.* (1889); *S. flaccidum* Meinsh., *Mel. Biol. Acad. St. Petersb.*, 13, 393–4 (1893); *S. perpusillum* Meinsh., *loc. cit.* (1893).

The original description was based on plants from the southern Harz Mountains in Germany. No specimens have been found in Wallroth's herbarium at Halle.

Floating (very rarely erect) aquatic. Leaves flat, usually translucent, barely inflated at the base. Inflorescence simple, unbranched; male capitula one (rarely two), if two then close together and appearing as one; female capitula (1–) 2–3, usually sessile; leaf-like bract subtending lowest female capitulum 1–5 (–8) cm. long, barely exceeding the whole inflorescence. Fruit sessile, obovoid with very short persistent style, uniform, shiny light brown in colour. (Fig. 2b).

In lochs, pools or ditches with a rich organic substratum, in 10–50 cm. of water. Temperate and arctic regions of North America, Europe and Asia. Found throughout Britain in suitable habitats.

NOMENCLATURE

The nomenclature of the British *Spargania* is difficult to elucidate, mainly because the earlier taxonomists chose to diagnose the species on characters that do not remain constant under all ecological conditions.

Linnaeus in his *Species Plantarum*, 971 (1753), recognised two species of *Sparganium* :

1. *S. erectum* (*foliis erectis triquetris*).
2. *S. natans* (*foliis decumbentibus planis*).

Hudson (*Flora Anglica*, ed. 2 (1778), 2, 401) was apparently not satisfied with Linnaeus's classification, so he dropped the Linnaean species and proposed two new ones :

1. *S. ramosum* (*foliis ensiformibus triquetris, caule ramoso*).

2. *S. simplex* (*foliis ensiformibus planis, caule simplice*).

The original description of *S. erectum* L. covers the plant later described as *S. ramosum* by Hudson. *S. erectum* L. is cited by Hudson as a synonym of *S. ramosum* Huds., so that the latter is an illegitimate superfluous name.

Within his *S. simplex* Hudson described a variety β *natans* (*foliis decumbentibus planis*); as this is the same diagnosis as that of *S. natans* L., the varietal name must be based on the Linnaean species, so that the name *S. simplex* Huds. is illegitimate also.

Curtis in *Flora Londinensis* (c. 1788), 5, 66, produced the earliest known full descriptions and illustrations of the two Hudson species. The Curtis description of *S. simplex* Hudson is the one accepted today; unfortunately it differs from the *S. simplex* diagnosed by Hudson. *S. simplex* Huds. was originally diagnosed as having flat leaves, while Curtis illustrated and described it with triquetrous leaves.

In the Linnaean herbarium there are three specimens of *Sparganium*: one of *S. erectum* L. and two of *S. natans* L.; of these, the specimen of *S. erectum* L. and one of the sheets of *S. natans* L. bear these names in Linnaeus' handwriting.

The specimen of *S. erectum* L. was found to be *S. simplex* Hudson *sensu* Curtis. The specimen in Clifford's herbarium based on the *Hortus Cliffortianus* (referred to in synonymy by Linnaeus) was examined in the British Museum, and was also found to be *S. simplex* Hudson *sensu* Curtis.

Linnaeus in *Species Plantarum* cited under *S. erectum* L. a variety β (*non ramosum*) with a reference to Bauhin's *Theatre*, (1620, p. 231) and *Pinax*, (1623, p. 15). Under Bauhin's list of synonyms there is a reference to *S. alternum* in L'Obel's *Historia Plantarum* (1570), 41. The illustration of *S. alternum* shows a plant that is undoubtedly *S. simplex* Hudson *sensu* Curtis.

On the other hand, under *S. erectum* (var. α), Linnaeus cites *S. ramosum* in Bauhin's *Theatre* and *Pinax*. By referring back to the illustrations in L'Obel's *Historia Plantarum*, it can be seen that var. α refers to *S. ramosum* Hudson.

It appears justifiable to assume that Linnaeus recognised the differences between the plants later described as *S. ramosum* Hudson and *S. simplex* Hudson *sensu* Curtis, but did not think them worthy of specific rank. It is quite likely that Linnaeus chose to represent only var. β in his herbarium as var. α is a large and difficult plant to mount on a small herbarium sheet.

Today it is recognised that there are two species within *S. erectum* L. From the preceding argument, *S. ramosum* Hudson should bear the name *S. erectum* L. For the plant which has been called *S. simplex* (following Curtis's misinterpretation of Hudson's name), the earliest available legitimate name must be used. This appears to be *S. emersum* Rehman, *Verh. Nat. Ver. Brünn*, 10, 80, (1871).

The sheet of *S. natans* L. bearing this name in Linnaeus's handwriting has on it a well-preserved specimen of *S. minimum* Wallr. while the other sheet bears a poor specimen of *S. emersum* Rehman. Hylander (1945) rejected *S. natans* as a *nomen ambiguum*. This decision was fully justified and the earliest available legitimate name appears to be *S. minimum* Wallr.

In 1903 Fernald examined type material of *S. angustifolium* Michx. and declared it to be the same as *S. affine* Schnizl. Apparently this had been noticed before as Morong (1888) remarked "Engelmann has seen Michaux's specimen at Paris and it is the same as *S. affine*," but he then proceeded to drop the name *S. angustifolium* and use the later name *S. affine*. *S. angustifolium* is the earlier name and must of course be used in place of *S. affine*.

BREEDING BEHAVIOUR

Sparganium is strongly protogynous and in *S. erectum* the lower female capitula have frequently passed their fertile stage before the first male capitulum matures. This insures cross-fertilization for some flowers at least, but the lower capitula rarely set much seed. No self-incompatibility or agamosperous mechanisms have been found.

Many hybrids have been reported, but the only hybrids I have seen (including examination of herbarium material) are between *S. emersum* and *S. angustifolium*. These two species are fairly widely separated ecologically, the former being a species of eutrophic and the latter a species of oligotrophic waters, but they occasionally grow close together in parts of western Scotland. The hybrids appear to be fully fertile and many plants have been found that showed introgression. At Stoer in Sutherland and on the Isle of Raasay the appearance of the hybrids tends towards *S. emersum* while in Galloway introgression appears to be towards *S. angustifolium*. This allopatric introgression appears to be similar to the type found in *Typha* by Fassett & Calhoun (1952).

EVALUATION OF THE TAXONOMIC CHARACTERS

The object of much of this study was to ascertain those characters which are of most value in separating the species. Many of the characters that have been used by previous authors have proved inconstant or readily modified by environment. The characters are annotated below and their value assessed. The key to the species is based on those characters that have proved most constant.

a. Leaf

Habit. The difference between erect and floating leaves is relative and is controlled largely by the habitat. *S. erectum* usually has erect leaves but in deep or flowing water they may be floating. *S. emersum* has erect and floating leaves, the floating leaves being found on deep-water forms and on forms exposed to wave action or water currents. *S. angustifolium* has floating leaves, but occasionally erect ones are found in very sheltered habitats. *S. minimum* is very rarely found with erect leaves.

Cross-section. *S. erectum* and *S. emersum* show a triangular cross-section. This is a good character when examining specimens in the field, but cannot easily be seen on herbarium specimens. *S. angustifolium* and *S. minimum* both have a flat cross-section. This character breaks down in *S. emersum* in the north of Scotland, possibly owing to hybridization.

Apex. In *S. erectum* the apex of the leaf has been used as a character to separate the various subspecies. Subsp. *neglectum* has been reported as having a truncate apex and subsp. *erectum* an apiculate one. These are not good characters and forms of subsp. *neglectum* have been seen with apiculate apices and forms of subsp. *erectum* with truncate apices.

Cross Veins. *S. erectum* has been described with obscure cross-veins and longitudinal veins appearing as pellucid lines without a dark border, while *S. emersum* is said to have distinct cross-veins and longitudinal veins with a dark green border. I can find no justification for these statements after examining living and dead material of both species.

Sheath. In *S. erectum* and *S. emersum* the leaf bases sheathe the stem. In *S. angustifolium* the leaf bases are inflated. This is a reliable taxonomic character for studies in the field especially when there are no flowers, but it is difficult to see in herbarium specimens. In *S. minimum* the leaf base is flat and barely sheathes the stem.

b. Stem

Colour. The base of the stem has been reported to be pink in *S. erectum* subsp. *neglectum*, but this is an unreliable character and is occasionally found in all subspecies of *S. erectum* especially when growing in stagnant water.

c. Inflorescence

Branching. The inflorescence is branched only in *S. erectum*; in all the other species it is simple.

Leaf-like bract subtending the lowest female capitulum. In *S. erectum* and *S. emersum* this bract is triangular in cross-section and about one to one-and-a-half times as long as the inflorescence. In *S. angustifolium* and *S. minimum* it is flat in cross-section. In *S.*

angustifolium it is usually between 10 and 60 cm long, the absolute length being directly proportional to the depth of water and the length of the peduncle supporting the lowest female capitulum. In *S. minimum* the bract is between 1 and 5 (-8) cm long; again, the absolute length is controlled by the habitat conditions. On this character *S. angustifolium* and *S. minimum* can easily be separated. In *S. angustifolium* the bract is usually more than twice as long as the whole inflorescence, but in *S. minimum* it barely exceeds it. The taxonomic value of this character does not appear to have been previously recognised.

d. Flower

Perianth segments. In *S. erectum* the perianth segments are thick with a black tip. In the other species they are thin with a translucent tip. This is a good character but is sometimes a little difficult to see on very old herbarium specimens. Beeby (1885) described the perianth segments of the female flowers of subspecies *neglectum* as being linear with a broad spatulate apex, while those of subspecies *erectum* were described as mostly ligulate, more membranous and scarcely or not enlarged at the apex. No distinctions can be made between these two types as intermediates appear to be more common than the extremes. In all the subspecies of *S. erectum* the perianth segments are very variable and determinations can not be made using this character.

Anther. In *S. erectum* and *S. emersum* the anthers are six to eight times as long as broad, and in *S. angustifolium* and *S. natans* they are only three to four times as long as broad. This is a good character, but it breaks down in *S. emersum* in the north of Scotland.

Carpel. In *S. erectum* the carpel is sessile and frequently plurilocular. Subsp. *erectum* usually has bilocular ovaries, whereas subspp. *microcarpum* and *oocarpum* usually have unilocular ovaries though bilocular ones are occasionally seen. *S. emersum* and *S. angustifolium* have shortly pedunculate carpels with long styles which persist in fruit. *S. minimum* has sessile carpels with short styles that do not persist in fruit; these characters are constant.

Seed. The seed has 6-10 longitudinal ridges in *S. erectum* but is smooth in the other species. This character does not appear to have been previously noted.

ACKNOWLEDGMENTS

This study was started at Edinburgh University under the direction of Dr. P. H. Davis. I would like to thank him, Dr. S. M. Walters and Prof. Dr. H. Merxmüller for valuable discussions. I would also like to thank Mr. J. E. Dandy for sparing so much time on the nomenclatural problems.

REFERENCES

- CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1952). *Flora of the British Isles*. Cambridge.
- ASCHERSON, P. F. A. & GRAEBNER, P. (1897). *Synopsis der mitteleuropäischen Flora*, 1. Leipzig.
- BAUHIN, K. (1620). *Prodromus Theatri Botanici*. Frankfurt-am-Main.
- BAUHIN, K. (1623). *Pinax Theatri Botanici*. Basel.
- CURTIS, W. (c. 1788). *Flora Londinensis*, 5. London.
- FASSETT, N. C. & CALHOUN, B. (1952). Introgression between *Typha latifolia* and *T. angustifolia*. *Evolution*, 6, 367.
- FERNALD, M. L. (1922). Notes on *Sparganium*. *Rhodora*, 24, 26.
- GLÜCK, H. (1911, 1924). *Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse*, 3, 547-558; 4, 1-5. Jena.
- GRAEBNER, P. (1900). Sparganiaceae. *Pflanzenreich*, 2.
- GRONTVED, J. (1945). Spargania in Denmark. *Bot. Tidsskr.* 50, 215.
- HAGERUP, O. (1941). Nordisk Kromosom-Tal. I. *Bot. Tidsskr.* 45, 385.
- HOLMBERG, (1922). Anteckningar till nya Skandinaviska Floran, II. *Bot. Notis.*, 203-9.
- HUDSON, W. (1778). *Flora Anglica*, 2, Ed. 2. London.
- HYLANDER, N. (1945). *Nomenklatorische und systematische Studien über nordische Gefäßpflanzen*. Stockholm.
- HYLANDER, N. (1953). *Nordisk Kärlväxtflora*. Stockholm.
- KIRCHNER, O. VON, LOEW, E. & SCHRÖTER, C. (1908). *Lebensgeschichte der Blütenpflanzen Mitteleuropas*. Stuttgart.
- LINNAEUS, C. (1737). *Hortus Cliffortianus*. Amsterdam.

- LINNAEUS, C. (1753). *Species Plantarum*. Stockholm.
- L'OBEL, M. DE (1570). *Historia Plantarum*. Antwerp.
- LOHAMMER in LÖVE A. & LÖVE, D. (1941). Chromosome numbers of Scandinavian plant species. *Bot. Notis.*, 27.
- LÖVE, A & LÖVE, D. (1948). *Chromosome Numbers of Northern Plant Species*. Reykjavik.
- LÖVE, A. & LÖVE, D. (1956). Cytotaxonomical conspectus of Icelandic Flora. *Acta Hort. Gotob.*, 20, 65.
- MORONG, T. (1888). Studies in the Typhaceae. II, *Sparganium*. *Bull. Torrey Bot. Cl.*, 15, 73-81.
- MUENSCHER, W. C. (1944). *Aquatic Plants of the U.S.A.* Ithaca.
- STEINBAUER, G. P. & NEAL, (1948). U.S. Spargania. *Papers Mich. Acad. Sci.*, 34, 33.
- WULFF, H. D. (1938). Chromosomenstudien an der schleswigholsteinischen Angiospermen-Flora. *Ber. deutsch. Bot. Ges.*, 56, 247-254.