# Assessing the status of *Stratiotes aloides* L. (Water-soldier) in Co. Fermanagh, Northern Ireland (v.c. H33)

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#### ABSTRACT

A case is argued for considering *Stratiotes aloides* L. (Water-soldier) (Hydrocharitaceae) of native status in Co. Fermanagh (v.c. H33), and possibly elsewhere in Ireland. The case is circumstantial in the absence of fossil evidence from the current interglacial, and consists of early 19th century discovery, long persistence in natural water bodies, rare and scattered occurrence, and lack of the "boom and bust" dynamics of many introduced aquatic species. No new stations have been found for over 100 years which strongly suggests that either *S. aloides* is not much used in Irish water gardens, or it does not readily escape into the wild. The species complement of two vegetation communities involving *S. aloides* in Upper Lough Erne, Co. Fermanagh is strikingly similar to communities described in the Norfolk Broads, where the species has long been considered native. Conservation arguments for sites frequently revolve around the occurrence of rare indigenous species, making the question of status more than a purely academic matter.

KEYWORDS: Hydrocharitaceae, aquatic macrophyte, native status, garden history.

#### INTRODUCTION

Botanists for too long have uncritically accepted notions of indigenous or introduced plant status largely derived from early observations and old studies made in southern England, and have continued to apply them to situations elsewhere without a great deal of reconsideration (Watson 1883; Bentham & Hooker 1900; Hyde & Wade 1957; Clapham *et al.* 1962; Webb 1985). Progress in botanical knowledge in Ireland has always lagged behind that in Great Britain, originally by up to a century or more, but it has tended to tramp the same path. However, it needs to be said that what is true and self-evident for the south of England does not necessarily apply in the different biological, historical and human circumstances operating in Ireland, or in other parts of these islands. Wealth, leisure and education combine in promoting both natural history and garden pursuits, and in timing and intensity these endeavours developed differently in the two major islands. In particular, the passion for gardening and the fashions in it did not in Ireland slavishly follow the English scene, but had a regional, climatically-governed identity, frequently constrained by limited resources rather than by any lack of imagination (Nelson & Brady 1979; Lamb & Bowe 1995).

The status of *Stratiotes aloides* L. (Water-soldier) is a case in point, a species whose native distribution throughout its whole European range is problematic, since it has been grown as an aquatic ornamental for nearly three centuries and its native occurrence has been obscured by numerous escapes from cultivation (Cook & Urmi-König 1983; Preston & Croft 1997).

*S. aloides* is described by Stace (1997) as native, its distribution in the British Isles summarised (abbreviations expanded here) as, "now very local in E Anglia, N and S Lincolnshire, SE Yorkshire and Denbighshire, formerly locally frequent in central Great Britain, introduced in scattered places in Great Britain, north to central Scotland." He makes no mention whatsoever of *S. aloides* occurring in Ireland. The species is described as being a dioecious perennial, and Stace adds the significant remark, "only female plants occur in Britain" (but see below). Perring & Walters (1976) in the *Atlas of the British Flora* are less dogmatic with regard to the status of the plant, their map distinguishing between "probably native" and "probable or certain introductions". On the basis of the 17th century records, Preston & Croft (1997) regard it as likely that *S. aloides* is native in eastern England "and perhaps also in Cheshire" (v.c. 58) (but see below).

With regard to *S. aloides* in Ireland, Perring & Walters (1976) indicate five widely scattered stations of "probable or certain introduction" status: three around Belfast Lough, Co. Antrim, one on Upper Lough Erne, Co. Fermanagh, and one in Co. Cork. Webb *et al.* (1996) state that the plant is naturalised in Upper Lough Erne and near Cork. The *Census Catalogue of the Flora of Ireland* (Scannell & Synnott, 1987), lists *S. aloides* as an introduction in three vice-counties: West Cork, Fermanagh and Antrim.

R. D. Meikle, on the other hand, takes a totally different view of the status of *S. aloides* in his unpublished (1957) typescript *Flora of Co. Fermanagh*, based on collaborative field work with E. N.Carrothers, R. C. Davidson & J. McK. Moon. In this Meikle states his opinion that, *"Stratiotes aloides* has as good a claim to be considered indigenous in Fermanagh as *Hydrocharis morsus-ranae* (Frogbit) or any other aquatic".

The present paper considers the status of *S. aloides* in Fermanagh in the light of definitions and criteria for such deliberation which were carefully delineated by Webb (1985), and supplemented by Preston (1986). Basic to Webb's definition of native or alien plant status is the consideration of human involvement (i.e., Neolithic man onwards). Fossil evidence from the period before Neolithic farming activity is the only concrete proof of native status that Webb accepts; all other evidence is circumstantial and, as such, for each species it must be subjected to careful, *objective* scrutiny and the balance of probabilities weighed.

I will begin by reviewing the distribution and history of the species in relation to human activities in Europe and the British Isles, in order to determine what patterns emerge, how they might apply in Ireland, and how the status of *S. aloides* in Fermanagh appears in the light of such investigation.

#### FOSSIL EVIDENCE

*S. aloides* can be recognised to species level both from macro-fossils and from fossil pollen (Andrew 1970). Dickson (1970) describes how the species can be distinguished from the extinct *S. intermedius* Hartz by its tough resistant leaf spines, which have a main pointed cell and subsidiary basal cells. Both species are illustrated by Katz *et al.* (1965). The species is also recognised from its fossil seeds which are often abundant, and the history of the genus has been traced back by means of these seeds into the Tertiary Era for some 48 million years, through as many as 15 fossil species (Chandler 1923; Cook & Urmi-König 1983).

In the South of England, fossil pollen has been discovered in early Pleistocene interglacial sands and clays of the Pastonian (West 1961). This interglacial pre-dates both the Anglian (the first East Anglian glacial stage) and the preceding Cold Beestonian stage. S. aloides also occurs as fossil pollen in the shelly sands of the Corton Beds, the name given to warm interstadial deposits within the Anglian glacial in East Anglia, which are of Middle Pleistocene age (Godwin 1975). In the Late Pleistocene it is found as seed in the Hoxnian interglacial, and again as macroscopic remains in the Ipswichian interglacial at Wretton and Selsey. Fossil pollen from the Ipswichian has also been recorded from Bobbitshole and Selsay (Godwin 1975). Other aquatics associated with S. aloides in the Selsay fossil record included Hydrocharis morsus-ranae, Sagittaria sagittifolia (Arrowhead) and Butomus umbellatus (Flowering-rush). Godwin obliquely poses an unanswered question about S. aloides' means of dispersal when he comments that, "It is of interest that whilst the fossil record provides no evidence whatever of this thermophilous plant in the glacial stages, it occurs nevertheless in every interglacial (my emphasis) from the Pastonian onwards" (Godwin 1975). Despite the implication contained in this quote, no specific reference is given here to a fossil presence of S. aloides in the early part of the current interglacial, the Flandrian, and I am not aware of any such record.

The above plentiful fossil occurrences, read in conjunction with early first records, help support the native status of *S. aloides* in at least south-eastern England, yet fail to prove it conclusively in Webb's terms. Fossil material has been noted in only one Irish deposit so far, at Shortalstown, Co. Wexford, where a single grain of *Stratiotes* pollen, thought to be of Ipswichian (Late Weichselian) age, was discovered by Colhoun & Mitchell (1971). Although this appears to be the only Irish fossil of *Stratiotes*, the reason for this may well be that no one has been looking for it; in addition, to date no palynological studies of Holocene lake sediments have ever been made in Fermanagh or Cavan, the region of *S. aloides'* main past and current distribution (Dr Valerie Hall, pers. comm., 1998).

# STATUS OF STRATIOTES ALOIDES IN CO. FERMANAGH

# GEOGRAPHICAL DISTRIBUTION AND HISTORICAL EVIDENCE

#### EUROPE

The map produced by Cook & Urmi-König (1983) shows *S. aloides* occurring in the British Isles and in Europe south to Spain, Italy, Bulgaria and European Turkey, north to Finland, and east to Siberia (Fig. 1). Throughout the range Cook & Urmi-König discovered it difficult to determine its status, but they reviewed the scientific opinion in relation to the fossil occurrences, floristic literature (sometimes documenting definite introductions), and herbarium records. They showed that the distribution of *S. aloides* today agrees very closely with the distribution of the 15 fossil species. The single exception was the find of *S. tuberculatus* E. M. Reid from the Pliocene in Portugal, which alone supports the two unconfirmed literature records of *S. aloides* in Spain from the 18th and 19th century (Willkomm & Lange 1861). This is a particularly interesting disjunction in the species range, as it is generally accepted that *S. aloides* is not native to France on grounds of its late first mention in the relevant literature (1810), a series of documented introductions, and the lack of any fossil finds. A similar puzzle exists with respect to Italy (where it is considered native in the eastern part of the Po Plain) and Switzerland ("certainly not native") (Cook & Urmi-König (1983)).

Cook revised his opinion of the native range of *S. aloides* two years later, asserting that it is indigenous only in Central Europe and is introduced and established in Western Europe (Cook



FIGURE 1. Distribution of *Stratiotes aloides* L. in Europe, with sexes determined from herbarium material (after Cook & Urmi-König 1983), and with the British Isles updated by the author.  $\bullet$  female plant,  $\blacktriangle$  male plant, O plant of unknown gender, L record from the literature only.

1985). No explanation accompanies this reassessment, but in the light of his earlier *Stratiotes* review (Cook & Urmi-König (1983)) I believe it may involve the distribution of a dragonfly associate (see section on insect associates below).

# GREAT BRITAIN

In the British Isles, on the basis of early records, the species is regarded by most naturalists as indigenous in the east of England (Geldart 1906; Stewart *et al.* 1994; Preston & Croft 1997) (Fig. 2). It was first reported by Thomas Johnson in the East Riding of Yorkshire in 1626 (Crackles 1990), followed by Lincolnshire in 1633 by the same finder (Gerarde 1633; Gibbons 1975). Old records from the 17th and early 18th centuries must be accepted with caution, as the name *Stratiotes* was applied by different authors to a number of quite unrelated plants, including *Achillea millefolium, Hydrocharis, Hottonia palustris* and even some Umbelliferae (Geldart 1906). Geldart also lists the English common names given by Johnson in the second edition of Gerard's *Herball* (Gerarde 1633) as, "Water houseleek, Knights' pondwort, Knights' water sengreen, Freshwater soldier, Wading pondweed, Soldier's yarrow and Knights' water woundwort". The fact that seven English common names for the plant were in use by 1633 suggests that it was already widely known by local people when the first plant record was published.

The native range of *Stratiotes* has contracted sharply in the last 150 years (Fig. 2). It is now extinct in its previous stronghold, the Cambridgeshire fens (Preston & Croft 1997), and it has largely disappeared from Lincolnshire and Yorkshire also (Stewart *et al.* 1994). The greatest concentration of surviving *Stratiotes* sites regarded as native in England occur in East Norfolk (v. c. 27), where it is currently found in 43 tetrads (nine 10 km squares), in ditches (or dykes) in grazing marshes around the River Waveney. Even in this corner of England, however, there are ten to twelve more-or-less isolated sites where the species is suspected of being introduced.

Apart from S.E. England and East Yorkshire, where the plant has a long history, there is justifiable doubt and uncertainty with regard to its status in the rest of Great Britain due to a combination of late first records, documented introductions, colonies in man-made or heavily disturbed habitats, and a lack of local fossil evidence, very much paralleling the situation in France (Watson 1883; Cook & Urmi-König 1983; Stewart *et al.* 1994; Preston & Croft 1997).

Preston & Croft (1997) suggested that S. aloides might be native in Cheshire (v.c. 58). It transpires that this assertion was made on the same basis as that used by Stewart et al. (1994) while working on the Scarce Plants in Britain project, i.e., that when required to separate native from alien records, unless there are good grounds for a difference, the treatment of the species follows that given by the Atlas of the British Flora (Perring & Walters 1962 and subsequent reprints with minor corrections and additions). "We think that this (i.e., The Atlas) presents a realistic assessment of the status of most species, and also recognise that there is an arbitrary element to the decisions which have to be made and there is no point in presenting alternative opinions if the evidence to support them is weak." (Stewart et al. 1994). Perring & Walters (1962) accepted the view of De Tabley (1899) who stated in his Flora of Cheshire that S. aloides seemed to him as native in central Cheshire as anywhere in Britain, although he gave no reasons for making this assertion. In the same work De Tabley also cited several known introductions of the species in Cheshire (G. McKay, pers. comm., 1998). The more recent Flora of Cheshire (Newton 1971) does not claim native status for S. aloides in the county, and C. D. Preston (pers. comm., 1998) now agrees that in retrospect, "the case for native status in Cheshire is weak and we should perhaps have shown less deference to the Atlas map."

S. aloides occurs in four 10 km squares in Denbighshire, and Ellis (1983) claimed them native (J. Green, pers. comm., 1998). The first Denbighshire record was made by the Rev. W. E. Jones in 1938 and was included in the 2nd edition of *Welsh Flowering Plants* by Hyde & Wade (1957), who assumed it to be native. Ellis updated the records from the same area for his *Flowering Plants* of *Wales*, and repeated the assumption of native occurrence since he had no reason to question it (Ellis 1983). In the light of the *Stratiotes* map published in Stewart *et al.* (1994), Ellis has revised his opinion and has written, "without any firm evidence to the contrary, I would probably class the v.c. 50 populations as introduced." (G. Ellis, pers. comm., 1998).

It is not at all surprising that the older Cheshire and Denbighshire records were simply assumed to be native by the botanists of the time. While describing the range of circumstantial evidence that needs to be assembled and weighed to enable a realistic consideration of a plant's status, Webb



FIGURE 2. Distribution of *Stratiotes aloides* L. in the British Isles. Symbols represent at least one record in a 10 km square. O pre-1975 putative native records,  $\bullet$  putative native records made in or after 1975, + records of introduced population made before 1950, × records of introduced populations made in or after 1950. Based on Preston & Croft (1997) and updated by the Biological Records Centre as requested by the author.

(1985) commented that in assigning native status there is often an element of wishful thinking, sometimes amounting to local patriotism, or an impression that the amount present in an otherwise undisturbed "natural looking" habitat was sufficient evidence in itself to claim a find as being native. Webb also gave telling examples of why this level of assessment is unreliable.

# IRELAND

# Co. Antrim (H39)

The first Co. Antrim record was made in 1815 by John Templeton, a well-known and respected amateur naturalist. He described the site at Stranmillis on the (then) outskirts of Belfast as, "In the back drain of the Belfast watercourse". Praeger (1938) and Hackney (1992) both regarded this and

the other Co. Antrim records as introduced, noting that three out of four stations were extinct by 1938. Hackney also records that the plant has not been seen since 1930 at the last remaining Co. Antrim station, the mill-dam at Woodburn, where it was reported as "occupying two acres" (Fisher 1930). Praeger (1938) commented in the second edition of *The Flora of the North-East of Ireland* that *Stratiotes*, "should be looked on as planted in our district; *in Ireland it seems fully naturalised in Lough Erne alone*" (my emphasis). In Co. Antrim the arrival, spread and departure of *S. aloides* fits the "boom and bust" behaviour pattern shown by many plant introductions (Simpson 1984; Clement & Foster 1994) and, apart from the early first discovery in a natural water course, there is no evidence with which to argue the contrary. I would *prefer* to consider Templeton's Lagan site as of "possibly native" status but, mindful of Webb's warning of vision clouded by local patriotism and recognising that the evidence really is insufficient, it must remain a (now extinct) "probable introduction".

# Co. Fermanagh (H33)

*S. aloides* was first found in Fermanagh in 1805, placing it amongst the very first plants recorded in the county. The discoverer of *S. aloides*, the Rev. Robert Scott, M.D., was Professor of Botany at Trinity College, Dublin from 1785 until 1808, and is regarded as the father of Fermanagh botany. A native of the county from Scottsborough House, Magheraveely, while primarily a bryologist, Scott evidently had a good eye for flowering plants (especially aquatics), and he was responsible for adding *Utricularia intermedia* Hayne (Intermediate Bladderwort), to the flora of the British Isles (Praeger, 1949).

The Fermanagh records of Dr. Scott were published along with his finds in other parts of Ireland in the first edition of J. T. Mackay's *Catalogue of Rare Plants found in Ireland* (1806). Mackay himself visited Fermanagh and the adjoining part of Cavan (H30) shortly after Scott, for in the same work he records his own find of *S. aloides*, "in drains on the roadside near Castle Saunderson, in the vicinity of Lough Erne". Scott's original *S. aloides* site is described as, "... growing in a drain near Crum Castle, on the banks of Lough Erne, county of Fermanagh, in August last," Crum is currently spelt, "Crom", and this locality near the Fermanagh-Cavan boundary where the Erne connects southwards with Belturbet, is still the main area of distribution for the plant today. S. aloides has recently been recorded again from the Cavan side of the border; the species was refound in 1996 at two loughs near Belturbet (Round Lough, H15.39, and Anoneen Lough, H22.35) (P. Reilly, pers. comm., 1998). This represents a gap of 128 years since the species was last listed in the same area by David Moore (Moore & More 1866). Robert Northridge and I, as joint B.S.B.I. vice-county recorders for Fermanagh (H33), have assembled a total of 44 S. aloides records in 15 tetrads (Fig. 3). Fourteen tetrads contain post-1975 records. The species was first recorded at the S.E. boundary of the county and subsequent finds extended its known occurrence northwards along Upper Lough Erne rather slowly. It was not found at Belleisle, about eight km. south of Enniskillen, until 1900. In 1990 a major survey of aquatic vegetation, commissioned by the Department of the Environment for Northern Ireland, extended the known distribution as far north as Lough Yoan, within 2 km of the town. In reality, however, the evidence is much too scant to conclude that the species is spreading in Fermanagh. Botanical recording in the county (as elsewhere in Ireland) has been extremely occasional, sporadic and unsystematic until the 1980s, and it has involved only a handful of people, few of whom resided locally. One can say with confidence, however, that S. aloides has not exhibited an explosive spread in the manner characteristic of some definitely introduced aquatic species, such as Elodea canadensis (Canadian Waterweed), or E. nuttallii (Nuttall's Waterweed). Neither has it declined or disappeared on Upper Lough Erne as it has in its Co. Antrim stations, where its occurrence on man-made or disturbed aquatic habitats always tended to support the suspicion it might be an introduction.

The headquarters of *S. aloides* in Fermanagh remains very much where it was first found almost two centuries ago, the southernmost fen-fringed lakes and inlets of Upper Lough Erne, where it sometimes dominates open water. In mid-August 1994, at the southern of two lakes in the district, both called "Corracoash", Robert Northridge and I came across a striking example of its growth potential; a dense population covered the lake surface, approximately 3 ha in extent. In 1998 the communicating Mill Lough, approximately twice the size of Corracoash Lough, was so overgrown with *S. aloides* that it was difficult to row a boat through it (J. Bullock, pers. comm., 1998).



FIGURE 3. Tetrad distribution of *Stratiotes aloides* L. (Water-soldier) in Co. Fermanagh (H33). Hatched symbols represent pre-1975 records, black symbols post-1975 records.

# Other stations in Ireland

Following the Fermanagh, Cavan and Antrim finds already discussed, Mackay published a further site for *S. aloides*, "on the banks of the Shannon, near Portumna" (Co. Tipperary, H10) in his *Flora Hibernica* (1836). Mackay's listing for this site showed *S. aloides* occurring on the major river of central Ireland with *Sagittaria sagittifolia* and *Eleocharis acicularis* (Needle Spike-rush). The Tipperary *S. aloides* had gone by 1866 when Moore & More published their *Cybele Hibernica*.

In addition to its earlier northern sites, Moore & More (1866) also list *S. aloides* occurring, "*naturalized* (my emphasis) in Ballyphehane Bog" (Cork city; H4), a site which Mackay (1825) previously mentioned in passing, and which was near the Cork Botanic Garden. Significantly, Mackay (1825) does *not* list *S. aloides* for this site, although twelve other species from Ballyphehane Bog are attributed to his major Cork contributor, Mr Drummond. The Ballyphehane station is again ignored by Mackay in his *Flora Hibernica* (1836), which also suggests he knew it was not a native occurrence of the species. Drummond was the curator of the short-lived Cork Botanic Gardens, which was situated on a low limestone hillock in the city. It appears that Drummond simply used the nearby marsh (it was never a bog), as a convenient out-station for growing aquatic plant species for the Botanic Garden (M. Scannell, pers. comm., 1998). This is the only unequivocally introduced site for *Stratiotes* in Ireland.

Colgan & Scully (1898) mention *S. aloides* as having occurred fleetingly (in 1829) in a canal near Drogheda, Co. Louth (H31). The lack of persistence and artificial nature of the waterway both suggest that a garden origin is likely in this case.

Moore & More (1866) considered *S. aloides*, "probably not indigenous" in southern Ireland, but suggested it might possibly be native in the north of Ireland. They recognised that the species was a rapidly spreading introduction elsewhere in the British Isles, and compared it with *Elodea canadensis*, (a plant which made its first appearance in these islands in Co. Down around 1836).

As was the case in Co. Antrim, the *S. aloides* plants in these three widely scattered locations in southern Ireland between 1829 and 1836 appear to have become extinct soon after their discovery, except at Ballyphehane Bog where the species survived until some date after 1900. The apparently short-lived nature of the other two south of Ireland stations is typical of most introductions; the persistence of the species at Ballyphehane may be the result of deliberate management.

The fact that there have been so few sightings of *S. aloides* in Ireland over the 192 years since its first discovery suggests that it is either truly rare, or so hard to detect that it is seldom found. As is the case with many Irish lakes, the waters of Upper Lough Erne are an opaque dark brown colour due to peat staining, so that a grapnel is an essential item of equipment to drag for submerged macrophytes. Even if one is actively looking for *S. aloides*, it can be difficult to see the characteristic "pineapple-like" leaf rosettes in deep murky lake water, and there could be very many plants invisible at depth. Under conditions of low illumination the leaves do not develop sufficient gas in their air-canals and intercellular spaces to raise the plant rosettes to the surface, and it is quite normal to find it as a bottom-dwelling plant in water between 1 and 5 m deep (Cook & Urmi-König 1983). In more shallow waters, particularly after a prolonged spell of warm weather, very rapid growth can produce the sort of *Stratiotes* "explosion" that occurred at Corracoash and Mill Loughs.

#### HABITAT

The typical habitat of *Stratiotes* is still or slow-flowing, meso-eutrophic water (Preston & Croft 1997). Upper Lough Erne consists of a multitude of small, shallow, linked lakes and intervening islands - a drowned drumlin landscape - and although there is a channel navigable for motor launches, the great majority of its shores are undisturbed. Drainage ditches are cleared from time to time by local farmers and, although fringing emergents encroach, open water is plentiful, as is rainfall throughout the year. Agriculture is entirely pastoral and low intensity on the surrounding rushy meadows and, while slurry is spread, eutrophication from run-off has not become a widespread problem. In recent years 60% of Fermanagh farmland has been covered by a government-funded Environmentally Sensitive Area farm subsidy scheme.

In England S. aloides was formerly found in lakes and slow-moving rivers but now is virtually confined to drainage ditches (Preston & Croft 1997). In the Broads of south-eastern England S. aloides occurs in three habitats, all of them man-made. The Broads are flooded peat excavations, the fen dykes were created to allow boat access into the fens, and the network of ditches in the reclaimed marshes were created for land drainage (R. J. Driscoll, pers. comm., 1998). S. aloides appears to prefer the still water of grazing marsh ditches, particularly where the water is moderately rich in nutrients and calcareous, and it grows where regular cleaning of the ditches or ponds, (often grazed on their margins), suppresses the growth of shading reeds and other tall emergent species. S. aloides is even more intolerant of fluctuating water levels than its relative and frequent associate, Hydrocharis morsus-ranae, and unlike it does not survive on mud to form turions (Cock & Lüönd 1982).

Eutrophication, and habitat disturbance and destruction due to agricultural changes, are readily identified as the major reasons for the rapid decline in distribution and decreasing abundance in the 20th century. In east Norfolk, the main area of surviving populations considered indigenous, habitat loss continues due to a change from pasture to arable agriculture, subsequent pollution and, since the area is low-lying and near the coast, sporadic tidal inundation (A. Bull, pers. comm., 1998). On the other hand, Wheeler & Giller (1982) suggested that *S. aloides*, in the dyke system of the Catfield and Irstead fens in the Norfolk Broads, showed abundant growth at the fen margins, possibly in response to a degree of agricultural nutrient run-off, whilst the species has become rare in the central areas of these fens during the last 30 years. On the basis of water chemistry they considered it at least possible that this decline might be due to nutrient depletion associated with oligotrophication and acidification.

A similar catastrophic decline of the species in the Netherlands from the 1960s onwards followed increased drainage associated with modern agricultural practices, which diminished the

influence of ground water. To prevent the low-lying peat soil from drying out, sulphate-enriched alkaline water from the Rhine was admitted, which produced a complex of environmental stresses involving iron limitation, sulphide toxicity, a strong increase of non-rooted species due to internal and external eutrophication, and ammonium toxicity (Smolders *et al.* 1996).

The habitat requirements and tolerances of *S. aloides* are thus very specific and narrow (see community ecology section below).

#### REPRODUCTIVE PATTERN

Phytogeographically, *Stratiotes* is regarded as a Continental species by Matthews (1955), a position refined by Preston & Hill (1997), who described it as Eurosiberian Boreo-temperate. When trying to relate a species' distribution to geography and climate, however, one must take particular account of the fact that different optimum and minimum conditions may occur for life processes such as seed set, germination and vegetative growth, and that biotypic variation may modify these physiological characteristics within the total range of a species. This is certainly the case with regard to growth and sexual reproduction of *Stratiotes*.

Currently, reproduction of *S. aloides* in the British Isles and in most of Europe is entirely vegetative and is carried on by the production of new open leaf rosettes (or closed turions (Kornatowski 1979)), budded off on monopodial lateral shoots (Cook & Urmi-König 1983). Renman (1989) studied the life histories of two clonal populations of *S. aloides* in northern Sweden and found that emergent forms of the plant produced more daughter turions than did submerged forms.

There is the added complication of the dioecious nature of the plant and the present-day distribution of the sexes. The dioecy of *Stratiotes* is not absolute. Dioecy is secondary in origin and in *S. aloides* flowers of both sexes contain whorls of staminodes, which in the female flowers secrete nectar at their base (Daumann 1931). Although the staminodes are normally sterile, rarely the female flowers contain a few apparently fertile stamens on their outer whorl (Geldart 1906; Cook & Urmi-König 1983; Preston & Croft 1997). Hutchinson (1948) went so far as to describe *S. aloides* as "subdioecious". The existence of hermaphrodite plants (even at low frequency) casts a different light on the possible reproductive history of the species in the post-glacial period.

Full dioecy is represented when plants (or genets - defined as genetically distinct individuals), are totally male or totally female. According to Richards (1986), who was writing on dioecy in general terms, when sex is phenotypically unstable, hermaphrodites that are capable of selfing may occur. When only some of the flowers on a female genet become hermaphrodite (as in the case of *S. aloides*), they are termed subgynoecious, and this is considered the result of unstable sex expression in a genetically dioecious plant (Richards 1986). (When <u>all</u> the flowers of a female plant or genet become hermaphrodite, the species is said to show gynodioecy (i.e. female and hermaphrodites occurring together), but this does not apply in the case of *Stratiotes*). Plants that are fickle in their sex expression are often subject to environmental influence and, in the case of thermophilous species such as *S. aloides*, temperature is clearly the most likely significant factor possibly linked with daylength. Sex expression in plants and its physiological control is a fascinating area of study (Meagher 1988), and touching on it ought to remind us that concepts such as "incompatible" and "dioecy", are decidedly "leaky", and that our description of the natural world is frequently a convenient oversimplification of the variation that really exists (Proctor *et al.* 1996).

Cook & Urmi-König (1983) reviewed the current distribution of the sexes in *S. aloides*, and found that while female plants strongly predominate north of a line drawn from Cherbourg to Leningrad (St Petersburg), isolated male plants have been found in Denmark, Sweden and Finland (Fig 1). North of the Cherbourg/Leningrad line, however, they did not find any evidence of *S. aloides* bearing seed and, although fruits may form, no viable seed has been found in the British Isles either, since the Pleistocene (Crackles 1982). This suggests three non-exclusive possibilities; (a) that for successful seed production, *S. aloides* requires a warmer summer than that currently found north of the Cherbourg/Leningrad line; (b) that <u>male *S. aloides* plants are more susceptible to cold and have become extinct in what is now a scattered, relict population; or (c) male flowers are never or only rarely triggered to occur by the longer summer daylength or other environmental factors to the north.</u>

The fossil assemblage found with S. aloides in the Corton Beds in East Anglia of Middle Pleistocene age indicated to West & Wilson (1968) a strong northerly aspect to the vegetation, with some persistence of Arctic-alpine species which occurred, "together with a number of aquatics, including S. aloides and Potamogeton crispus, with a mainly southern distribution", (my emphasis). Considering the occurrence of fossil Stratiotes along with Cladium mariscus, Hydrocharis morsus-ranae and Lemna minor, West (1961) suggested that their joint presence indicated a considerable summer warmth in the Cromerian and Pastonian interglacials of the Norfolk coast.

Evidence like this supports the notion that the prevailing temperature in the north and west of *S. aloides*' current range is too cool for successful sexual reproduction, as even in regions where both sexes occur today (i.e. Sweden, Finland and Denmark), no viable seed appears to be set. Further south, in a warmer climate, seed *is* successfully produced, e.g. in the Netherlands (Smolders *et al.* 1993). Palynologists tell us that we are past the climatic optimum in the current interglacial period (the "Littletonian" in Ireland (Mitchell & Ryan 1997)), so it is arguable that *S. aloides* flourished, reproduced and spread by seed in an ancient warmer climatic phase, and when cooler conditions developed it declined to its current disjunct relict areas, persisting by vegetative reproduction. To explain the occurrence of single sex populations in the British Isles, we have to postulate differential survival capacities of the sexes. A similar explanation involving differential vigour, ecology and survival between the sexes is used to account for the restricted occurrence of female plants of *Petasites hybridus* in the British Isles (one site only in Ireland), while males are widespread throughout both islands (Valentine 1946, 1947; Perring & Sell 1968).

#### DISPERSAL ABILITY

As Preston & Croft (1997) point out, without seed *S. aloides* appears to lack a means of long-range dispersal over land. The current lack of fruiting ability may have arisen, however, *after* small founder populations of seed successfully established in both England and Ireland, some plants perhaps temporarily retaining a degree of fertility through the possession of a subgynoecious habit.

"Baker's Law" (Baker 1955; Stebbins 1957) suggests that dioecious species appear to be at a major disadvantage when colonising islands compared to self-compatible hermaphrodite plants. Bawa (1982), however, has suggested that dioecious taxa may have been disproportionately successful in colonising islands. Analyses of numerous oceanic island floras by Baker & Cox (1984) indicated that dioecious taxa do not do better in long-distance dispersal than self-compatible hermaphrodites, but neither do they fare worse, a result that was unexpected and was not predicted by extensive numerical simulations (Cox 1985). While the distances and the timescales involved in colonisation of oceanic islands are far greater than those associated with continental islands such as the British Isles, the evidence remains that jump dispersal is effective and plants do colonise islands. The fact that in *S. aloides* dioecy is not absolute but "leaky" (Cox 1985), and that it is capable of producing subgynoecious self-compatible hermaphodites from time to time, overcomes some of the conceptual difficulties we face in imagining jump dispersal of the species to Britain and Ireland.

Like two aquatics often associated with *Stratiotes*, *Ceratophyllum demersum* (Rigid Hornwort), of which Scannell (1976) found that it flowered but failed to ripen fruit in Ireland, and *Hydrocharis morsus-ranae*, which flowers erratically and seldom fruits (Cook & Lüönd 1982; Preston & March 1996), *S. aloides* possesses a successful means of vegetative multiplication. It is possible that a single founder or a single aggressive clone may have survived many years of asexual competition and a slowly changing, cooling environment, giving rise to high levels of sterility, even in species or regions where both sexes are currently sympatric (Richards 1986). Throughout north-west Europe *S. aloides* appears to fit this pattern closely, and on offshore islands the probability of a restricted genome is clearly increased.

The occurrence of fertile seed-producing plants across the North Sea in the Netherlands, and the small but possibly highly significant seed set which self-compatible subgynoecious plants could produce, provide an ancient seed source for colonisation of the British Isles, most likely through transportation by birds. Jump-dispersal of turions is possible, but diaspores adhering securely tc the dispersal agent externally (i.e. exozoic transport) is somewhat more difficult to envisage thar endozoic transport of ingested seed.

Fruit of *S. aloides* ripens late, (end of September to end of October), at a time when birds are migrating. Fresh seeds of *S. aloides* are heavily clothed with mucilaginous hairs and are liberated in a gelatinous mass by longitudinal splitting of the fruit (Cook & Urmi-König 1983), which suggests the possibility that they might stick to feet or feathers of birds feeding among fertile fruiting plants. The exotesta which bears the mucilaginous hairs is however shed, shortly after the seed is released from the fruit (Cook 1987), and in any case the mucilage tends to be sticky when dry, or almost so, but non-sticky when wet (Sculthorpe 1967). However, while *S. aloides* is said to attract a range of herbivores including water snails, beetles, insects and "several vertebrates" (Cook & Urmi-König 1983), birds are not specifically mentioned as feeding on the plant. This may simply reflect the fact that, at present, seed is rare on *Stratiotes* plants anywhere in Europe.

Similar dispersal circumstances attend other non- or seldom-fruiting aquatic macrophytes, including several that are commonly associated with *Stratiotes* in Britain and Ireland and generally considered native. Other native aquatic species of the same community freely set seed, yet appear to remain poorly adapted for long-range jump dispersal as their seeds are totally digested when eaten by birds and fish, e.g. *Nymphaea alba* (White Water-lily) and *Nuphar lutea* (Yellow Water-lily) (Preston & Croft 1997).

All long-range or jump-dispersal events are rare and unlikely and as such are difficult to envisage (Carlquist 1974; Cook 1985). Birds, particularly waterfowl, are often cited as agents of dispersal. Because of their rarity, natural transport events are almost impossible to observe and, for the same reason, they are not readily open to experiment. In the great majority of cases we do not know how or when the dispersal event(s) happen, but we have indisputable evidence that they do occur.

#### GENETIC DIVERSITY

As noted by Webb (1985), this is one area where data for most plants are very rarely available. I doubt that there are any relevant data on *S. aloides* apart from comments made by Cook & Urmi-König (1983). These authors undertook in their revision of *S. aloides* to rid the accumulated literature on it of contradictory observations and views, by reviewing the species on the basis of their own direct experience of fresh and fixed material. After their study they concluded that they had found no genetic or ecotypic variability worthy of formal taxonomic recognition. Three features they mentioned were:

- a. minor differences existed with respect to seed sizes between Swiss and Czechoslovakian plants,
- b. British specimens were somewhat stouter than Continental and Scandinavian ones, yet fell within the overall pattern of variation for the species,
- c. totally submerged plants with more flaccid, stomata-less leaves up to 100 cm long were more common in the north of the range of the species.

The reproductive pattern and current behaviour of *S. aloides* suggest that a small or very small founder population might well be all that the species succeeded in dispersing across the North Sea and the Irish Sea, so that plants on each island may represent one clone or a small range of clones. Comparative genetic investigation using isozymes is required to answer the questions posed by this clonal hypothesis.

# COMMUNITY ECOLOGY

The Middle Pleistocene fossil assemblage in East Anglian sediments described by West & Wilson (1968) showed *S. aloides* occurring with *Potamogeton crispus* (Curled Pondweed), *Cladium mariscus* (Sword Sedge), *Hydrocharis morsus-ranae* and *Lemna minor* (Common Duckweed). All these fossil allies occur today with *S. aloides* in Upper Lough Erne, Co. Fermanagh, together with numerous other frequently associated aquatics, e.g., *Lemna trisulca* (Ivy-leaved Duckweed),

Sagittaria sagittifolia (Arrowhead), and several narrow-leaved Potomogeton species typical of more shallow waters, such as *P. pusillus* (Lesser Pondweed), and *P. pectinatus* (Fennel Pondweed). In phytosociology, communities are drawn floristically by species presence, *plus* a particular set of frequency and abundance values of all the species found in the samples or relevés. A sample may be pigeon-holed into a previously described community even if the name-giving species, or some of the other characteristic "constant species", are absent. The information available from Upper Lough Erne forms part of the substantial Fermanagh Flora database and consists, not of standardised quadrats or relevé samples, but of site specific species lists which do not incorporate frequency and abundance values. It is possible, however, to glean an idea of species frequency from the overall species statistics of records and tetrads occupied, and I present these estimates of species presence here (Table 1).

The National Vegetation Classification survey of aquatic vegetation in Great Britain (Rodwell 1995) shows *S. aloides* present in two plant associations, prominently as a characteristic constant species in the *Hydrocharis morsus-ranae–Stratiotes aloides* community (A4) (Table 1), and as a rare companion species in the *Potamogeton pectinatus–Myriophyllum spicatum* community (A11). The *Hydrocharis morsus-ranae–Stratiotes aloides* community is equivalent to the continental

Species	Norfolk Broads		Fermanagh	
	Frequency	Cover value	No. recs.	No. of tetrads
Hydrocharis morsus-ranae	V	1-4	78	19
Stratiotes aloides	V	1-7	44	12
Lemna minor	V	1-3	720	50+
L. trisulca	V	1-5	487	50+
Callitriche platycarpa	V	1-3	13	5
Polygonum amphibium	IV	1-3	370	47+
Utricularia vulgaris	IV	1-7	98	30+
Ceratophyllum demersum	IV	1-7	0	0
Myriophyllum verticillatum	III	1-3	26	6
Nuphar lutea	III	1-2	619	50+
Potamogeton obtusifolius	III	1-6	240	50+
Elodea canadensis	III	1-4	604	50+
Potentilla palustris	II	1-2	674	50+
Hottonia palustris	II	1-2	0	0
Berula erecta	Ш	1	23	6
Ceratophyllum submersum	II	1-6	0	0
Oenanthe aquatica	II	1-3	126	27
Sparganium erectum	II	1-3	613	50+
Nasturtium officinale	II	1-3	432	35+
Sium latifolium	II	1-3	377	50+
Alisma plantago-aquatica	I	1-3	708	50+
Nymphaea alba	I	1-3	185	18
Ranunculus lingua	I	1-3	181	35+
Sagittaria sagittifolia	Ι	1-3	87	28
Potamogeton crispus	I	1	98	18
Sparganium emersum	Ι	3-4	267	50+
Number of samples	12			
Number of species/sample	14 (11-19)			

 TABLE 1: FLORISTIC TABLE FOR THE HYDROCHARIS MORSUS-RANAE–STRATIOTES

 ALOIDES COMMUNITY (A4) OF RODWELL (1995)

Based on data (columns 1 & 2) from the Norfolk Broads (Wheeler & Giller 1982), compared with data from the Co. Fermanagh Flora database (unpub.). Column 3 lists the total number of records for the species in the database, and column 4 indicates the number of tetrads in around Upper Lough Erne in which it occurs.

Hydrochario-Stratiotetum (Westhoff & den Held 1969) or the Hydrocharitetum of Oberdorfer (1977). Rodwell admits that he has characterised this community in Great Britain almost entirely on what he refers to as, "the small data set of Wheeler & Giller (1982)" from the Norfolk Broads, and he recognises that more comprehensive sampling is needed to arrive at a satisfactory definition of this kind of assemblage in Britain. Keeping this reservation in mind, examination of the published floristic table for the Hydrocharis morsus-ranae-Stratiotes aloides community demonstrates that in addition to the two eponymous aquatics, there are 24 additional species listed, of which 21 occur in Upper Lough Erne (Table 1). The only plants missing from Upper Lough Erne are the two Hornworts, Ceratophyllum demersum and C. submersum (Soft Hornwort), plus Hottonia palustris (Water Violet). Of these three, C. demersum alone has a prominent role as a "constant species" in the plant community, but the other seven "constant" species are all present.

The fact that S. aloides occurs in Fermanagh backed up by a very nearly complete complement of the characteristic species of the Ceratophyllum–Stratiotes nodum (Wheeler & Giller 1982), or the Hydrocharis morsus-ranae–Stratiotes aloides community of Rodwell (1995) - and this despite the depauperate flora of Ireland - must lend very strong circumstantial support to the claim for Water-soldier's native status in Upper Lough Erne.

With regard to the second community, in which *Stratiotes* plays a much more minor role, the *Potamogeton pectinatus–Myriophyllum spicatum* community (A11) of Rodwell (1995), Upper Lough Erne supports 47 of the 56 characteristic species listed by Rodwell for the three subcommunities he recognises (neglecting the moss *Fontinalis antipyretica*). The nine missing species include five which are nationally scarce in Great Britain, two that are strictly coastal, and two which have never been recorded anywhere in Ireland.

Thus we can say with confidence that *Stratiotes* occurs in Upper Lough Erne with very much the same vascular plant species complement that accompanies it in Great Britain and, importantly, that in turn these match Continental equivalents.

#### INSECT ASSOCIATES

Preston (1986) suggested an additional criterion for assessing native status of plants to the eight discussed by Webb (1985), namely, the relationship of the plant species in question to oligophagous herbivorous insects. Entomological evidence, Preston indicated, needs to be used with the same degree of caution as Webb's criteria, for introduced plant species may attract insect feeders from related long recognised native species, as is known in the case of *Impatiens nolitangere* (Touch-me-not Balsam), which supplies oligophagous insects to the definitely introduced garden escape *I. parviflora* (Small Balsam) when the two species are adjacent.

With regard to *S. aloides*, the absence of the dragonfly *Aeshna viridis* Eversmann, which is described as dependent on the macrophyte, led Cook & Urmi-König (1983) to argue that *S. aloides* might not be native in Great Britain and other areas of Europe from which the insect is missing. These authors report the findings of Münchberg (1956), who researched the habits and life history of the insect: it is carnivorous and, although the larvae live on *S. aloides* rosettes for two or three years until they reach maturity, they do not appear to harm the leaves of the host plant at all. Knowing this, it is not at all clear why the dragonfly should be specifically associated with *S. aloides* in the Dutch broads, but apart from a few Lepidopteran caterpillars, which did insignificant damage, none of the other species appeared to feed on the living plant tissues - they merely used the plant as a habitat surface or shelter. The argument linking *Aeshna viridis* to the native status of *S. aloides* is further weakened by the fact that the distribution of the dragonfly only partially overlaps that of *S. aloides*, and the dragonfly is absent from N.E. Italy and the mouth of the Danube where Cook & Urmi-König believe *S. aloides* is likely to be native (Cook & Urmi-König 1983).

Another dragonfly, Anaciaeshna isosceles (Müller) (Norfolk Hawker), a protected, endangered species, is restricted in Great Britain to the Broadlands and there heavily dependent on S. aloides, again apparently purely for shelter, although it is also found to a lesser extent on Glyceria maxima (Reed Sweet-grass), Juncus effusus (Soft-rush) and Iris pseudacorus (Yellow Iris) (Leyshon & Moore 1993). This dragonfly was found in the examined Suffolk Broadland dykes only where a dense population of S. aloides occurred.

#### EASE AND SOURCE OF KNOWN NATURALIZATION

### GREAT BRITAIN

S. aloides was recommended by Philip Miller as a suitable plant for water gardens in his famous Gardener's dictionary, first published in 1724 and with many subsequent revisions and abridged editions. Until Loudon's An encyclopaedia of gardening appeared in 1822, Miller's publication was the most widely used and influential garden handbook and his ideas became fashionable. William Robinson's The English flower garden (first published in 1883 and which also ran to many subsequent editions), continued the fashion, although he was not impressed with Stratiotes, "spike of unattractive blossoms". A recently published manual of water gardening sponsored by the Royal Horticultural Society (Robinson 1997) continues to recommend S. aloides as a hardy submerged aquatic species for garden pool decoration.

The map of the British Isles distribution of *S. aloides* in Preston & Croft (1997) and the revised version published here (Fig. 2) provide a convenient summary of current knowledge of the distribution of the species, the extent to which it has become naturalised in Great Britain, and its decline this century. (The coverage of Preston & Croft's map gives a very much more complete and detailed picture of the status of *S. aloides* than the *Atlas* map (Perring & Walters 1976), having information plotted for 216 squares compared with just 93). It requires only a cursory glance to appreciate that only a small minority (16%) of the post-1969 symbols represent native occurrences, the balance being records of introduced populations. The revised map (Fig. 2) contains four classes of record symbols, 25% representing post-1969 native occurrences. The introductions extend north to Brechin (v.c. 90), south to Portsmouth (v.c. 11), and west to Bideford (v.c. 4) but are, as one might expect, centred on the major conurbations of the English midlands.

The other impression quickly gained from Fig. 2 is the extent to which *S. aloides* as a species (irrespective of the status of the particular station) is declining in the Britain Isles. Even after revising the status of the Fermanagh and Cavan records, the number of native symbols on the map has dropped from a total of 75 10-km squares pre-1950 to just 23 today, while in areas where it was introduced, the decline has only been from 149 squares pre-1950 to 69 squares after that date.

#### IRELAND

In Co. Fermanagh the main garden activities in the late 18th and early 19th centuries were still landscaping with trees, and the less formal, more natural Rococo style of gardening initiated by Alexander Pope, his friend Dean Jonathan Swift and *his* friend, the Dean of Down, Patrick Delaney. The Rococo style involved vistas of trees grown in a natural manner, rather than the clipped dress of the formal baroque garden, and it had subsidiary vistas in the form of meanders or angles, the whole effect being intricate, whimsical and natural (Lamb & Bowe 1995). It is known that Delaney advised on garden improvements in Co. Fermanagh, certainly at Belleisle near Enniskillen, and perhaps also at Manor Waterhouse (Malins & the Knight of Glin 1976). The Manor Waterhouse estate (H3730), a few km south of Lisnaskea and five km north of the Crom estate, belonged to an Englishman, John Madden (1652–1703). Madden and his son Samuel were interested in plants (Nelson 1981), and gardening (including the use of water features); however, there are no records of *S. aloides* from Manor Waterhouse and no evidence suggesting that the Maddens knew the species, or that they had any hand in introducing it to the county.

The grounds of Crom Castle, where (or close to where) *S. aloides* was first discovered in 1805, at that particular time were probably extremely neglected from the gardening point of view, since Crom Castle had been destroyed by a major fire in 1764, and was not rebuilt until 1834. The grounds around the castle were then laid out in the new classical Landscape style, complete with false ruins and a picturesque cottage or garden house on nearby islands in Upper Lough Erne.

Miller's Gardener's dictionary (1724 and subsequent editions) had many Irish subscribers, and three Dublin editions were published, in 1732, 1741 and 1764 (Nelson 1980). Although Miller recommended S. aloides for use in garden water features, I cannot unearth any evidence that the plant was ever fashionable or widely available in Ireland. The Garden History Society has published The availability of hardy plants of the late eighteenth century (Harvey 1988), in which there is no mention of either S. aloides, or its often associated relative, Hydrocharis morsus-ranae, indicating that S. aloides was not available for purchase in the horticulture trade immediately prior to its discovery in Ireland.

*S. aloides* was first found associated with or close to landed estates e.g., Crom and Castle Saunderson. Does this not suggest a cultivated origin? Such estates were sited in places that were visually interesting and strategically important and, being large enough, often contained relatively undisturbed habitats that were likely to contain interesting plants. Educated people lived in these surroundings and they used the lakes for sailing and pleasure boating and were likely to notice unusual plants. *S. aloides* has an unusual life-cycle, rising and sinking as the year progresses, and we can surmise that estate residents would comment on it to each other and to interested visitors. Botanists like Scott and Mackay, while not directly involved in the life of the grand houses, through their knowledge of plants and gardens, had access to the estates, their owners and gardeners, a tradition of hospitality amongst plantspeople which happily continues to the present day. The botanists would thus gain knowledge of local wild plants from the residents of the large country houses, and very many of the older plant records in the Fermanagh Flora database are associated with the names of old estates, e.g., Florencecourt, Belleisle, Crom and Castle Coole (R. H. Northridge pers. comm., 1998).

If, contrary to published information (Harvey 1988), sources of *S. aloides* were widely available and it was used for decorative effect in water gardens throughout Ireland for a period, why, if it readily escapes (as it appears to do in Great Britain), have there been no further reports of it in the wild in Ireland during the last 160 years?

#### CONCLUSIONS

The only incontrovertible proof of native status for *S. aloides* in Co. Fermanagh, pre-Neolithic macrofossil material, is absent so far - here and elsewhere in the British Isles. Therefore we must weigh up the circumstantial evidence offered here to decide if it is sufficient to allow us to say, as Meikle did in 1957 (unpub. ms.), that *S. aloides* is as indigenous to Co. Fermanagh as *Hydrocharis morsus-ranae*, or any other aquatic plant species.

The major points in favour of an indigenous origin for S. aloides in Fermanagh are:

- 1 Early discovery (in an Irish context at least), by a reputable and very experienced botanist who knew the locality intimately and could therefore have judged the likelihood of garden origin, yet did not argue for it, or comment on it as a possibility.
- 2 The rare and scattered occurrence of records and the lack of spread of the species when compared to other known aquatic introductions.
- 3 The total lack of new stations for the species for well over 100 years, despite the recording efforts of a growing body of botanical recorders, suggests either that *S. aloides* is not widely grown in Ireland, or if it is, it does not escape or spread.
- 4 *S. aloides* was not available in the horticulture trade in the late 18th century and no information suggests that it ever became a popular or fashionable garden plant in Ireland.
- 5 Persistence for almost 200 years in a natural watercourse (i.e. Upper Lough Erne) compared with its relatively rapid disappearance at sites where introduction is either known (i.e. Ballyphehane Bog), or possible.
- 6 The remarkable degree of similarity in the range of associated species when compared to the vegetation described from the Norfolk Broads, the most likely native station in Great Britain.
- 7 The existence in Upper Lough Erne of accepted native aquatic plant species, some rare, some with disjunct distributions, and some which also currently lack seed dispersal.
- 8 The habitat in Upper Lough Erne fits the habitat typical for *S. aloides* everywhere in Europe, namely slow-flowing meso-eutrophic water.

The main evidence suggesting S. aloides could be an introduction is:

- 1 Miller's *Dictionary of Gardening* (1724 & subsequent editions) recommended *S. aloides* to gardeners creating water features. Early 19th century occurrences of the species in a few widely scattered stations in Ireland, including canals, flax dams and other artificial waterways, might imply some level of cultivation and subsequent escape.
- 2 Some of these possibly escaped *S. aloides* colonies persisted for up to 120 years before dying out and could therefore appear naturalised for a time.
- 3 *S. aloides* appears to lack an obvious means of long-range "jump" dispersal over land, and it is thus difficult to account for its presence anywhere in the British Isles, and more so on the offshore and more ancient island of Ireland.
- 4 The restricted distribution of its extant Irish populations, especially its absence from other watercourses in drumlin regions (and even from the lower parts of the River Erne catchment). However, as discussed earlier, the habitat requirements and tolerances of *S. aloides* are very specific and narrow, and locations that *look* appropriate may not provide suitable sites (e.g., the physiography and water chemistry of Lower Lough Erne differs considerably from the Upper Lough).

I believe that, on balance, the circumstantial evidence assembled here strongly supports Meikle's assertion that *S. aloides* has as much right to indigenous status in Ireland as *Hydrocharis* or any other aquatic species. Like Webb (1985), I feel sure that there are other cases where the current status of a plant species is heavily dependent on received wisdom rather than reasoned debate over assembled facts. Conservation arguments for sites frequently revolve around the occurrence of rare and declining indigenous species, making the question of status much more than a purely academic matter.

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### REFERENCES

- ANDREW, R. (1970). The Cambridge pollen reference collection, in WALKER, D. & WEST, R. G., eds. *Studies in the vegetational history of the British Isles*. Cambridge University Press, Cambridge.
- BAKER, H. G. (1955). Self-compatibility and establishment after 'long-distance' dispersal. Evolution 9: 347–349.
- BAKER, H. G. & COX, P. A. (1984). Further thoughts on islands and dioecism. Annals of the Missouri Botanical Garden 71: 230-239.
- BAWA, K. S. (1982). Outcrossing and the incidence of dioecism in island floras. American naturalist 119: 866-871.
- CARLQUIST, S. (1974). Island biology. Columbia University Press, New York.
- CHANDLER, M. E. J. (1923). The geological history of the genus *Stratiotes*: an account of the evolutionary changes which have occurred within the genus during Tertiary and Quaternary times. *Quarterly journal of the Geological Society* **79**:117–138.

- CLEMENT, E. J. & FOSTER, M. C. (1994). Alien plants of the British Isles. Botanical Society of the British Isles, London.
- COLGAN, N. & SCULLY, R. W. (1898). Cybele Hibernica, 2nd. ed. Ponsonby, Dublin.
- COLHOUN, E. A. & MITCHELL, G. F. (1971). Interglacial Marine formation and Lateglacial Freshwater formation in Shortalstown Townland, Co. Wexford. Proceedings of the Royal Irish Academy 71 (B): 211 - 245.
- COOK, C. D. K. (1985). Range extensions of aquatic vascular plant species. Journal of aquatic plant management 23:1-6.
- COOK, C. D. K. (1987). Dispersal in aquatic and amphibious vascular plants, in CRAWFORD, R. M. M., ed. Plant life in aquatic and amphibious habitats. British Ecological Society Special Publication No. 5, pp. 179-190. Blackwell, Oxford.
- COOK, C. D. K. & LÜÖND, R. (1982). A revision of the genus Hydrocharis (Hydrocharitaceae). Aquatic botany 14: 177-204.
- COOK, C. D. K. & URMI-KÖNIG, K. (1983). A revision of the genus Stratiotes (Hydrocharitaceae). Aquatic botany 16: 213-249.
- Cox, P. A. (1985). Islands and dioecism: Insights from the reproductive ecology of Pandanus tectorius in Polynesia, in WHITE, J., ed. Studies on plant demography: a Festschrift for John L. Harper, pp. 359-372. Academic Press, London.
- CRACKLES, E. (1982). Stratiotes aloides L. in the East Riding of Yorkshire. Naturalist (Leeds) 107: 99-101.
- CRACKLES, E. (1990). Flora of the East Riding of Yorkshire. Hull University Press, Hull.
- DAUMANN, E. (1931). Zur Morphologie und Oekologie der Blüte von Stratiotes aloides L. Planta 4: 766-776. DE TABLEY (Lord) (1899). The Flora of Cheshire. Longmans, Green & Co., London.
- DICKSON, C. A. (1970) The study of plant macrofossils in British Quaternary deposits, in WALKER, D. & WEST, R. G., eds. Studies in the vegetational history of the British Isles. Cambridge University Press, Cambridge.
- ELLIS, R. G. (1983). Flowering plants of Wales. National Museum of Wales, Cardiff.
- FISHER, N. (1930). Water-Soldier, Stratiotes aloides, L., at Woodburn. Irish naturalists' journal 3: 112.
- GELDART, A. M. (1906). On Stratiotes aloides, L. Transactions of the Norfolk & Norwich Naturalists' Society 8: 181-200.
- GERARDE, J. (1633). The Herball or Generall Historie of Plantes, 2nd ed., revised by T. Johnson. London.
- GIBBONS, E. J. (1975). The Flora of Lincolnshire. Lincolnshire Naturalists' Union, Lincoln.
- GODWIN, H. (1975). The history of the British Flora, 2nd ed. Cambridge University Press, Cambridge.
- HACKNEY, P., ed. (1992). Stewart & Corry's Flora of the North-East of Ireland, 3rd ed. Institute of Irish Studies, The Queen's University of Belfast, Belfast.
- HARVEY, J. H. (1988). The availability of hardy plants of the late Eighteenth Century. The Garden History Society, sine loc.
- HIGLER, L. W. G. (1977). Macrofauna-cenoses on Stratiotes plants in Dutch broads. Verhandelingen Rijksinstituut voor Natuurbeheer 11: 1-86.
- HYDE, H. A. & WADE, A. E. (1957). Welsh flowering plants, 2nd ed. National Museum of Wales, Cardiff.
- KATZ, N. J., KATZ, S. V. & KIPIANI, M. G. (1965). Atlas and keys of fruits and seeds occurring in the Quaternary deposits of the U.S.S.R. Publishing House Nauk, Moscow.
- KORNATOWSKY, J. (1979). Turions and offsets of Stratiotes aloides L. Acta Hydrobiologica 21: 183-204.

LAMB, K. & BOWE, P. (1995). A history of gardening in Ireland, Stationary Office, Dublin.

- LEYSHON, O. J. & MOORE, N. W. (1993). A note on the British Dragonfly Society's survey of Anaciaeschna isosceles at Castle Marshes, Barnby, Suffolk, 1991–1992. Journal of the British Dragonfly Society 9: 5-
- LOUDON, J. C. (1822). An encyclopaedia of gardening. Longman. Hurst, Rees, Orme and Brown, London
- MACKAY, J. T. (1806). A systematic catalogue of rare plants found in Ireland. Transactions of the Royal Dublin Society 5: 127–184.
- MACKAY, J. T. (1825). Catalogue of the indigenous plants of Ireland. Transactions of the Royal Irish Academy, B, 14: 103-198.
- MACKAY, J. T. (1836). Flora Hibernica. William Curry jun. & Co., Dublin.
- MALINS, E. & THE KNIGHT OF GLIN (1976). Lost Demesnes: Irish landscape gardening 1660–1845. Barrie & Jenkins, London.

MATTHEWS, J. R. (1955). Origin and distribution of the British Flora. Hutchinson, London.

- MEAGHER, T. R. (1988). Sex determination in plants, in LOVETT DOUST, J & LOVETT DOUST, L., eds. Plant reproductive ecology: patterns and strategies, pp. 125–138. Oxford University Press, Oxford.
- MILLER, P. (1732). Gardener's dictionary. London.
- MITCHELL, G. F. & RYAN, M. (1997). Reading the Irish landscape. Town House, Dublin.
- MOORE, D. & MORE, A. G. (1866). Cybele Hibernica, 1st ed. Hodges, Smith & Co., Dublin.
- MÜNCHBERG, P. (1956). Zur Bindung der Libelle Aeschna viridis Eversm. an die Pflanze Stratiotes aloides L. (Odon.) Nachrichtenblatt der Bayerischen Entomologen 5: 113-118.

- NELSON, E. C. (1980). Works of botanical interest published before 1800 held in Irish libraries. Occasional papers No.1: National Botanic Gardens, Glasnevin, Dublin.
- NELSON, E. C. (1981). A late 17th century Irish herbarium in the library of Trinity College, Dublin. Irish naturalists' journal 20: 334-335.
- NELSON, E. C. & BRADY, A. (1979). Irish gardening and horticulture. Royal Horticultural Society of Ireland, Dublin.
- NEWTON, A. (1971). Flora of Cheshire. Cheshire Community Council, Chester.
- OBERDORFER, E. (1977). Süddeutsche Plfanzengesellschaften. Teil 1. Fischer, Stuttgart.
- PERRING, F. H. & SELL, P. D. (1968). Critical supplement to the Atlas of the British flora. Nelson, London.
- PERRING, F. H. & WALTERS, S. M., eds. (1962). Atlas of the British flora. Nelson, for Botanical Society of the British Isles, London.
- PERRING, F. H. & WALTERS, S. M., eds. (1976). Atlas of the British flora, 2nd ed. EP publishing, Wakefield.
- PRAEGER, R. L. (1938). The flora of the North-east of Ireland, 2nd ed. Quota Press, Belfast.
- PRAEGER, R. L. (1949). Some Irish naturalists. Dundalgan Press, Dundalk.
- PRESTON, C. D. (1986). An additional criterion for assessing native status. Watsonia 16: 83.
- PRESTON, C. D. & MARCH, M. D. (1996). Hydrocharis morsus-ranae L. (Hydrocharitaceae) fruited in Britain in 1995. Watsonia 21: 206–208.
- PRESTON, C. D. & CROFT, J. M. (1997). Aquatic plants in Britain and Ireland. Harley, Colchester.
- PRESTON, C. D. & HILL, M. O. (1997). The geographical relationships of British and Irish vascular plants. Botanical journal of the Linnean Society 124: 1-120.
- PROCTOR, M. C. F., YEO, P. F. & LACK, A. J. (1996). The natural history of pollination. Harper Collins, London.
- RENMAN, G. (1989). Life histories of two clonal populations of *Stratiotes aloides* L. *Hydrobiologia* **185**: 211–222.
- RICHARDS, A. J. (1986). Plant breeding systems. Allen & Unwin, London.
- ROBINSON, P. (1997). RHS Water Gardening. Dorling Kindersley, London.
- ROBINSON, W. (1883). The English flower garden and home grounds. John Murray, London.
- RODWELL, J. S., ed. (1995). British plant communities 4: Aquatic communities, swamps and tall-herb fens. Cambridge University Press, Cambridge.
- SCANNELL, M. J. P. (1976). Ceratophyllum demersum L. and fruit performance. Irish naturalists' journal 18: 348–349.
- SCANNELL, M. J. P. & SYNNOTT, D. M. (1987). Census catalogue of the Flora of Ireland. Stationary Office, Dublin.
- SCULTHORPE, C. D. (1967). The biology of aquatic vascular plants. Edward Arnold, London.
- SIMPSON, D. A. (1984). A short history of the introduction and spread of *Elodea* Michx in the British Isles. Watsonia 15: 1–9.
- SMOLDERS, A., VAN DUYNHOVEN, A. H. N. & ROELOTS, J. G. M. (1993). Vruchzetting en zaadproductie van Krabbescheer (*Stratiotes aloides* L.) in Nederland. *Gorteria* 19: 55–61.
- SMOLDERS, A. J. P., ROELOFS, J. G. M. & DEN HARTOG, C. (1996). Possible causes for the decline of the water soldier (Stratiotes aloides L.) in the Netherlands. Archiv fur Hydrobiologie 136: 327–342.
- STACE, C. A. (1997). New flora of the British Isles, 2nd ed. Cambridge University Press, Cambridge.
- STEBBINS, G. L. (1957). Self-fertilization and variability in the higher plants. American naturalist 41: 337-354.
- STEWART, A., PEARMAN, D. A. & PRESTON, C. D. (1994). Scarce plants in Britain. Joint Nature Conservation Committee, Peterborough.
- VALENTINE, D. H. (1946). The Butterbur in Yorkshire. Naturalist 1946: 45-46.
- VALENTINE, D. H. (1947). The distribution of the sexes in Butterbur. N.W. Naturalist 1947: 111-114.
- WATSON, H. C. (1883). Topographical Botany, 2nd ed. Quaritch, London.
- WEBB, D. A. (1985). What are the criteria for presuming native status? Watsonia 15: 231-236.
- WEBB, D. A., PARNELL, J. & DOOGUE, D. (1996). An Irish Flora, 7th ed. Dundalgan Press, Dundalk.
- WEST, R. G. (1961). Vegetational history of the early Pleistocene of the Royal Society borehole at Ludham, Norfolk. Proceedings of the Royal Society B, 155: 437–453.
- WEST, R. G. & WILSON, D. G. (1968). Plant remains from the Corton Beds, Lowestoft, Suffolk. Geological magazine 105: 116–123.
- WESTHOFF, V. & DEN HELD, A. J. (1969). Plantengemeenschappen in Nederland. Thieme, Zutphen.
- WHEELER, B. D. & GILLER, K. E. (1982). Status of aquatic macrophytes in an undrained area of fen in the Norfolk Broads, England. Aquatic botany 12: 277-296.

WILLKOMM, M. & LANGE, J. (1861). Prodromos Flora Hispanicae. E. Schweizerbart, Stuttgart.

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