

PROJECT 352

DATABASE AND ATLAS OF AQUATIC VASCULAR PLANTS IN THE BRITISH ISLES

Part I : Species Accounts

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Database and Atlas of Aquatic Vascular Plants in the British Isles

Part I: Species Accounts

C D Preston and J M Croft

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Research Contractor:
Institute of Freshwater Ecology
Monks Wood
Abbots Ripton
Huntingdon
Cambridge
PE17 2LS

National Rivers Authority
Rivers House
Waterside Drive
Almondsbury
Bristol
BS12 4UD

Project Record 352/2/N&Y

ENVIRONMENT AGENCY



136210

Commissioning Organisation

National Rivers Authority
Rivers House
Waterside Drive
Almondsbury
Bristol
BS12 4UD

Tel: 01454 624400

Fax: 01454 624409

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This document provides information on the occurrence and distribution of aquatic plants in Britain and provides a valuable source of data for NRA staff..

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Institute of Freshwater Ecology
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PE17 2LS

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The NRA's Project Leader for Project 352 was:
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No further copies of this document are available. Both volumes of the Project Record will be incorporated into a book to be published in Spring 1996 as "An Atlas of Aquatic Vascular Plants in Britain and Ireland" by Harley Books, Colchester, Essex.

Project Record 352/2/N&Y

CONTENTS

PAGE

SUMMARY

1

INTRODUCTION

3

SPECIES ACCOUNTS

5

REFERENCES

303

INDEX

351

SUMMARY - VOLUME I

The objectives of the Atlas and Database of Aquatic Plants Project are to develop a database of the distribution of aquatic plants in Britain and Ireland, and to prepare summaries of the data for publication. The project is funded by the Joint Nature Conservation Committee, the National Rivers Authority and the NERC Institute of Terrestrial Ecology.

This report consists of draft accounts of the families, genera, species and subspecies covered by the project. The habitat and reproductive biology of each species is outlined, trends in its British and Irish distribution discussed and its world distribution is summarised. Additional notes on other topics of interest are sometimes provided.

The text should be read in conjunction with the distribution maps, Volume II. The text will be revised in the light of any comments received from referees and the modified text, maps and necessary introductory material and illustrations will be submitted to Harley Books for publication as a book, *Aquatic Plants in Britain and Ireland*.

INTRODUCTION

The objectives of the Database and Atlas of Aquatic Plants Project are :

1. to develop a database on the distribution of aquatic plants;
2. to prepare summaries of the data for publication as a book *Aquatic Plants in Britain and Ireland*.

The project is jointly funded by the Joint Nature Conservation Committee (JNCC), the National Rivers Authority (NRA) and the Institute of Terrestrial Ecology (ITE). It builds on the existing records of aquatic plants held by the Biological Records Centre (BRC) at ITE Monks Wood.

An outline of the project is provided in an earlier report (Preston *et al.*, 1993). Distribution maps of the taxa covered by the project are also included in that report. This report consists of text to accompany these maps.

The species covered by the project are those vascular plants in Britain and Ireland which characteristically grow in permanent fresh or brackish water. They include submerged macrophytes, free-floating species and emergents which are rooted in permanent water but have aerial leaves. The project excludes plants which are not usually found in permanent water but which are rooted in floating masses of vegetation, or occur in seasonally flooded sites, fens or bogs. The dividing line between land and water is not clear-cut, but is marked by seasonal and non-seasonal fluctuations and more gradual changes. It cannot, therefore, be expected that there will be a clear division between terrestrial and aquatic plants, and many species have actually evolved to exploit the various transition zones between land and water. Many species undoubtedly qualify for inclusion under our criteria, but decisions about borderline cases are inevitably somewhat arbitrary. As the dividing line is so fuzzy, we have had no hesitation in occasionally including borderline species when it was convenient to do so: we have, for example, included both *Ranunculus hederaceus* and *R. omiophyllus* in order to provide an account of all the species in *Ranunculus* Subgenus *Batrachium*.

During the preparation of the text, it has become clear that a few changes need to be made to the list of species covered by the project to bring it into line with the criteria outlined above. A number of species are mapped by Preston *et al.* (1993) but have subsequently been dropped and are not included in this report: these are *Carex appropinquata*, *C. nigra*, *Equisetum palustre*, *Hydrocotyle vulgaris*, *Iris versicolor*, *I. × robusta*, *Lythrum salicaria*, *Mentha aquatica*, *Ranunculus lingua* and *Typha × glauca*. Most of these can be found in permanent water but are not sufficiently frequent in this habitat to qualify for inclusion. However, we have added *Carex recta*, *Hydrocotyle ranunculoides*, *Ranunculus reptans* and *R. × levenensis*.

There are only three species of vascular plants which grow in sea water in our area, namely *Zostera angustifolia*, *Z. marina* and *Z. noltii*. These are not covered by this project but accounts of all three are provided by Stewart *et al.* (1994).

The numbering of the families and the genera follows Kent (1992). The scientific names of

British and Irish taxa are taken from Kent (1992) and the English names from Stace (1991). Synonyms are not given in the accounts of individual taxa, but synonyms which have been in recent use are included in the index.

The text which follows gives a brief account of each family covered by the project. This attempts to set the British and Irish representatives in the context of the family as a whole. The accounts of the genera and species in the family follow. The generic accounts also attempt to set our species in the world context. If certain information is common to all the members of a genus this is usually given in the generic account rather than repeated under each species. The generic accounts are therefore variable in length, and tend to be short if there is only one aquatic plant in the genus in our area. *It is important that the reader should realise that the account of the genus and that of the species should both be read to obtain all the information about the species.*

The first paragraph of each species account describes the habitat in Britain or Ireland. The altitudinal limit is given, and 'lowland' denotes altitudes less than 300 m. The altitudinal limit may not be given explicitly for plants which are clearly confined to the lowlands (e.g. certain coastal species). The next paragraph outlines the reproductive biology and the third paragraph discusses any historic trends in the distribution in Britain and Ireland. If a species is thought to be under-recorded, this is mentioned here. The world distribution is described in the fourth paragraph. Other information may be added in a fifth paragraph.

The species accounts presented here are final drafts. Some points which still require clarification are identified in bold in the text, and full details of a few references still need to be added. The maps and text, together with introductory material and illustrations, will be submitted to Harley Books on 10 July 1995 for publication as a book *Aquatic Plants in Britain and Ireland*.

3. ISOETACEAE

The Isoetaceae is a small and taxonomically isolated family of pteridophytes. In addition to *Isoetes*, it includes only one other genus, *Stylites*, which is endemic to the Peruvian Andes.

3/1. *Isoetes* L.

Isoetes is a genus of c. 100 species, of which 11 are recognised in Europe. They have linear leaves (or 'sporophylls') arising from a bulb-like structure or 'corm'. The base of the sporophyll is expanded and contains a sporangium. The large female megaspores and the smaller male microspores are borne in sporangia on separate sporophylls on the same plant. The spores are released as the sporophylls die and decay. Both male and female prothalli develop within the spore walls, the mobile male gametes emerging from the microspores to effect fertilisation.

The simple structure of *Isoetes* offers few characters to the taxonomist, and this (coupled with extreme phenotypic plasticity) means the taxonomy of the genus has always been difficult. Recent evidence indicates that interspecific hybridisation can take place in the genus, and that some species have arisen as fertile allopolyploids (Hickey *et al.*, 1989). There are still a number of taxonomic problems to be resolved even in Europe. Three *Isoetes* species are known in Britain and Ireland, two of which are aquatic (*I. echinospora*, *I. lacustris*) and one terrestrial (*I. hixtrix*, a rare Mediterranean-Atlantic species restricted in our area to S.W. England and the Channel Islands). Plants which are apparently intermediate between *I. echinospora* and *I. lacustris* have recently been found in Britain (Camus *et al.*, 1988). Their taxonomic status has still to be elucidated and they are not considered further in this account.

The aquatic *Isoetes* species exemplify the 'isoetid' growth habit. Isoetids have a rosette of short stiff leaves (often with extensive internal air spaces) arising from a short stem. This growth habit is found in a number of other British and Irish species in unrelated families: *Subularia aquatica* (Brassicaceae), *Littorella uniflora* (Plantaginaceae), *Lobelia dortmanna* (Campanulaceae) and *Eriocaulon aquaticum* (Eriocaulaceae). These plants are so similar in habit that they are sometimes confused by field botanists. Isoetids are found in nutrient-poor habitats, often in areas which are disturbed by wave-action. They are slow-growing, evergreen plants. A high proportion of their biomass is accounted for by their roots, which are often mycorrhizal (Farmer & Spence, 1986). They are unable to utilise bicarbonate ions as a source of CO₂, and are thus restricted to using CO₂ in the sediment in which they grow. It has recently been shown that *Isoetes* species and *Littorella uniflora* possess Crassulacean Acid Metabolism (CAM), a photosynthetic pathway more usually associated with desert succulents (Keeley, 1982, Farmer & Spence, 1985). This pathway allows carbon dioxide to be accumulated at night in malic acid, which is then released in the day and used in photosynthesis. Desert plants are thus able to minimise water loss by opening the stomata at night. The CAM pathway allows *Isoetes* and *Littorella* to recycle CO₂ released into the leaf lacunae at night by respiration, a valuable adaptation for plants which characteristically grow in habitats where the inorganic carbon content is low (Boston, 1986).

I. lacustris is a characteristic species of oligotrophic lakes. It usually grows over rocky substrates with skeletal soils or over base-poor sands or clays, being absent from silty mud. Scattered plants often grow in shallow water at the edge of lakes, where they are frequently accompanied by *Littorella uniflora* and *Lobelia dortmanna*. However, the species is usually more frequent at greater depths and it can be the dominant (and sometimes the only) macrophyte at depths below 1.5-2.5 m. It has been recorded in water as deep as 6 m at Loch Lundie (West, 1905). The freshwater sponge *Spongilla lacustris* is often a conspicuous associate in these deep water stands (Spence, 1964). In addition to natural lakes, *I. lacustris* has also colonised artificial reservoirs and the Muirtown Basin of the Caledonian Canal. It is recorded from sea-level to 825 m at Ffynnon Llyffaint.

Little information is available about the reproduction of *I. lacustris* in Britain or Ireland, but the presence of small plants at the edge of lakes suggests that establishment from spores is not infrequent. Laboratory studies of the closely related *I. macrospora* Durieu in N. America showed that neither megaspores nor microspores required a cold treatment for germination (Kott & Britton, 1982). A high proportion of megaspores germinated (an average of 87%), the maximum germination being reached in 45 days or less. Megaspores from dried plants failed to germinate. *Isoetes* lacks any means of vegetative reproduction.

I. lacustris was clearly under-recorded in the *Atlas of the British Flora* (Perring & Walters, 1962), presumably because it is most abundant in deeper water and scattered plants are easily overlooked when growing with *Littorella uniflora* in the shallows. It is probably still under-recorded in areas which have not been covered by intensive surveys. There is little evidence for any major decline in *I. lacustris* in Britain or Ireland. Like other isoetids, it is extinct at some of its more easterly sites, which are now eutrophic, and other such populations are probably vulnerable (Farmer & Spence, 1986). It formerly grew, for example, at Bomere Pool but, like *Lobelia dortmanna*, it is now extinct there (Sinker *et al.*, 1985). It has been suggested that *I. lacustris* and other isoetids have declined in Scandinavia as a result of acidification. The evidence is discussed by Rørslett & Brettum (1989), who conclude that it is extremely scanty. There is much clearer evidence of a decline in The Netherlands, where acidification has followed the increased input of ammonium into water bodies in recent years. **Add reference here.**

I. lacustris is frequent in Europe north of *c.* 53°N; it extends south as scattered populations to N. Spain (Jalas & Suominen 1972). *I. lacustris sensu lato* (including the N. American species *I. macrospora* and *I. occidentalis*, which may be conspecific with it) has a circumboreal distribution.

Over much of its British and Irish range *I. echinospora* grows, like *I. lacustris*, in oligotrophic lakes; it has also been found at the edges of slow-flowing rivers and in pools. It occurs over a wide range of nutrient-poor substrates including rocky and stony areas, base-poor sands and gravels, sandy mud or silt and peaty deposits. In Shetland it favours a finer substrate than *I. lacustris* and apparently prefers the sheltered S. and W. sides of lochs (Scott & Palmer, 1987); this is probably true elsewhere in Britain. Although it usually grows in oligotrophic sites, *I. echinospora* has occasionally been found in eutrophic lakes, notably Llyn Llygerian and Llyn Llywenan in Anglesey (Seddon, 1965). Here it is found in areas where the growth of emergent species is restricted by rocky outcrops or by heavy wave action. *I. echinospora* has colonised an artificial reservoir in Cumbria, flooded gravel pits at Capel Bangor and disused clay pits in Dorset and Devon. It ascends from sea-level to 470 m at Llyn Glas.

Little or no information is available about the reproduction of *I. echinospora* in Britain or Ireland. Experimental studies in N. America have shown that a cold period of 4°C for 12 weeks stimulates megaspore germination, but even with such a treatment total germination was very low (15%). Spores subjected to shorter pretreatments and control samples failed to germinate as did megaspores from dried specimens. Microspores germinated without a cold pretreatment but a 4°C pretreatment for 12 weeks resulted in a higher percentage germination (Kott & Britton, 1982). It would be interesting to know if *I. echinospora* from Britain and Ireland has similar requirements.

Although *I. echinospora* often has more flaccid, gradually tapering leaves than *I. lacustris*, the two species can only be identified with certainty by microscopic examination of the megaspores. Although *I. echinospora* has been known from [add first record here] it is almost certainly under-recorded both because *Isoetes* plants are themselves often overlooked and because *I. echinospora* may be assumed to be *I. lacustris* or not noticed when the species are growing together. Fossil evidence indicates that *I. echinospora* has been present in Britain from the late Weichselian onwards, and long-term persistence through the Flandrian has been demonstrated at some sites (Godwin, 1975). The botanical records are insufficient to provide any evidence of change in its distribution since it was first reported in 18??.

I. echinospora has a similar European range to *I. lacustris*: it is frequent in N. Europe and present as very scattered populations south to N. Spain and Greece (Jalas & Suominen, 1972). *Isoetes echinospora sensu lato* is a very variable and taxonomically complex species which has a circumboreal distribution, with isolated occurrences in Barbados and Chile.

I. echinospora and *I. lacustris* are ecologically similar in Britain and Ireland, and can grow together (Stokoe, 1978). In Scandinavia *I. lacustris* "occurs mainly in oligotrophic to mesotrophic lakes" whereas *I. echinospora* "is a ubiquitous species of clayey riverside habitats and intermittently dried-out mudflats", also occurring in dystrophic lakes, clear-water lakes, turbid eutrophicated sites and in slightly brackish water (Rørslett & Brettnum, 1989). This suggests that *I. echinospora* has a much wider habitat range in Scandinavia than in Britain or Ireland, with a correspondingly clearer distinction between *I. echinospora* and *I. lacustris*. In Scandinavia *I. echinospora* tends to occur in shallower water than *I. lacustris* (although there is considerable overlap between the two species). Unfortunately, critical observations on the depth at which *I. echinospora* grows in Britain are not available.

4. EQUISETACEAE

This family contains a single extant genus, *Equisetum*. The species of *Equisetum* are the only living representatives of the Sphenopsida, a class which is known from fossil evidence to have been in existence for over 250 million years. In the Upper Carboniferous members of the class included both tall trees which were co-dominant in the coal-measure swamp forests and herbaceous plants similar to modern *Equisetum* species.

4/1. *Equisetum* L.

A small genus containing 15 species (Hauke, 1974). The genus is widespread in both hemispheres, but is absent from Australia and New Zealand. Cook (1990) classifies two species as aquatics, and several others are plants of damp or wet terrestrial habitats. Descriptions of the ecology of the British and Irish taxa are given by Page (1982, 1985, 1988) and their distributions are mapped by Jermy *et al.* (1978).

The genus is divided into two subgenera. The species in subgenus *Equisetum* have annual stems which develop in the spring and die back in autumn; the cones are obtuse. The species in subgenus *Hippochaete* (Milde) Baker usually have persistent stems and the cones are apiculate. Both subgenera have been monographed by Hauke (1963, 1978). Representatives of both subgenera occur in our area but the taxa treated here are in subgenus *Equisetum*.

Equisetum species are rhizomatous perennials. The jointed stems are the main photosynthetic structures; they often have whorls of branches at the nodes. The leaves are reduced to inconspicuous scales. The sporangia are borne in cones at the apex of the stems or, in some non-European species, at the end of the branches. The plants are homosporous and the short-lived spores germinate to produce prothalli which are green and photosynthetic. In *Equisetum* subgenus *Equisetum* the prothalli are either male or bisexual; the bisexual individuals initially produce archegonia and later develop antheridia. Detailed studies of the reproductive biology of species in this subgenus have been published by Duckett (1970a,b,c, 1979) and Duckett & Duckett (1980).

Hybrids have been recorded between species within a subgenus, but not between members of different subgenera. They normally become established on moist, freshly exposed soil surfaces. They are partially or totally sterile but can form persistent clones which spread by growth or fragmentation of the rhizome. There is a particularly rich concentration of hybrids in western Britain and Ireland, where the chances of hybridisation and the subsequent establishment of hybrid clones may be favoured by the oceanic climate (Page, 1985).

E. fluviatile is found in fens and as an emergent in swamps. It grows in a wide range of water bodies from ditches and small ponds to large lakes and the sheltered backwaters of rivers, growing in marshes and fens and as an emergent in standing water. In fens it occurs as scattered stems in closed vegetation where the dominant species are often tall sedges; common fen species such as *Galium palustre*, *Menyanthes trifoliata*, *Potentilla palustris* and *Calliergon cuspidatum* are amongst the most frequent of its numerous associates. It can also be found in open fen carr. In small lakes and the more sheltered bays of larger lakes it is frequently found with *Carex rostrata* in swamps where the water is at least 0.3 m deep; in shallower water it is usually replaced by *C. rostrata*. In more exposed lakes it forms open stands in water up to 1.5 m deep; here it often grows in the absence of other emergents but with a range of aquatics with submerged or floating leaves including *Littorella uniflora*, *Myriophyllum alterniflorum*, *Potamogeton natans* and *P. gramineus*. *E. fluviatile* is a species with a notably wide ecological amplitude, not only tolerating a range of water depths but also found in oligotrophic, mesotrophic and eutrophic water and over a variety of aerobic to highly anaerobic substrates including inorganic sands, clays, and muds with an appreciable organic content. It extends from sea level to 550 metres at Pin Seat (Wilson, 1956) and up to 900 metres in the Breadalbanes (White, 1898). There is an unlocalised record from 1050 metres (Grime *et al.*, 1988). **CHK NVC swamp descriptions.**

The spores of *E. fluviatile* are released as soon as the cones are mature. The normal period of release is from mid-May to the end of June; a few fertile shoots are sometimes produced throughout the summer and spores can continue to be released from these into September (Duckett 1970a). The spores are short-lived (Duckett 1970b). The gametophytes require newly exposed, bare mud on which to develop and are typically found around the edge of reservoirs where the water-level fluctuates markedly or on mud left when lakes have been drained. Gametophytes only develop into sporophytes if the mud remains exposed above the water during the subsequent winter. For a detailed description of the ecology of the gametophyte, see Duckett & Duckett (1980). Established stands of *E. fluviatile* spread vegetatively by means of the extensive rhizome system. Stems are often detached by waterfowl or broken off by waves, and even short lengths root from the nodes when floating on water or stranded on wet mud (Praeger, 1934b).

E. fluviatile is a distinctive species. It has presumably decreased in abundance in areas where wetlands have been drained in historic times. It is widespread and locally abundant in Britain and Ireland and in most of our area there is no evidence to suggest that its distribution is changing. In the London area Burton (1983) suggests that it may have been eliminated from some sites by *Typha latifolia*, which has become more frequent in recent years.

E. fluviatile is widespread in the boreal and temperate zones throughout the northern hemisphere. In Europe it is frequent from Iceland and northern Scandinavia south to France, northern Italy and Romania, but rare in the Mediterranean region (Jalas & Suominen, 1972).

The ecological requirements of *E. fluviatile* and *Schoenoplectus lacustris* are rather similar, but Spence (1964) comments that they can rarely be found together in Scottish lakes. The reasons for this are unclear.

As a hybrid between a terrestrial and an aquatic species, *E. × litorale* can be found in a wide variety of moist lowland habitats, and occasionally in water up to 0.3 m deep. Many of its sites are on marshy ground near bare or disturbed soil. It has been recorded from the edge of quarry pools, ponds, lakes, reservoirs, streams and rivers, the dried-out beds of canals, moist ditches, roadsides and railway cuttings, open peaty mud in bogs, damp pastures, open willow scrub and the edges of moist woods. In the Hebrides it is particularly frequent by the eroding edge of streams flowing over shingle or machair, where *Iris pseudacorus* is a characteristic associate (Page 1988). The hybrid can form large and vigorous stands which may displace the parent species. Some colonies along streams and canals can extend for over 1.5 kilometres. Like the parents, it is found over a wide range of substrates from calcareous sand to acidic peat.

E. × litorale produces cones, although cone-bearing stems are infrequent in some colonies. The spores are infertile. Clones spread by the growth of rhizomes, and perhaps also by water-borne shoot fragments. Experiments in North America have shown that cut stems of the hybrid can become established if they are buried in mud, and rhizome fragments can regenerate even if placed on the surface of the mud. The ability of the hybrid to regenerate in this way is greater than that of its parents (Peck, 1980).

E. × litorale has been known from Britain since 1886, when it was first reported (as a species) by Beeby (1886), but for many years it was regarded as a very rare plant. It was discovered in Ireland by Praeger (1917), who subsequently found it in numerous Irish sites. It is still overlooked by many botanists and is probably much more frequent than the map suggests. Like other *Equisetum* hybrids, it is probably more frequent in northern and western areas than in the south and east.

The distribution of *E. fluviatile* is described under that species; *E. arvense* is even more widespread. *E. × litorale* is the most frequent hybrid in the genus, having been recorded at many localities in Europe and North America.

This is a variable hybrid, but the variation is thought to be environmentally induced (Duckett & Page, 1975). The hybrid nature of this taxon has been demonstrated by cytological studies (Manton, 1950) and by the artificial synthesis of the hybrid. In experimental studies the hybrid has only been synthesised with *E. fluviatile* as the female parent; attempts to produce the reciprocal hybrid have been unsuccessful (Duckett, 1979).

9. MARSILEACEAE

This is a small and taxonomically isolated family of aquatic ferns, containing three genera and some 72 species. *Marsilea* is the largest genus; the 65 species are found in tropical and warm-temperate areas north to southern Europe. *Pilularia* is the only genus in Britain and Ireland.

9/1. *Pilularia* L.

Two of the six *Pilularia* species occur in Europe, but only one is represented in the British Isles. The species are rhizomatous and have erect, thread-like leaves which lack a lamina. The sporangia are borne in spherical sporocarps ('pills') which form in the axils of the leaves. Both megasporangia and microsporangia are found in the same sporocarp. The unit of dispersal is probably the sporocarp, which dehisces to release the spores.

This is a plant of lowland, non-calcareous silty or peaty lake and pond margins, ditches and shallow pools. It is an opportunist species, which can rapidly colonise an open substrate exposed by falling water levels or created as a result of gravel or brickearth extraction. Characteristic associates include *Apium inundatum*, *Hydrocotyle vulgaris* and *Ranunculus flammula*. Some colonies on newly disturbed ground may be short-lived but the plant can persist in lakes and reservoirs, appearing in abundance when water levels are low (cf. Stewart 1988). Occasionally it maintains itself in denser plant communities as a submerged aquatic in base-poor pools, or in fens with *Carex diandra*, *Menyanthes trifoliata*, *Calliergon cuspidatum* and other pleurocarpous mosses. *P. globulifera* is not a competitive species, and at some of its sites suitable conditions are maintained by the trampling of cattle and horses. Most sites are at low altitudes, but the species is recorded up to 380 metres (Page, 1982 - where?).

P. globulifera is a perennial which dies back during the winter, but some 'sub-evergreen fragments' persist and regrow in the following spring (Page, 1982). Sporocarps are formed in most populations except those in permanent deep water. Field observations suggest that the spores can remain viable for many years, but there is no hard evidence for this. Spores released from the sporocarp in late summer can develop through the gametophyte stage to produce new sporophytes within 17 days.

Pilularia was lost from many sites before 1930, largely because of habitat destruction. It is an inconspicuous species which was recently the subject of a special survey led by A.C. Jermy (ref?), but which may still be under-recorded in northern and western areas. The current distribution is probably stable: the species may disappear from some sites as a result of successional changes but these losses will perhaps be balanced by the colonisation of new areas.

P. globulifera is endemic to western Europe, with lowland areas in Britain, France, northern Germany and southern Sweden containing the bulk of the populations and outliers extending to Portugal, Italy and Czechoslovakia (Jalas & Suominen, 1972). It is decreasing in much of mainland Europe and the British sites are therefore particularly significant in a national context.

19. AZOLLACEAE

The Azollaceae is a small family of pteridophytes which contains a single genus, *Azolla*.

19/1 *Azolla*

Azolla is a very distinctive genus of 6 rather similar species. The sporophytes are small free-floating plants with pinnately branched stems which bear scale-like leaves and pendulous roots. The leaves have an upper photosynthetic lobe, which is borne above the surface of the water, and a lower colourless lobe which rests on the water. The lower lobe is usually inhabited by the cyanobacterium *Anabaena azollae* Strasburger. The presence of this nitrogen-fixing organism has led to the use of *Azolla* in E. Asia as a food for livestock and as a green manure for rice fields, a practice which originated in China at least 2000 years ago, (Shi & Hall, 1988).

Sporocarps of two different sizes are produced on the lower surface of the mature frond. The smaller sporocarps contain microsporangia which produce the mobile male gametes. These fertilise the megaspores in the larger sporocarps. After fertilisation the embryo develops within the wall of the megaspore until the first leaf grows, when it emerges as a free-floating sporophyte. For an illustrated account of the life-cycle of *Azolla* and a taxonomic review of the species, see Tan *et al.* (1986).

Azolla caroliniana Willd. has been reported from Britain and Ireland, but all records are referable to *A. filiculoides*. *A. caroliniana* is 'the least understood species in the genus' (Tan *et al.* 1986); plants from mainland Europe hitherto named *A. caroliniana* are referred to *A. mexicana* by Lawalrée & Jermy (1993).

Azolla filiculoides Lam. Water Fern

A small but highly gregarious floating fern, which can occur in abundance on the surface of lowland canals, ditches, ponds and small lakes or in the sheltered backwaters of larger water bodies. Dense stands exclude almost all competitors; less dense aggregations are often intermixed with *Lemna gibba*, *L. minor* and *L. minuta*. *Ceratophyllum demersum* and *Elodea canadensis* or *E. nuttallii* often grow under the *Azolla* layer. *Azolla* is most frequent in eutrophic, calcareous waters and is often particularly frequent in ditches near the sea.

Plants are dispersed by water and, according to Page (1988), perhaps also as fragments on the feet or feathers of birds. They increase very rapidly in the summer by clonal spread; colonies develop a striking red colour in autumn and persist into the early winter but then break up and disappear from view. Regeneration in the spring is thought to be from surviving fragments. However, examination of herbarium specimens shows that sporocarps are regularly produced and British and Irish populations may therefore reproduce sexually.

Like *Rhododendron ponticum*, *Azolla* was native to Britain and mainland Europe in previous interglacials (West, 1953; Tralan, 1959; Godwin, 1975) but in this interglacial it only occurs as an introduction. In Britain it was first recorded at Pinner in Middlesex in 1883, but did not become well-established until some 25 years later. By 1914 it was well naturalised in the Thames valley and Norfolk Broads, and had been recorded at other scattered localities (Marsh, 1914). In Broadland its spread was assisted by floods in 1912. It has continued to spread, and established populations doubtless arose from several different introductions. It can invade a region very rapidly, but although persistent at some sites it only survives for a few years at others or reappears after long intervals. There is much anecdotal evidence about the fluctuations of *Azolla* but an absence of critical study. Sporophytes have been eliminated from particular sites by hard winters (cf Muscott, 1983). It is not known whether populations can overwinter as spores even if mature sporophytes are killed. Warm summers apparently favour *Azolla*.

A. filiculoides is a native of N. & S. America which is now widely naturalised elsewhere. In Europe it is widespread south of 55° N, but does not extend into colder latitudes (Jalas & Suominen, 1972).

26. NYMPHAEACEAE

This family includes the familiar water-lilies in the genera *Nuphar* and *Nymphaea*, as well as four small genera native to S. and E. Asia, S. America and Australia. Most members of the family have floating leaves and emergent flowers; many species also have delicate submerged leaves and in a few species these are the only leaves present. The non-European genera include the giant water-lily *Victoria amazonica*.

Mabberley (1987) has stressed the fact that the family, although classified in the dicotyledons, has many of the characters of the monocotyledons. The individual species possess characters which are not normally found in members of the same family (eg inferior and superior ovaries, orthotropous and anatropous ovules). Mabberley suggests that they are successful, specialised relics of a primitive stock which existed before the monocots were distinct from the dicots. They were able to penetrate temperate latitudes from a presumably tropical origin as they are rhizomatous plants which can over-winter in the buffered under-water environment.

26/1 *Nymphaea*

A genus of c.40 species, of which 4 are native to Europe. There is no recent monograph of the genus, and even in Europe there are unsolved taxonomic problems. These arise partly from the variability of the species, and the apparent occurrence of natural hybrids, and partly from the artificial hybridization of species by horticulturists followed by the planting of such hybrids in ornamental waters or semi-natural habitats. In addition to the native *N. alba* treated below, plants of horticultural origin have been planted in Britain in disused gravel pits and other waters managed by anglers. They can usually be recognised by their pink-tinged or yellow flowers. Stace (1992) states that most are hybrids of *N. alba*, but suggests that they need further study. A detailed account of the ecology of *N. alba* in Britain and Ireland is provided by Heslop-Harrison (1955b).

N. alba often grows in abundance in the still water of lakes, ponds and pits, and in slowly-flowing large ditches and the backwaters of lowland rivers. It is usually found at depths of 0.5-1.5 m in open water or in very sparse stands of emergents, but it can grow in very shallow water, and is even found with aerial leaves in swamps in W. Ireland (Praeger, 1934) and Broadland (Wheeler, 1980). In lakes stands of *N. alba* are often bordered on the landward side by emergents, and in deeper water by *Potamogeton natans* or submerged species. Stands of *N. alba* are usually species-poor, and few species occur as associates with any degree of constancy (Heslop-Harrison, 1955b; Spence, 1964). The species tolerates a wide range of water chemistry from oligotrophic and mesotrophic lochs to eutrophic lakes and rivers. It is, however, notably intolerant of disturbed and turbid water, and in windswept areas it is usually confined to small lakes and sheltered bays. It is also absent from rivers and canals with appreciable boat traffic. It occurs over a range of fine-grained substrates including peat, sand, silt, marl, mud and clay. Although primarily a lowland species, it is recorded up to 456 m at Angle Tarn, Place Fell.

N. alba is a rhizomatous perennial which, when mature, only possesses floating leaves. It sheds its leaves in autumn, coming into leaf in spring and flowering from early June to late August. The flowers close at night and open during the day. They are visited by insects but pollen is shed directly onto the stigmas and cross-pollination is probably not essential for fertilisation. After fertilisation the peduncles coil and draw the fruits under water, where they mature and eventually burst. The arillate seeds can float for 1-3 days (often in a mass resembling frogspawn) before sinking. Floating seeds are often eaten by birds and fish, which digest them completely and are therefore unlikely to act as agents of dispersal. The seeds have no adaptations to facilitate transport by animals and are also unable to withstand 28 days' desiccation. Natural dispersal is probably dependant on transport by water. The seeds do not germinate in the season when they are shed. Thereafter germination is erratic, and in favourable years large crops of seedlings can be found. Germination is possible in anaerobic conditions. For details of the reproductive biology of the species see Heslop-Harrison (1955b), Smits & Wetzels (1986), Smits *et al.* (1989) and Van der Velde (1986).

N. alba is certainly native in both Britain and Ireland; pollen evidence shows that *Nymphaea* was present throughout the late Weichselian and Flandrian. Its exact native distribution is more difficult to determine. It is clearly native in much of W. Scotland, N.W. England and W. Ireland, although even in Shetland the situation has been confused by introductions (Scott & Palmer, 1987). Its status in S.E. England has been greatly obscured by the drastic modification of natural river systems and the popularity of the species as an ornamental plant. It is probably less frequent as a native plan in S.E. England than the map suggests. In recent years some stands of *N. alba* have been lost through excessive eutrophication [is this true? **What has happened in Broads?**], but these have been counterbalanced by the planting of *N. alba*, or related hybrids, in new localities.

N. alba is widespread in Europe, reaching 66° N in Norway; it is, however, scarce in the Mediterranean region. It is also recorded from N. Africa and W. Asia. In N.E. Europe and much of Asia it is replaced by the closely related *N. candida*, with which it hybridises. For maps of both taxa, see Jalas & Suominen (1989) and Hultén & Fries (1986).

Plants of *N. alba* in Britain and Ireland are variable in size. Small populations in oligotrophic sites in N. and W. Scotland and W. Ireland have been distinguished as *N. alba* subsp. *occidentalis* (Ostenf.) Hylander. The consensus of opinion is that these plants do not merit taxonomic recognition (Heslop-Harrison, 1953a, 1955b; Tutin *et al.*, 1993), and few observers have recorded subsp. *occidentalis* in recent years. However, the subspecies has recently been taken up by Stace (1991). The map excludes records known to be cultivated water-lilies doubtfully referable to *N. alba*, but some of these will almost certainly have been reported as *N. alba* and will consequently appear on the map.

The taxonomy of this genus is more problematical than that of *Nymphaea*, and Cook (1990) can only estimate the number of species as between 7 and 20. Most authors, including Stace (1991) and Tutin *et al.* (1993), recognise two native species in Britain and Europe, *N. lutea* and *N. pumila*, with the hybrid *N. × spenneriana*. In addition, the alien *N. advena* has recently been recorded from Britain. Beal (1956) considers that both *N. pumila* and *N. advena* are subspecies of a very broadly defined *N. lutea*. For an account of the ecology of all three native taxa in Britain and Ireland, see Heslop-Harrison (1955a).

N. lutea is a plant of mildly acidic or basic, mesotrophic or eutrophic water in lakes and in slowly-flowing lowland rivers, canals and large drains and ditches. It is normally found in open water at depths of 0.5-2.5 m, but it has been recorded as deep as 3.6 m. Stands of *N. lutea* are at least as species-poor as those of *Nymphaea alba*; *Elodea canadensis*, the aquatic form of *Juncus bulbosus*, *Littorella uniflora* and *Potamogeton obtusifolius* are the most frequent associates recorded in Scottish lochs (Spence, 1964). Although it is tolerant of a range of water chemistry, *N. lutea* does not extend into sites which are as base-poor and oligotrophic as those tolerated by *Nymphaea alba*. Consequently it is rare in N.W. Scotland and the Hebrides and absent from Shetland. In richer lakes the species can often be found at the same site, with *N. lutea* usually growing in slightly deeper water than *N. alba*. *N. lutea* is notably more tolerant of mechanical disturbance than *N. alba*, and it can often be found along the edge of rivers and canals which carry considerable boat traffic. In very disturbed sites it persists as plants with submerged leaves which rarely produce floating leaves or flowers. *N. lutea* is usually found over mud or silt and rarely over peat; in rivers it is particularly characteristic of clay substrates (Holmes, 1983). Although primarily a lowland plant, it ascends to 510 m at Llyn Crugnant.

N. lutea over-winters as a rhizome, producing translucent submerged leaves in early spring and coriaceous floating leaves in April and May. It flowers from June to August. The flowers, which remain open at night, are not automatically self-pollinated, but are visited by insects which may effect either self- or cross-pollination. The fruits ripen above the water. The seeds are embedded in the spongy tissue of the carpel, which normally sinks within a day of its release. The seeds resemble those of *N. alba* in lacking morphological adaptations for animal dispersal, and in being killed by desiccation and completely digested when eaten by birds or fish. The main chance of dispersal must be by water movement. Otherwise long-distance dispersal must be a rare event: Heslop-Harrison (1955a) found viable seed in the excreta of a heron which had presumably eaten a fish which had been recently feeding on *N. lutea*! A proportion of seeds can germinate in the year they are shed. Germination can take place in anaerobic conditions, but is erratic. In some years enormous numbers of seedlings can be found in favourable localities, but few survive to maturity. For further details of the reproductive biology of the species, see Heslop-Harrison (1955a), Smits & Wetzels (1986), Smits *et al.* (1989) and Van der Velde (1986).

The fossil history of *N. lutea* is well documented, and Godwin (1975) concludes that it has probably persisted in the British Isles right through the Pleistocene, though with a restricted distribution in glacial periods. Its distribution has doubtless been somewhat modified by planting, but it is now less frequently introduced into semi-natural habitats than *Nymphaea alba*, probably because it is less suited to the shallow waters of ponds and gravel pits. It is still a frequent plant in S. England.

N. lutea has a similar distribution in Europe to *Nymphaea alba*, being widespread up to 66° N but scarce in the Mediterranean region (Jalas & Suominen, 1989). It is more frequent in N.E. Europe than *N. alba*, occurring in the areas where that species is replaced by *Nymphaea candida*, and extends much further east in Asia. Related species occur in N. America (Hultén & Fries, 1986).

Nuphar × *spenneriana* Gaudin (*N. lutea* L. × *N. pumila* (Timm.) DC.) Hybrid Water-lily

This hybrid is found in oligotrophic and mesotrophic lakes, pools, rivers and streams. It is recorded from water up to c. 2 m deep over both peat and mineral soil. At some sites it can occur in abundance in the absence of both parents, a notable example being Chartners Lough where *N. × spenneriana* covers almost the whole area of the lake and "the bottom .. in the area of the *Nuphar* is entirely covered with entangled rhizomes" (Heslop-Harrison, 1953b). Although most localities are lowland, it is found at 476 m in Blea Tarn.

N. × spenneriana, like its parents, is capable of a limited degree of vegetative spread by the growth of its rhizomes. Heslop-Harrison (1953b) suggests that some colonies, such as that at Chartners Lough, may even consist of a single enormous individual of great age. The hybrid is less fertile than its parents, with 85% of the pollen grains and 80% of the ovules being sterile. Nevertheless, some ripe seed is set every year. In cultivation seeds of the hybrid appear to germinate more rapidly than those of the parent species, and develop into vigorous young plants. Seedlings have not been observed in the wild, but the only detailed study of *N. × spenneriana* in Britain has been at Chartners Lough, a site where the cover of mature plants is so great that there is little opportunity for seedlings to become established.

Colonies of *N. × spenneriana* are persistent: the Chartners Lough plant was first found by Sir John Trevelyan before 1824 and is still extant. The hybrid can occur in the absence of both parents and some colonies are a considerable distance from the rarer parent, *N. pumila*. The seeds of *Nuphar* are not adapted to long-distance dispersal, and it seems likely that isolated colonies of *N. × spenneriana* are relic populations dating from a period (perhaps in the early Flandrian) when the parents grew in closer proximity. Unfortunately, direct evidence for this hypothesis from pollen analysis is lacking.

N. × spenneriana is widespread in N. Europe, and extends into Asia. In Britain, it can occur in pure populations in the absence of both parents and in some areas of Lapland it is more frequent than either.

Heslop-Harrison (1953b) investigated the taxonomy of *Nuphar* × *spenneriana* in detail, concluding that it was a partially sterile hybrid between *N. lutea* and *N. pumila*. The mapped records from N. England and Scotland are likely to be correct, but the hybrid may well have been overlooked at other localities or reported as one of its parents. Heslop-Harrison (1975) queried records from Wales, but the record from the southerly locality, Tal-y-llyn Lake, has subsequently been confirmed by Benoit (1984).

This species grows in water 0.6-2.4 m deep in sheltered lakes, the oxbows and sheltered bays of rivers, ditches, and in pools in marshes and bogs. In Scotland it is found in oligotrophic or, more frequently, mesotrophic sites, some of which receive base-rich drainage water. At the isolated sites in Shropshire it is found with *N. lutea* and *Polygonum amphibium* in sheltered bays in base-rich, eutrophic meres over glacial drift. These meres might, however, have been less eutrophic in former times. The species has been planted and is now established at Cow Pond, Windsor Great Park. It is found over a range of substrates including mud, silt and peat. It ranges from near sea-level to 300 m; a record from 520 m near Lochan nan Damh (White, 1898) is probably correct but requires confirmation.

The reproductive biology of *N. pumila* is similar to that of *N. lutea*. Most populations are fertile, but a population at Avielochan shows reduced fertility, probably because the plants have suffered introgression with *N. lutea*. The seeds are unable to survive drying for 28 days. Little is known of their germination, and seedlings have not been seen in the wild.

Although there is no direct fossil evidence of the history of *N. pumila* in Britain, it seems likely that it was widespread in the early Flandrian and has since retreated to its current range. This is consistent with the occurrence of populations of *N. × spenneriana* in the absence of *N. pumila*. Although there are hints in the literature that the Shropshire plants are not native, there seems to be no evidence to support this and the suggestion probably arose from botanists who were unable to accept the possibility of such a disjunct distribution. The Shropshire meres have a rich flora, which formerly included the demonstrably relict *Scheuchzeria palustris*, and Sinker's (1962) conclusion that *N. pumila* is "a probably survivor from early post-glacial times" is the most likely explanation of its presence there. The plant is now restricted to a single site in Shropshire, having been recorded in two others from which it has probably been lost because of eutrophication. There is no evidence of a marked decline elsewhere, but this would be difficult to obtain because of the paucity of reliable historical records.

N. pumila is a circumboreal species. It is frequent in N. Europe; further south it is known from the Alps and from other very scattered localities south to 43 °N in Spain. It extends eastwards at similar latitudes through much of Asia and also occurs in eastern N. America. For maps of its European and world distribution, see Jalas & Suominen (1989) and Hultén & Fries (1986).

The widespread occurrence of the hybrid *N. × spenneriana* was not appreciated by British botanists until the publication of Heslop-Harrison's (1953) paper. Many old records of *N. pumila* are therefore dubious. It is difficult to provide an adequate revision on the basis of herbarium material, as specimens are not available for many localities and are less useful than a survey of population in the field. The mapped distribution is probably broadly accurate, but it may incorporate some errors. A detailed field survey of the British populations of *N. pumila* and *N. × spenneriana* would be worthwhile.

This species is established in a number of lowland lakes and ponds, where it is found in water up to 1.5 m deep. At most of the sites where it has been recorded it has clearly originated from planted stock, but the presence of a large clump of *N. advena* with *Nuphar lutea* and *Nymphaea alba* at Loch Ard is more difficult to explain.

N. advena is a rhizomatous perennial. Little is known of its reproductive biology in Britain, but it has presumably occupied most of its known sites by vegetative spread after planting. Riemer (1985) found that the seeds germinated slowly and sporadically over a long period of time; they were still germinating when he put a stop to his experiments one year after they had begun.

Specimens of *N. advena* were first collected by Miss M. McCallum Webster from an old curling pond at Auchnagairn House, Kirkhill, in 1963, but not identified until 1990. Miss McCallum Webster also noted that the same plant grew in a small loch in the policies of Darnaway Castle. From 1979 onwards the plant was noted at sites in Surrey (in some of which it had clearly been established for a long time), and in 1990 the species was recognised in Loch Ard, where an unidentified exotic *Nuphar* had been noted eight years previously.

N. advena is a native of N. America, where it extends from Wisconsin and Maine south to Mexico and Cuba. In its native range it grows in lakes, ponds, pools in marshes and swamps, ditches, canals and sluggish streams.

This species is related to *N. lutea*, and Beal (1956) treats it as *N. lutea* subsp. *macrophyllum* (Small) Beal. It is unlikely to be overlooked, as the leaves do not float but are held above the water surface, but it may be under-recorded as botanists might have failed to identify it or considered that as an introduced species it was not worth noting.

27. CERATOPHYLLACEAE

This is a small but distinctive family with only one genus, *Ceratophyllum*. The species are so reduced morphologically that the affinities on the family are difficult to assess. Cronquist interprets the Ceratophyllaceae as a highly reduced and specialised member of the Nymphaeales, the order which includes Nymphaeaceae and Cabrombraceae (Mabberley, 1987).

27.1 *Ceratophyllum*

Ceratophyllum lacks roots; the stems float in the water or are anchored to the substrate by buried branches. Small minuscule flowers develop in the leaf axils. The male flowers release anthers which float just below the water surface, shedding pollen into the water. The fruits are small, hard nuts. Little is known of the germination requirements of either species. Vegetative reproduction is probably frequent as plants are brittle and are able to regenerate from fragments. In winter plants sink, regrowing in spring from unspecialised buds.

It is difficult to delimit species in this genus, as taxa which appear to be distinct in one region intergrade in another. The two species recognised in Britain and Ireland were confused until Sandwith (1927) demonstrated that the leaves of *C. demersum* branch once or twice whereas those of *C. submersum* branch three or four times. In a worldwide revision of the genus Wilmot-Dear (1985) recognised only these two species. Each of them shows extraordinary variation in the surface and armature of the fruits, variation that is well-illustrated in Wilmot-Dear's paper. Wilmot-Dear treats these variants as infraspecific taxa, but other authorities have recognised some of them at specific rank.

C. demersum is frequent and sometimes abundant in a wide range of still or slowly-flowing lowland water bodies including lakes, ponds, canals, ditches and sluggish streams and rivers. As it lacks roots it is unable to become established in rapidly flowing water. Murphy & Gaton (1983) noted that in canals it was particularly frequent where boat traffic was low, suggesting that its fragile stems were vulnerable to mechanical damage in more heavily used channels. Its strong preference for eutrophic waters is well illustrated by its history in the Broads (George, 1992). It colonised the Broads as nutrient levels rose in the post-war years, and in some Broads it became very abundant. As eutrophication increased further populations crashed and the Broads became dominated by phytoplankton. At Alderfen Broad, for example, the excessive abundance of *C. demersum* was causing concern in 1963 but five years later the plant had virtually disappeared. When the flow of eutrophic water was diverted from Alderfen Broad, *C. demersum* again became abundant. *C. demersum* is shade-tolerant, and small quantities can persist in ditches under a heavy carpet of *Azolla filiculoides* or *Lemna* species.

C. demersum flowers freely. Many observers have noted that *C. demersum* rarely produces mature fruit (e.g. Burton, 1983; Norman, 1978; Tabley, 1899; Scannell, 1976a). In a detailed study of the species in the London area Guppy (1894) failed to find fruiting plants in three successive summers. In the hot summer of 1893 fruits matured in shallow water but not in the cooler water of rivers. If fruits were kept moist only 15% germinated in the first year, but this increased to 80% if the fruits were dried for 2-3 months. The main method of spread is by vegetative fragmentation, and the spread of the species in canals may be facilitated by clearing operations which break the fragile stems (Scannell, 1970). *C. demersum* is sold as a plant for garden ponds and it may be released into the wild when overgrown ponds are cleared out.

C. demersum has fluctuated in abundance of some sites in response to changes in the nutrient status of particular water bodies, but there is no evidence to suggest that there is any change in its overall distribution or abundance in Britain or Ireland.

C. demersum is widespread in Europe. It is more frequent in Scandinavia than *C. submersum*, and almost reaches 70°N in N. Norway (Jalas & Suominen, 1989). It has a virtually cosmopolitan world distribution, being found in all continents except Antarctica. For a map of the world distribution, see Wilmot-Dear (1985).

An aquatic plant of shallow, sheltered, lowland waters. Like *C. demersum*, it grows as a floating mass or lightly anchored to the substrate by buried stems. It is found in eutrophic, often base-rich or slightly brackish water. In coastal sites its most characteristic habitats are shallow ponds and ditches (including grazing marsh ditches), where it grows with other plants which tolerate slightly brackish conditions (e.g. *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Ranunculus baudotii*, *Zannichellia palustris*) as well as species of wider habitat range. At inland localities it grows in similar habitats to the commoner *C. demersum*, including small field ponds, lakes and flooded marl and gravel pits. Both species can sometimes be found growing together. *C. submersum* is shade-tolerant, and can be found in ditches or small ponds surrounded by tall emergents. In both coastal and inland sites it can be so abundant that it virtually excludes all competitors.

Plants flower freely. It has been suggested that *C. submersum* fruits regularly more than *C. demersum* in S. England (Norman, 1978). Plants survive the winter as sunken stems, but are unable to tolerate prolonged freezing.

It is difficult to assess changes in the distribution of the species, as the simple vegetative distinction between *C. submersum* and *C. demersum* was not understood until they were described by Sandwith (1927). Older records of *C. submersum* are unreliable, and have only been accepted if supported by herbarium specimens. *C. submersum* is being recorded with increasing frequency in inland sites, and it was first found in Ireland in 1989 (Smith & Wolfe-Murphy, 1991). It is not clear if this reflects a real increase or whether it was previously overlooked. At some sites it has certainly increased in abundance in recent years, and it now fills entire ponds which formerly had a richer flora. As a species of eutrophic water, it is unlikely to be threatened by changes in water quality.

C. submersum sensu lato is widespread in Europe, north to S. Scandinavia (Jalas & Suominen, 1989). It is also found in Asia, Africa and N. and S. America, but it is absent from Australasia. For a map of its world distribution, see Wilmot-Dear (1985).

28. RANUNCULACEAE

A large family of 58 genera and some 1,750 species, most of which occur in temperate and boreal areas. Members of the family are very variable in vegetative form, floral structure and fruits. Only two of the genera contain aquatic species.

28/1. *Caltha* L.

The genus *Caltha* has been monographed by Smit (1973), who recognises 10 species. One of these is a true aquatic (*C. natans* Pallas) and the others are plants which grow in a variety of wet habitats. The only European representative is *C. palustris*.

C. palustris usually grows in sites which are flooded in winter and where the water-table remains at or near the soil surface during the summer months, but it is absent from permanently flooded ground. It is found in open habitats, tall-herb communities and woodland over base-rich or base-poor, peaty or mineral soils, although it avoids the most acidic and oligotrophic sites. Characteristic habitats include stony lakeshores, the edges of slow-flowing streams and rivers, moist meadows and pastures, willow carr, alder woods and montane springs and flushes. It is unpalatable to stock and is therefore frequent in poorly drained, rushy pastures. It grows from sea-level to 1100 metres on Braeriach and Lochnagar (Wilson, 1956).

C. palustris is a rhizomatous perennial. Plants flower in spring and are self-incompatible. They are pollinated by a wide variety of insects (including bees, flies and beetles) and usually set viable seed. Seeds can float for up to four weeks and may be dispersed by water (Ridley, 1930-CHK). They require chilling to break their dormancy and germination occurs in spring. Plants have a limited capacity for rhizomatous spread and detached shoots can root and become established (Grime *et al.*, 1988).

Flowering plants are very conspicuous in spring and the distinctive leaves persist through the summer, so the species is well recorded. It has declined in abundance in recent years in lowland England, often disappearing from wet pastures and streamside habitats as these have been drained but persisting in damp woodland (Simpson, 1982; Sinker *et al.*, 1985; Tarpey & Heath, 1990). It is often cultivated in water gardens and it can be found as an introduction by newly created or restored village ponds.

C. palustris is widespread in arctic, boreal and temperate regions of the northern hemisphere. In Europe it is rare in the Mediterranean region but frequent elsewhere (Jalas & Souminen, 1989).

This is a variable species, both morphologically and ecologically. Two genetically distinct varieties are recognised in Britain: var. *palustris* and var. *radicans* (Forst.) Beck. Var. *palustris* is the widespread plant, which includes the phenotypically dwarf montane populations which were formerly recognised as subsp. *minor* (Mill.) A.R. Clapham. Var. *radicans* differs from the typical plant in rooting at the nodes; it is found in lowland habitats in northern and western Britain and is widespread on lake shores in northern and western Ireland (Praeger, 1935; Woodell & Kootin-Sanwu, 1971). Cytologically, *C. palustris* is a polyploid complex. Most British and Irish populations of both varieties are hexaploid ($2n=56$) but octoploid plants ($2n=64$) are known from Dolbadarn, N. Wales. Tetraploids ($2n=32$) are widespread in mainland Europe and N. America but have not been detected in the British Isles (Kootin-Sanwu & Woodell, 1970, 1971, Smit, 1973).

This is the largest genus in the family, with 250 species. There are three rather distinct subgenera in Britain and Ireland. Subgenus *Ranunculus* and Subgenus *Ficaria* (Schaeffer) L. Benson include species with yellow petals; they are predominantly terrestrial but two species in Subgenus *Ranunculus* (*R. flammula* and *R. reptans*) and their hybrid are treated here. The species in these subgenera are relatively straightforward taxonomically; few of them hybridise and the main taxonomic problems concern the treatment of the considerable intraspecific variation shown by some widespread species.

The species in Subgenus *Batrachium* (DC.) A. Gray have white petals. They all grow in association with water, but vary in the extent to which they are adapted to the aquatic environment. All species are treated in the accounts below. Some (*R. hederaceus*, *R. omiophyllus*) have laminar leaves which cannot survive submersion, and these species are restricted to terrestrial habitats at the water's edge. Other species (*R. circinatus*, *R. fluitans*, *R. penicillatus* subsp. *pseudofluitans*, *R. trichophyllus*) have capillary leaves which can only survive if submersed, and these are obligate aquatics. The largest group of taxa are heterophyllous, with the capacity to produce both capillary and laminar leaves (*R. aquatilis*, *R. baudotii*, *R. peltatus*, *R. penicillatus* subsp. *penicillatus*, *R. tripartitus*; the three hybrids treated below also fall into this category). These taxa usually grow in shallow water, with the capillary leaves submersed and the laminar leaves floating on the surface, but can sometimes develop in water as young plants with capillary leaves and then grow terrestrially with laminar leaves when they are mature. Both the species with capillary leaves and the heterophyllous species can grow as small, terrestrial forms if exposed above the water level. The leaves of these forms resemble flattened, short capillary leaves. Terrestrial forms can survive on damp substrates during the summer but they are frost-sensitive and only survive the winter if they are flooded and revert to the capillary-leaved form before the onset of cold weather.

Taxonomically, Subgenus *Batrachium* is perhaps the most difficult group of aquatic plants in the British Isles. All available evidence indicates that the species are closely related. Like many aquatic plants they have undergone morphological reduction, and this limits the possible taxonomic characters which can be used to separate the species. Barriers to hybridization within the subgenus are slight, and Cook (1970) suggests that all species may potentially be capable of exchanging genetic material. Both fertile and sterile hybrids can be found as persistent populations in the wild and have been synthesized in cultivation. *Ranunculus penicillatus* is particularly critical taxonomically. It is believed to have evolved by hybridization between *R. fluitans* and other species, and is almost certainly polyphyletic in origin. Cook (1970) has suggested that some other species (including *R. aquatilis*, *R. peltatus* and *R. trichophyllus*) may also have a polytopic origin and perhaps represent no more than particular combinations of characters which are well adapted for survival in the aquatic or amphibious environment.

The breeding system of the species in Subgenus *Batrachium* is similar for all species, and is outlined here. The flowers are protogynous and the stigmas are ready to receive pollen 2-6 days before the anthers dehisce. Self-fertilisation takes place once the anthers dehisce and most species are self-compatible. At least some of the ovules in the species with smaller flowers tend to be self-pollinated before the flower buds open, especially if flowering is delayed by cold weather (Cook, 1966a; Haag, 1991).

The modern taxonomic treatment of Subgenus *Batrachium* is based on a revision by Cook (1966); older records of the more critical species are of little value unless supported by herbarium specimens. The treatment of the subgenus in Stace (1991) follows Cook (1966), with modifications for *R. penicillatus* group suggested by Webster (1988a). In mainland Europe there is little consensus about the taxonomic rank or even the definition of the taxa in the subgenus; the main differences of opinion are summarised by Jalas & Suominen (1989).

Much of the information in the accounts of *R. flammula*, *R. reptans* and *R. × levenensis* is taken from papers by Padmore (1957), Gibbs & Gornall (1976) and Gornall (1987). The accounts of the taxa in Subgenus *Batrachium* is based on the work of Cook (1966a, 1966b, 1970, 1975) and Webster (1988a, 1988b, 1990, 1991).

R. flammula subsp. *flammula* is found in a wide range of moist, wet or seasonally flooded habitats, but only occasionally occurs in permanently flooded sites. It is restricted to areas where tall vegetation is unable to become established because of shallow or infertile soils, disturbance or grazing (*R. flammula* is unpalatable to stock). Typical habitats include stony or gravelly soil at the edge of pools and lakes, where it sometimes grows in shallow water, streamsides, springs and flushes, marshes, damp hollows in heathland and moorland, dune slacks, ditches, damp grassland and deeply rutted woodland rides. It is sometimes found as a colonist of old gravel and brickpits. It is usually found over neutral or moderately acidic substrates associated with oligotrophic or mesotrophic water, and occurs on both peaty and mineral soils. In the Sheffield area it generally occurs where the soil pH is between 4.5 and 6.5, but there (as elsewhere) it is occasionally found in highly calcareous sites (Grime, Hodgson & Hunt, 1988). It is recorded from sea-level to 930 m on Carnedd Llewelyn, and perhaps ascends to higher altitudes in the Scottish highlands (Wilson, 1956).

This is a perennial which overwinters as very small rosettes. It is a predominantly self-incompatible species, which scarcely sets any seed if self-pollinated (Gibbs & Gornall, 1976). The seeds lack buoyancy, but may be dispersed by animals as they have survived ingestion by horses (Ridley, 1930). There is a persistent seed bank in the soil, and germination occurs in spring (Grime, Hodgson & Hunt, 1988). The seed of American plants only germinates sporadically when fresh but rapidly after subjection to alternate freezing and thawing (Cook & Johnson, 1968). Prostrate plants root at the nodes and if their shoots are accidentally detached they may also give rise to new plants.

R. flammula is frequent in suitable habitats in much of northern and western Britain and Ireland. In the south and east it is widespread but local, and in some counties such as Cambridgeshire it has decreased markedly because of drainage (Perring *et al.*, 1964). Subsp. *flammula* is much commoner than subsp. *minimus* or subsp. *scoticus*, and all records except those definitely attributable to the rarer subspecies have been included on the map.

R. flammula subsp. *flammula* is widespread in Europe, although absent from the extreme north and rare in the Mediterranean region (Jalas & Suominen, 1989). It extends south to N. Africa and east to western Asia; it is also naturalised in New Zealand. Plants in the *R. flammula* aggregate (which includes *R. reptans*) are widespread in N. America, and some of those in western and eastern parts of its range may be referable to *R. flammula sensu stricto*, but the relationship of the American plants to those in Europe requires investigation.

This is a polymorphic taxon, with variants which range from procumbent phenotypes which resemble *R. reptans* to erect, large-leaved genotypes (var. *ovatus* Pers.) which can be mistaken for the fenland species *R. lingua*.

Ranunculus flammula subsp. *minimus* (A. Bennett) Padmore

This dwarf, fleshy, semi-prostrate subspecies of *R. flammula* grows in dense mats on exposed sea-cliffs. It is recorded from dry moorland, short, damp turf and wet flushes. All localities must lie below 300 m.

This is a fertile perennial which sets viable seed. Its reproduction in the wild has not been studied.

R. flammula subsp. *minimus* is a little-known taxon. It was described (as forma *minimus*) from North Uist by Bennett (1904), and has subsequently been collected from a number of scattered localities in Scotland and Ireland. Some observers have confused this subspecies with dwarf variants of subsp. *flammula* (Silverside, 1984); only records based on reliably determined herbarium specimens have been accepted for the map. Silverside (1984) notes that subsp. *minimus* has not been refound recently at two of its known localities, Cape Wrath and Holburn Head, and Scott & Palmer (1987) have also failed to relocate it in Shetland.

The only confirmed records of this subspecies are from Britain and Ireland.

Well-marked specimens of subsp. *minimus* are very distinctive, and retain their characters in cultivation (Padmore, 1957). This suggests that the plant merits its subspecific status, but the taxonomy of the *R. flammula* aggregate in the northern hemisphere requires revision. Cook (1983) notes that he has seen herbarium specimens which appears to be this plant from America and perhaps elsewhere, but gives no further details. The current status of the British populations also requires investigation, but this will not be easy to achieve in view of the remoteness of the sites.

Ranunculus flammula subsp. *scoticus* (E.S. Marshall) A.R. Clapham

This plant usually grows in water up to 0.6 m deep at the edges of lakes. It is sometimes found exposed on stony or, more rarely, peaty shores. It is recorded at altitudes up to 485 m at Loch Builg.

R. flammula subsp. *scoticus* is a fertile perennial which sets well-formed and apparently viable seed. Little is known of its reproduction in the wild.

This plant was discovered and described by Marshall (1889, 1892, 1898) but was subsequently misinterpreted by many observers, both before and after Padmore's (1957) account. The map is based on reliably determined herbarium specimens. Few botanists are familiar with the plant, and it may be more frequent in Scotland and Ireland than the map suggests.

The only confirmed records of this subspecies are from Britain and Ireland. Unconfirmed records from the Faeroes are reported by Jalas & Suominen (1989) but not taken up by Tutin *et al.* (1993).

R. flammula subsp. *scoticus* retains its characters in cultivation (Padmore, 1957). At a loch near Tongue it grows at a level below subsp. *flammula*, with intermediate plants between them (Silverside, 1984). Plants which are intermediate between the subspecies occur at most or perhaps all of the sites for subsp. *scoticus*, and this has contributed to the taxonomic confusion between the plants. Typical subsp. *scoticus* is illustrated by Marshall (????) and the distinguishing characters discussed by Padmore (1957) and Silverside (1984). Cook (1983) suggests that this subspecies, like subsp. *minimus*, may occur in America and perhaps elsewhere, but gives no further details.

Ranunculus × *levenensis* Druce ex Gornall (*R. flammula* × *R. reptans*) Loch Leven Spearwort

This hybrid grows on lake shores, where it is usually found in a zone near the low water level where the shore is damp and occasionally flooded in summer. It occurs on a variety of substrates including stones, gravel, silt-covered gravel and sand. *Carex* spp., *Juncus bulbosus* and *Littorella uniflora* are recorded as associates. All sites are below 300 m.

R. × levenensis is a perennial which creeps and roots at the nodes. It is fertile and some hybrid plants are partially self-compatible. The hybrid produces a full complement of well-formed fruit.

R. × levenensis is known to have been present at its best-known British localities for many years. Plants from Loch Leven illustrated on the title page of Lightfoot's *Flora Scotica* (1777) are clearly referable to this hybrid (Gornall, 1987), and the plant is still present at this site. It also persists at Ullswater, where it was first collected in 1880. These populations were first reported as *R. reptans* but are now known to be of hybrid origin (Padmore, 1957, Gibbs & Gornall, 1976).

There are records of *R. × levenensis* from southern Scandinavia and the Alps, the main areas where the distributions of the parents overlap. The hybrid is also recorded from northern Germany which, like the sites in Britain and Ireland, is south of the main range of *R. reptans*.

Ranunculus flammula and *R. reptans* are completely interfertile, and there is an argument for treating them as a subspecies of a single species (Gibbs & Gornall, 1977). Plants of *R. × levenensis* in the wild are similar to synthesised hybrids. The hybrid is very variable, both genotypically and phenotypically. Genotypes in Britain range from those which closely resemble *R. reptans* to those which are very difficult to distinguish from dwarf phenotypes of *R. flammula* unless they are taken into cultivation. British populations probably consist for the most part of backcrosses with *R. flammula* rather than F1 hybrids. At Loch Leven and Ullswater hybrids along the water's edge tend to be closest to *R. reptans* and above this they give way to hybrids closer to *R. flammula*, prostrate phenotypes of *R. flammula* and above the high water mark to erect *R. flammula* (Padmore, 1957, Gibbs & Gornall, 1976).

Plants which are referable to *R. reptans* are known from four localities in Britain: the gravelly shores of Ullswater and Loch of Strathbeg, where it has been recorded with *R. × levenensis*, the shore of Loch Leven, where it was almost certainly associated with the same hybrid, and Loch Awe, where it has recently been found on silty sand near the top of the shore.

This species is a stoloniferous perennial, which creeps and roots at the nodes. It is partially self-compatible.

R. reptans appears to be a transient member of the British flora. It was collected at Ullswater in 1887 and from 1911 to 1917, and at Loch Leven in 1869, 1896 and 1935. It is currently known from Loch of Strathbeg, where it was collected in 1876, 1900 and 1989 and was still present in 1994, and Loch Awe, where it was collected in 1992. Gornall (1987) suggests that it is introduced repeatedly by waterfowl migrating in autumn from Iceland, Scandinavia or northern Russia. Mallard, Pink-footed Geese and Wigeon appear to be the most likely species to have carried the seeds to Loch Leven. Plants of *R. reptans* hybridise with *R. flammula* and give rise to persistent populations of the hybrid *R. × levenensis*. The reason that *R. reptans* itself fails to survive is not clear, but Gibbs & Gornall (1976) have shown that it is less phenotypically plastic than the hybrid and may therefore be at a disadvantage on lake shores where the water level fluctuates. *R. × levenensis* has been recorded from sites in north-east Scotland and northern Ireland where *R. reptans* has never been reliably recorded, but where it was presumably once present.

R. reptans has a circumpolar distribution, being widespread in the boreal zone and extending southwards in the mountains of Europe, Asia and N. America. In Europe its main range is in Scandinavia and the north-east, but it is found at scattered sites south to the Alps, central Italy and Bulgaria (Hultén & Fries, 1986; Jalas & Suominen, 1989).

The distinction between *R. reptans* and the variable hybrid *R. × levenensis* is difficult and somewhat arbitrary. This account is based on specimens determined by R.J. Gornall and P.D. Sell.

R. hederaceus is usually found at the edge of small water bodies such as ponds, ditches, streams, springs and flushes, although it can also occur by the sheltered backwaters of larger rivers. It is a low-growing species which is often found in areas where wet soil has been disturbed; characteristic sites include the cattle-poached edges of streams and ponds, recently cleared roadside ditches, places where trickles of water flow over footpaths and ruts on unsurfaced tracks. It also grows in very shallow water as a form with floating leaves. It can colonise a range of substrates from gravel to mud, is found in both acidic and calcareous sites and it can also be found over slightly saline soil at the upper edge of salt marshes. It tolerates a range of nutrient levels, and often grows in rather nitrophilous situations. It is found from sea-level to 680 m (Milburn Common).

Plants of *R. hederaceus* are annuals or short-lived perennials. The seeds germinate very erratically if they are kept wet, but if dried then rewetted almost all will germinate simultaneously (Cook, 1966). In the field seeds germinate in autumn or spring and plants begin to flower from March to May. Pollination usually takes place within a flower bud before the flower opens, and after fertilisation the pedicel bends down, forcing the fruits into the substratum. Growth of the parent plants continues until they are smothered by competing species such as *Lythrum portula*, *Montia fontana* or *Ranunculus sceleratus*, or are killed by desiccation. Individuals which survive these hazards overwinter as small, tight cushions.

R. hederaceus is one of the most distinctive members of *Ranunculus* Subgenus *Batrachium*, and the distribution map is therefore much more complete and reliable than those of the more difficult taxa. The species, like many other plants of similar habitat, has declined in south-east England. The decline is partly due to habitat destruction: streams have been canalised, ponds filled in and tracks surfaced. Those habitats that remain are often unsuitable as they are no longer used for watering stock, and consequently the vegetation around them has become overgrown. In northern and western England and in much of Wales, Scotland and Ireland the species remains frequent.

In Europe this species has a western distribution. It extends from Portugal and Spain through France northwards and eastwards to central Germany, Denmark and southern Sweden. It is extinct in Norway, where it formerly occurred near Trondheim, and in Latvia. *R. hederaceus* also occurs on the east coast of North America, where it may have been introduced. The European localities are mapped by Jalas & Suominen (1989) and the American sites by Cook (1966a,b). On the European mainland, as in Britain, the species has declined in the eastern part of its range (de Sloover, Iserentant & Lebrun, 1977; Cook, 1983).

R. hederaceus and *R. omiophyllus* are the two species in Subgenus *Batrachium* which lack the ability to produce capillary submersed leaves; they are therefore found in more terrestrial habitats than the others. Cook (1966b) suggests that they have evolved from ancestors which had the capacity to produce such leaves, and that they represent two homozygous strains that have arisen from a common polymorphic stock. A detailed account of the ecology of *R. hederaceus* in the Low Countries is provided by Segal (1967).

The habitat requirements of this species are similar to those of *R. hederaceus*. It is found in open communities on disturbed soil at the edges of ponds and streams, in ditches, flushes and damp depressions in pastures and by the sheltered backwaters of lakes and rivers. It also grows in shallow water as a form with floating leaves. Unlike *R. hederaceus*, *R. omiophyllus* is confined to acidic, mesotrophic or oligotrophic soils. It often occurs over acid sands or peat and it is much more frequent than *R. hederaceus* in heathland pools. *Montia fontana* is a characteristic associate. *R. omiophyllus* is recorded from sea-level to 1000 m on Carnedd Llewelyn.

R. omiophyllus has a similar life-history to *R. hederaceus*. It can behave as a winter or summer annual or, if conditions are suitable, persist as a short-lived perennial. Fresh seeds germinate erratically but most will germinate if they are dried then rewetted. Plants may begin to flower as early as February and the flowering period can extend until November. Flowers are usually self-pollinated before the flower buds open and the fruits are deposited in the substrate by the recurved pedicels. The spreading summer growth form, like that of *R. hederaceus*, is susceptible to desiccation or shade but the small compact overwintering plants are more tolerant of shade, desiccation and freezing.

This is a distinctive species and the map probably presents an accurate summary of its distribution since 1950. As a plant of acid soils it has always had a restricted distribution in south-east England, and it has declined in some areas for similar reasons to *R. hederaceus*. It is still frequent in its western strongholds.

R. omiophyllus is endemic to Europe, where its distribution is even more restricted than that of *R. hederaceus*. In western Europe it is found in Portugal, Spain, France and the British Isles; it is extinct in The Netherlands. There are also outlying populations in southern Italy and Sicily.

The ecological requirements of *R. hederaceus* and *R. omiophyllus* overlap, and the two species can occasionally be found growing together. Cook (1966b) has suggested that *R. omiophyllus* is excluded from nutrient-rich sites by competition with *R. hederaceus*. In Sicily, where *R. hederaceus* does not occur, *R. omiophyllus* is found on disturbed soil which is calcareous and eutrophic. Hybrids between the two species have not been found in the wild but a highly sterile hybrid has been synthesized artificially by Cook (1966b).

Ranunculus × *novae-forestae* S. Webster (*R. omiophyllus* Ten. × *R. tripartitus* DC.) New Forest Crowfoot

This plant grows in shallow water or on damp clay at the edge of ponds, by small streams and drainage channels and in flushes and seasonally flooded hollows, sometimes in sites poached by cattle. It can be found with *R. omiophyllus*, but it appears to favour less acidic soils and is even found on calcareous clay in the southern New Forest.

There have been few detailed observations on the life-history of this hybrid. It normally behaves as an annual, but it may persist for over a year if submerged (Salisbury, 1974). It is variable in fertility, but some well-formed fruits usually develop from each flower. Like the parents, it presumably reproduces by seed rather than by vegetative spread.

In 1966 Cook (1966a) pointed out that material from the New Forest which had traditionally been ascribed to *R. tripartitus* or *R. lutarius* by British botanists was actually the hybrid between *R. omiophyllus* and *R. tripartitus*. The hybrid was given a binomial by Webster (1990). It is still widespread in the New Forest.

R. × novae-forestae is only known with certainty from the New Forest and from France.

Artificially synthesised hybrids are morphologically similar to the plant which grows in the New Forest. Both synthesized and wild hybrids are pentaploid, as would be expected from a hybrid between tetraploid (*R. omiophyllus*) and hexaploid (*R. tripartitus*) parents. In experimental studies both *R. omiophyllus* and *R. tripartitus* can be backcrossed to hybrids which have been collected in the wild. The fertility of some wild plants greatly exceeds that of synthesized F1 hybrids, but highly fertile strains can be selected from the F2 generation or the backcrosses. The New Forest populations of *R. × novae-forestae* are very variable, and some are very similar to *R. tripartitus*. Cytological examination of these plants is needed to establish whether any of these are actually *R. tripartitus*, which has not been recorded from the area with certainty.

R. tripartitus grows in shallow lowland pools which are flooded in winter but often dry out in the summer. Typical sites include ditches, heathland ponds, flushes in heaths and on sea cliffs, ruts in unsurfaced tracks and muddy depressions in field gateways. The species is a calcifuge which is found over a variety of soils ranging from peat to fine-grained loess. It is intolerant of competition and only persists where the development of a closed sward is prevented by fluctuating water levels, poaching by livestock or disturbance by vehicles. Typical associates include *Apium inundatum*, *Eleogiton fluitans*, *Lythrum portula*, *Montia fontana* and *Nitella flexilis*.

In cultivation *R. tripartitus* is perennial but in the field it behaves as a winter annual, germinating in autumn on damp mud or under water. Individuals can overwinter as aquatics with capillary leaves, or as terrestrial plants with laminar leaves. They flower from March to May. If the habitat dries out the plants are killed by desiccation; if it remains moist they are overwhelmed by more vigorous species.

R. tripartitus has undoubtedly undergone a marked decline in Britain. The reasons for this include the destruction of heathland, the draining or infilling of ponds, the improvement of rutted tracks and the reduction or cessation of grazing which has led to the development of rank vegetation or even willow carr around suitable habitats. The exact extent of the decline is difficult to assess as the plant has probably been overlooked in both the past and in recent years because of its early flowering season, and perhaps because of its similarity to *R. × novae-forestae* (q.v.). The conservation of this species will require the protection and appropriate management of existing colonies, and perhaps the restoration of suitable habitat at former sites where the plant may still be present as dormant seed.

This species has an Atlantic distribution, being found in Morocco and in western Europe from Spain and Portugal to The Netherlands and northern Germany. It has also been reported recently from the Aegean island of Mykonos (Jalas & Suominen, 1989; Dahlgren, 1991). The species is declining in the northern part of its range; it is extinct in Belgium and perhaps in The Netherlands. There is little published information on its current distribution in southern Europe.

R. tripartitus is clearly adapted to an oceanic climate: it can be cultivated without difficulty in botanic gardens in western Europe but only with much effort in central Europe, where the transition between winter and summer appears to be too abrupt (Cook, 1976).

This is a species of still or very slowly flowing, brackish water. It is confined to water less than 1 m deep, and usually found at depths shallower than 50 cm. It grows in a range of coastal habitats including lagoons, the seaward side of machair lochs, ditches, pools, dune slacks and borrow pits. It is a characteristic species of unfenced ditches in grazing marshes, where grazing and trampling by livestock prevent the growth of a dense sward of emergent vegetation. It is often found as a colonist of newly dug pools or pits, and even flooded ruts in unsurfaced tracks. It is often associated with species such as *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Ruppia maritima* and *Zannichellia palustris* in water which is sufficiently saline to exclude most macrophytes but not brackish enough to support a dense sward of *Ruppia*. Exceptionally, it can be found in much more brackish situations, including sites which are flooded at high tide. There are a few inland records from canals, gravel pits and brickpits, where it grows in fresh water.

R. baudotii can behave as an annual or a perennial, depending on the particular habitat in which it grows. Perennial plants persist through the winter in the capillary leaf state. In summer the species can persist as a small, terrestrial form on damp mud. Plants are well-adapted to self-pollination (Hong, 1991). The usual method of reproduction is probably by seed, but detached stems can also root and become established.

It is difficult to assess trends in the distribution of this species, which has been under-recorded in the past and is probably still overlooked in some areas. The species has almost certainly been lost from many sites in south-east England in recent years because of the conversion of much coastal grazing marsh to arable land, but these losses do not show at the scale of the map, and may have been partly compensated for by the ability of the species to colonise new sites.

R. baudotii is frequent along the Atlantic coast of Europe from Portugal to Denmark, and in the Baltic. It is apparently rarer along the Mediterranean coast and occurs at scattered inland localities in Europe (Jalas & Suominen, 1989). Outside Europe it is found in Morocco and the Canaries (Hultén & Fries, 1986).

R. baudotii is a variable species; much of the variation is phenotypic but some has a genetic basis (Cook, 1966a). Typical plants are not difficult to identify, but not all plants attributable to this species show the full range of diagnostic characters and because of this the map is likely to show some erroneous records. *R. baudotii* and *R. peltatus* are difficult to distinguish in southern Europe, where the morphological gap between them is bridged by *R. peltatus* subsp. *saniculifolius* (Vivani) Cook. Cook (1984) has recently reduced *R. baudotii* to *R. peltatus* subsp. *baudotii* (Godron) Meikle ex Cook, a treatment followed in *Flora Europaea* (Tutin *et al.*, 1993). However, in some areas, including the Outer Hebrides, *R. baudotii* is more difficult to distinguish from *R. trichophyllum*. It may be best to retain the plant at specific rank, while recognising that several species of Batrachian *Ranunculus* are less distinct than one would like them to be.

R. trichophyllus is a plant of shallow, still or very slowly flowing water. It is most frequently found in small water bodies such as ponds, dune slacks or drainage ditches, but it is also recorded from a wide range of other habitats including lakes, slowly-flowing streams, canals and turloughs. It is an early colonist of new habitats or of sites which have been disturbed, where it is often accompanied by *Ranunculus aquatilis* and *Chara vulgaris*. It cannot persist (except perhaps as buried seed) when the vegetation becomes dominated by more competitive macrophytes or emergents. It tolerates a wide range of water chemistry but is most frequent in mesotrophic or eutrophic water and is absent from the most oligotrophic sites; it is sometimes found in brackish habitats near the sea. It is a mainly lowland species; the maximum altitude of 550 m (Widdale Fell) given by Wilson (1956) is probably correct but the identity of the plant requires confirmation.

Like the other smaller members of Subgenus *Batrachium*, *R. trichophyllus* can behave as an annual or a perennial. It often begins to flower in March or April, being the first member of the subgenus to flower in most parts of its British and Irish range. Plants are often self-pollinated before the flowers open. When the habitat dries out *R. trichophyllus* can persist on damp mud in a terrestrial phenotype, but these plants do not survive severe desiccation. Individuals can overwinter as submersed plants with capillary leaves but the terrestrial forms are killed by frost, and only survive if re-submerged before the onset of cold weather. Reproduction is by seed, which can germinate on damp mud or under water.

This is the most frequent *Batrachian Ranunculus* in many lowland areas, and there is no evidence to suggest that it has decreased to any significant extent.

This species occurs throughout the northern hemisphere in arctic, boreal and temperate areas. It is also recorded from S.E. Australia and Tasmania (Hultén & Fries 1986). The plant in the British Isles is subsp. *trichophyllus*, which is replaced in arctic and montane areas by subsp. *eradicatus* (Laest.) C.D.K. Cook.

R. aquatilis has similar ecological requirements to *R. trichophyllus*, with which it often grows. It is a plant of shallow water in marshes, ponds and ditches, the sheltered edges of lakes and the margins of slow-flowing streams. It appears to favour eutrophic and often rather base-rich water, and perhaps for this reason it is often recorded from farm ponds. Like many of the smaller species in Subgenus *Batrachium*, it is favoured by disturbance and is often found in muddy water at the edge of streams and ponds where cattle congregate. *Callitriche obtusangula*, *Glyceria fluitans* and *Lemna minor* are characteristic associates. It is a primarily lowland species which is recorded up to 380 m at Malham Tarn (Sinker, 1960).

R. aquatilis is an annual or a short-lived perennial. Most plants flower in May and June, but the flowering period can extend into the late summer. Like *R. trichophyllus*, plants are often self-pollinated and isolated plants set a full complement of seed. If the water dries up plants can persist through the summer on damp mud. However, the species only produces laminar leaves in long days; in short winter days only capillary leaves are produced and plants therefore over-winter under water or perish (Cook, 1969). Seeds from a pond in Israel germinated after they had been stored for 10 years in dry conditions (Witztum, 1986).

Our knowledge of the distribution of this species is incomplete as most records collected for the *Atlas of the British Flora* (Perring & Walters, 1962) under the name *R. aquatilis* are only attributable to an aggregate which also includes *R. peltatus* and *R. penicillatus*, and are not plotted on the map. Because the taxonomy of this group has only recently been clarified, and because *R. aquatilis* is under-recorded, it is difficult to assess whether there have been any changes in its distribution.

R. aquatilis is widespread in Europe from southern Scandinavia southwards, but is rare in the Mediterranean region. It is recorded from N. Africa and in scattered localities across Asia to Japan. It is also found in western N. and western S. America.

In southern England *R. peltatus* is often found in the upper reaches of highly calcareous rivers flowing from a chalk aquifer, in stretches which often dry out during the summer months. Further downstream it is replaced by *R. penicillatus* subsp. *pseudofluitans*. In Ireland it is the characteristic Batrachian *Ranunculus* of streams and rivers over Carboniferous limestone. Away from calcareous bedrock it is found in a variety of other habitats, including slow-flowing, acidic streams and rivers over peat or clay, coastal lagoons, the shallow edges of lakes and nearby inflow streams, ditches, ponds and dune slacks. It can colonise newly created habitats such as gravel pits and in established vegetation it often benefits from disturbance. In many areas it shows some preference for base-poor water, but its trophic range seems to be broad and it has been recorded from both nutrient-rich and nutrient-poor localities. It is primarily a lowland species, which occurred up to 460 m in the R. Tees at a site now flooded by Cow Green Reservoir (Proctor, 1978). A record from 500 m at Llyn Anafon (Wilson, 1956) is dubious as recent collections from this site have been determined as a sterile hybrid of *R. peltatus*.

In permanently moist habitats *R. peltatus* is a perennial, which overwinters as an aquatic and persists through the summer in water or in a terrestrial form on damp mud. When the habitat dries out in summer it can behave as an annual. Cook (1966a) described the species as self-compatible and adapted to self-pollination. However, the flowers are large and Hong (1991) concluded that the plants he studied were well adapted for outbreeding, and were pollinated by beetles. Their anthers did not dehisce in the buds, and there was some evidence that plants were self-incompatible. Reproduction of the species is by seed.

R. peltatus has only been recorded systematically since the publication of Cook's monograph in 1966, and is still under-recorded. The patchy distribution shown on the map probably reflects this, but the species appears to be genuinely absent from some areas within its overall range, including the vice-county of Cambridgeshire. Some of the records plotted may be erroneous, as the species can be confused with *R. aquatilis*, *R. baudotii* or *R. penicillatus*. In the absence of adequate historical records it is impossible to assess whether its distribution has changed.

R. peltatus is widespread in Europe from the Mediterranean countries north to northern Scandinavia; in European Russia it is very rare or under-recorded (Jalas & Suominen, 1989). Elsewhere it is only known from North Africa. The closely related *R. sphaerospermus* Boiss. & Blanche, often classified as a subspecies of *R. peltatus*, extends from the Balkans through western Asia to the Himalaya.

In its ecological preferences *R. peltatus* is intermediate between the smaller species in Subgenus *Batrachium*, which are plants of shallow, still or very slowly flowing water, and the larger riparian species. Its exact ecological requirements, and in particular its relationship to *R. aquatilis*, have not yet been clearly defined, partly because of taxonomic confusion.

Ranunculus × *kelchoensis* S. Webster (*R. peltatus* Schrank × *R. fluitans* Lam.) Kelso Water-crowfoot

This hybrid has been recorded from number of major lowland rivers, most of which have a meso-eutrophic flora and are moderately base-rich. In the R. Teviot and the Whiteadder Water it is locally very abundant, forming large beds in shallows where the rivers flow rapidly over a stony substrate. Neither parent has been recorded in the vicinity of these stands, and the beds of *R. × kelchoensis* are normally sufficiently vigorous to exclude other species, but *R. penicillatus* subsp. *pseudofluitans* is sometimes present. The hybrid was also recorded from the River Welland, where the water is more calcareous and probably more eutrophic than at these sites, but little is known of the exact habitat or the associated species in this river.

This is a robust perennial. Most populations are highly sterile, but the stems root at the nodes and the plant can presumably reproduce and spread by vegetative fragments. Sterile populations are very persistent: the hybrid was collected in the Whiteadder Water at Allanton in 1841 and in the R. Teviot at Roxburgh Castle in 1876, and re-found in both sites in 1991. Plants from the River Wye which are also referable to *R. × kelchoensis* set well-formed fruit.

Brief accounts of this hybrid were given by Cook (1966a, 1975) but it was not until Webster (1990) gave it the binomial '*kelchoensis*' that it was brought to the attention of most British and Irish botanists. The hybrid has not yet been searched for in all the rivers from which old herbarium specimens are known. It will probably be rediscovered in some localities from which only pre-1950 records are available, and found in new stations elsewhere. However: it has not been possible to re-find the plant at sites in the R. Welland and its tributaries where it was present in the 1950s (Webster, 1990).

In addition to its British and Irish localities. *R. × kelchoensis* is known from France and Portugal.

Ranunculus penicillatus subsp. *penicillatus* is believed to be an amphidiploid derived from hybrids similar to *R. × kelchoensis*.

Ranunculus penicillatus (Dumort.) Bab. subsp. *penicillatus*

This is primarily a plant of rivers and streams, where it is sometimes found in dense stands which dominate the entire channel. In some rivers it grows in torrent conditions; in others it occurs in sections which are usually more slow-flowing but where the current velocity is high during floods (Holmes, 1980). In Britain it is confined to base-poor and usually more or less mesotrophic waters flowing over Palaeozoic or igneous rock. In Ireland it has a considerably greater ecological range, being found in both base-rich and base-poor rivers and streams over a range of parent materials including basalt and Carboniferous limestone. It is also recorded from some Irish lakes and from the Grand Canal in Dublin. It is not recorded above 300 m.

This is a fertile perennial which overwinters as shoots with capillary leaves. Its reproduction has not been studied. Plants can presumably spread by vegetative fragments, as lengths of stem are often detached and washed downstream. The degree to which it reproduces by seed is unknown.

R. penicillatus subsp. *penicillatus* has only been recognised as a distinct taxon in recent years, and is likely to be under-recorded, particularly in Ireland.

The distribution of *R. penicillatus* and its constituent subspecies is unclear because of taxonomic confusion. The species appears to be widespread in the middle latitudes of Europe, but absent from both northern countries and much of the Mediterranean region (Jalas & Suominen, 1989). The confirmed records of subsp. *penicillatus* are from western and central Europe, extending from the British Isles, Denmark and St Petersburg southwards to Portugal, Spain and the mountains of Sardinia (Cook, 1966a).

In Britain *R. penicillatus* subsp. *penicillatus* is replaced by subsp. *pseudofluitans* in base-rich rivers. In Ireland subsp. *pseudofluitans* is known from only one site, and Webster (1991) suggests that this has allowed subsp. *penicillatus* to occupy a wider range of habitats.

Ranunculus penicillatus (Dumort.) Bab. subsp. *pseudofluitans* (Syme) S. Webster

This is the dominant macrophyte in many British lowland, base-rich streams and rivers, where it often forms dense beds which span the entire channel. It is found in moderately or rapidly flowing, mesotrophic or meso-eutrophic water over a wide range of geological strata, but it is most frequent in calcareous water arising from chalk or limestone aquifers. It is also found in some rivers which are only moderately base-rich. In eutrophic or sluggish rivers it is usually replaced by other aquatics, including *Myriophyllum spicatum* and *Potamogeton* species. It also grows in clear calcareous water in canals, pools and ditches. In Ireland it is confined to a single, rather base-poor river which flows over schist and gneiss, the usual habitat of subsp. *penicillatus*. Subsp. *pseudofluitans* is virtually confined to the lowlands, reaching 310 m in the Carlcroft Burn.

Like subsp. *penicillatus*, subsp. *pseudofluitans* is a fertile perennial which overwinters as actively growing leafy shoots. Dawson (1980) noted that the first plants to flower in the R. Piddle were those near the source of the river, and there was then a progression of flowering downstream until the plants near the tidal limit flowered 2-3 months later. Material transplanted to other parts of the river retained its original flowering date. The extent to which subsp. *pseudofluitans* reproduces by seed or by the spread of vegetative fragments is unknown; reproduction by seed may be rare.

This species is so abundant in some rivers that it impedes the flow of water, and has to be removed by mechanical or chemical means. It is, however, vulnerable to pollution and it is, for example, much rarer in the R. Colne than it once was (Kent, 1975). However, it has also spread very rapidly in some rivers such as the R. Wear, which was formerly polluted by the coal industry and by sewage. It was first noted in the Wear in 1970 and it was perhaps the most abundant submerged flowering plant by 1976, having spread from a small population in a tributary (Holmes & Whitton, 1977a, Graham, 1988).

The distribution of *R. penicillatus* subsp. *pseudofluitans* is obscured by taxonomic confusion. It is recorded from western and central Europe by Cook (1966a), and has subsequently been reported from Greece.

Subsp. *pseudofluitans* differs from subsp. *penicillatus* in never having laminar leaves. The sole Irish population of subsp. *pseudofluitans* may actually be a variant of subsp. *penicillatus* which has lost the capacity to produce such leaves, and is therefore morphologically identical to subsp. *penicillatus* (Webster, 1991). Two varieties of subsp. *pseudofluitans* are recognised in Britain. Var. *pseudofluitans* is the commoner plant and is usually found in rivers, whereas var. *vertumnus* C. Cook can grow in rivers but is also found in streams, canals, ditches and pools. The distribution of both varieties is mapped by Webster (1988), who also summarises the extensive ecological literature on var. *pseudofluitans*. Murrell & Sell (1990) suggest that the varieties should each be recognised as species distinct from *R. penicillatus*.

Ranunculus × *bachii* Wirtgen (*R. aquatilis* L. × *fluitans* Lam. & *R. fluitans* Lam. × *trichophyllus* Chaix)

R. × bachii is known from a number of lowland rivers and streams, but most records are derived from herbarium specimens and there is little information about the nature of the sites in which it grows. In the R. Wharfe *R. × bachii* has recently been recorded in shallow, stony stretches of the river, growing with *R. penicillatus* subsp. *pseudofluitans* var. *vertumnus*, *Myriophyllum spicatum*, *Potamogeton crispus* and *P. perfoliatus*. The occurrence of the hybrid in lakes requires confirmation: plants collected as *R. cambricus* in Llyn Coron last century may be this hybrid, but they could be *R. fluitans* growing in an unfavourable habitat (Webster, 1990); they are not plotted on the map.

R. × bachii is a robust, highly sterile hybrid which can form large populations. Plants continue to grow though the winter months. Reproduction must be by vegetative spread, which presumably occurs when stems become detached and are carried downstream to become established at new localities. Established populations can be very persistent: the hybrid was first collected in the R. Wharfe in 1904, and is still present there.

Cook (1966a) confirmed the presence of *R. × bachii* in Britain, but few observers are familiar with it and it is probably more frequent the map suggests.

Plants attributable to *R. × bachii* have been recorded from a number of countries in western and central Europe, and, as in Britain, there is evidence that they have been established in some river systems for many years.

The name *R. × bachii* is used to cover the hybrids with *R. fluitans* as one parent and *R. aquatilis* or *R. trichophyllus* as the other. The type of *R. × bachii* is probably *R. fluitans* × *trichophyllus*, and the name is used in this restricted sense by Kent (1992). However, the two hybrids are genotypically and phenotypically variable and they cannot be distinguished with certainty on the basis of their morphology, although they differ in chromosome number. The population of *R. × bachii* at Monsal Dale has been identified as *R. aquatilis* × *fluitans* on the basis of a chromosome count. Hybrids similar to *R. × bachii sensu lato* are believed to have given rise to the fertile amphidiploid *R. penicillatus* subsp. *pseudofluitans*.

[Ask NTHH if he can provide any information about the ecology of this hybrid in the R. Dee]

R. fluitans is primarily a species of large rivers, where it usually grows in rapidly flowing water which is base-rich and meso-eutrophic. Its detailed distribution is often controlled by its requirement for a stable substrate. In Derbyshire, for example, it is present where rivers flow over non-calcareous rocks which weather to smooth pebbles around which silt collects, but replaced by *R. penicillatus* subsp. *pseudofluitans* in those stretches of the same rivers which flow over limestone, and where the substrate is much less stable. In many northern rivers, including the Tees and the Swale, *R. penicillatus* subsp. *pseudofluitans* is usually the dominant species in the upper reaches but is replaced by *R. fluitans* downstream (Holmes & Whitton, 1977b, 1977c); in the R. Dove the zone of overlap is less than 0.5 km (Clapham, 1969). It is not recorded above 300 m.

In Britain this species has been confused with other taxa, particularly *R. penicillatus* and sterile hybrids which may have *R. fluitans* as one parent. Only records from rivers where the presence of the species has been confirmed by experts have been accepted for the map. Nevertheless, some records are probably erroneous and in other areas the species is probably under-recorded. Cook (1966a) describes it as fairly tolerant of pollution as long as the water remains clear, but soon dying if the water becomes cloudy or shaded. He suggests that it has become extinct or rare in many of the large rivers in the English Midlands. The Irish population was eliminated from that part of the Six Mile Water where it was first discovered by industrial pollution last century (Hackney, 1992). In recent years *R. fluitans* appears to have decreased in abundance in some rivers, such as the R. Lark in Suffolk, where it was frequent in the 1950's. A critical reappraisal of its past and present distribution would be worthwhile.

R. fluitans is a fertile perennial. It overwinters as slow-growing, compact and prostrate patches of stems which root at the nodes. In April or May these clumps give rise to rapidly elongating and slightly hollow stems which lack the ability to root, and which flower from June onwards. Little is known of the relative importance of vegetative reproduction as opposed to reproduction by seed, but the species can spread fairly rapidly, as evinced by its colonisation of the R. Wear following the deliberate introduction of plants by a water bailiff in 1959 (Graham, 1988).

R. fluitans is endemic to Europe. Most records are from western and central Europe, where the species extends from the Pyrenees north to southern Sweden, but there are scattered localities southwards and eastwards to Sardinia, Italy and Romania (Jalas & Souminen, 1989).

This delicate species is found in standing or very slowly flowing, clear, base-rich, meso-eutrophic or eutrophic water. It is normally found in water 1-3 m deep; it can grow in more shallow sites but only if the water is permanent, as it is intolerant of desiccation. Typical habitats include grazing marsh and fenland ditches, ponds, canals and major fenland drains, natural and ornamental lakes, reservoirs and sluggish streams and rivers. It is also a frequent colonist of gravel pits, and it occasionally invades flooded quarries and newly dug garden pools. It often grows in species-rich assemblages of aquatic plants; some of the more frequent of its many associates are *Elodea canadensis*, *Myriophyllum spicatum*, *Potamogeton crispus*, *P. pectinatus*, *P. pusillus* and, in larger waters, *Nuphar lutea*, *Potamogeton lucens* and *P. perfoliatus*. It is confined to the lowlands.

R. circinatus is a perennial; Salisbury (1960) suggested that it might behave as an annual but there is little or no evidence to support this view. Plants overwinter as prostrate stems which root at the nodes and bear rather flaccid leaves. In summer erect shoots grow upwards towards the water surface. Populations often fail to flower or flower only sparingly, but the plant can flower profusely on the surface of a ditch, lake or reservoir (cf. West, 1910; Church, 1925). Flowering sometimes begins before the stems reach the water surface, and these submersed flowers are often cleistogamous. It has little resistance to desiccation and in cultivation the terrestrial form in moist conditions with long photoperiods. It is not known whether the plant colonises new sites by seed or by vegetative fragments. In Finland, where it rarely flowers, it is dispersed by fragments which become attached to boats (Cook, 1966a) and in Britain it might similarly be dispersed by anglers.

R. circinatus is the most distinctive aquatic *Ranunculus*, and it is therefore relatively well recorded. It has been lost from many sites because of habitat destruction, including the filling in of farm ponds and the loss of drainage ditches in areas where pastoral land has been converted to arable. Driscoll (1985), for example, noted a very marked reduction in its frequency when an area of grazing marsh in Norfolk was ploughed up and the drainage system modified. *R. circinatus* is intolerant of very eutrophic conditions, and it has therefore disappeared from sites which have become too eutrophic, including its northernmost localities Balgavies Loch, Loch of Forfar and Rescobie Loch. The species has, however, colonised newly available habitats and in some counties such as Bedfordshire (Dony, 1976) and Essex (Jermyn, 1974) it is confined to gravel pits or more frequent in this habitat than in any other.

R. circinatus occurs in temperate latitudes from western Europe to eastern Asia; in Europe it is virtually absent from the Mediterranean region, and reaches its northern limit around the Gulf of Bothnia (Hultén & Fries, 1986, Jalas & Suominen, 1989). Closely related taxa occur at similar latitudes in North America.

This large family of 50 genera and over 1,000 species is found throughout the world, but is particularly well represented in the temperate northern hemisphere. It includes a wide range of life-forms, and even in Britain the native and naturalised species include small, annual herbs (e.g. *Koenigia islandica*), giant perennial herbs (e.g. *Fallopia sachalinensis*), lianes (e.g. *F. baldschuanica*) and intricately branched shrubs (e.g. *Muehlenbeckia complexa*). An illustrated account of the British and Irish species is available (Lousley & Kent, 1981). The only genera to contain aquatic species are *Persicaria* and *Rumex*, both of which include true aquatics, emergents, plants of seasonally flooded ground and annuals which grow on mud exposed by falling water levels, as well as many terrestrial species.

47/1. *Persicaria* Miller

The species traditionally included in the genus *Polygonum* by British botanists are now classified in the three segregate genera *Fallopia*, *Persicaria* and *Polygonum sensu stricto*, following a revision of generic boundaries by Ronse Decraene & Akeroyd (1988). Some 100 of the 150 species formerly included in the genus *Polygonum* probably belong to *Persicaria*, including the aquatic *Persicaria amphibia*.

As an aquatic *P. amphibia* grows in standing or slowly moving water in lakes, reservoirs, canals, ditches, large fenland drains, and sluggish streams and rivers. In lakes it can form large, virtually pure stands in water from 0.5 to at least 2 metres deep; these stands often appear to represent a single clone. It is confined to mesotrophic or eutrophic water and is tolerant of turbidity caused by disturbed sediment or algal blooms, perhaps because it lacks submersed leaves. Colonies are found over a range of fine-textured substrates. *P. amphibia* also grows as a terrestrial plant in swamps and in herbaceous vegetation on ditchbanks, by canal towpaths, in wet meadows (where it is often dominant in winter flooded hollows) or as a weed in arable fields near rivers or fenland drains. It can be abundant in sites such as reservoir margins, dune slacks and the Breckland meres, where the water level fluctuates greatly. It is virtually confined to the lowlands; the only record above 300 metres is from 572 metres at Blind Tarn, Coniston (Stokoe, 1983).

P. amphibia is a rhizomatous perennial. The shoots of a single plant measured by Arber (1920) were 13 m long. The species can spread in water by regeneration from detached shoots and on land by growth from rhizome fragments following disturbance; in many such sites vegetative spread is probably more important than sexual reproduction. Aquatic populations often flower freely but even the most vigorous terrestrial stands usually produce only a few short inflorescences. The flowers have nectaries and are insect pollinated. The seeds are dormant when they are first shed, and will not germinate even if the pericarp is removed. Under experimental conditions they do not respond to treatments which stimulate germination in many other *Persicaria* and *Polygonum* species, but 75-85% germination can be obtained by storing intact seeds for 4-6 months, then removing the pericarp and keeping the naked seeds in moist conditions at 2-4°C for a further 4-5 months (Justice, 1940). In the wild seeds germinate in spring (Grime, Hodgson & Hunt, 1988).

P. amphibia is a frequent plant in lowland Britain and Ireland. There is little evidence that it is declining, and even in the densely populated London area it is common in suitable habitats (Burton, 1983, Kent, 1975). Its capacity to grow both terrestrially and as an aquatic perhaps enables it to withstand all but the most drastic habitat change.

The variable is found at temperate latitudes throughout the northern hemisphere, and has also been introduced to areas south of its native range (Hultén & Fries, 1986). In Europe it is frequent except in the far north and in the Mediterranean region (Jalas & Suominen, 1979).

The capacity of *P. amphibia* to exist as two markedly different phenotypes has been recognised since the 17th century. The aquatic plant has glabrous, floating leaves with a long petiole whereas the terrestrial plant has pubescent, short-stalked leaves.

Are fruits eaten by wildfowl? Ridley says gadwall eat them, citing D.C. Marrott, USA Dept. Agric. Bull. 862 (1920).

47/8. *Rumex* L.

This is a genus of some 200, predominantly terrestrial species. Thirteen species are native to the British Isles.

This robust species is found in lakeside vegetation, by the side of rivers or ditches, or on riverine sand banks. In these localities it grows amongst tall, emergent vegetation; its most frequent associates are *Carex vesicaria*, *Deschampsia cespitosa*, *Eleocharis palustris*, *Equisetum fluviatile*, *Filipendula ulmaria*, *Phalaris arundinacea* and *Sparganium erectum*. There is also a large colony in a clearing in a swampy alder wood. The plants grow on eutrophic, sandy, silty or muddy soils; at a lakeside site it has been recorded near a sewage outflow and some colonies receive nutrient-enriched water from farmland. All sites are at altitudes below 20 metres.

R. aquaticus is a perennial which, like other *Rumex* species, is believed to be wind pollinated. In the largest British colony at least 89% of the seed is viable; in most other colonies the percentage of viable seed ranges from 55 to 76 (Hull & Nicholl, 1982). Mature plants with ripe fruit tend to topple over like wind-blown trees. Little is known of the conditions under which seeds germinate and seedlings become established in the wild.

R. aquaticus is known from fossil evidence to have been present in the late glacial period in Cornwall and N. Wales (Godwin, 1975). The only records of the living plant are from the shore of Loch Lomond, and by the Endrick Water which flows into the south-east corner of that loch. Most colonies are found on the flood plain of the Endrick, in areas which were drained for agriculture in the 18th century, but subsequently reverted to marsh and damp woodland. The species was not discovered in Britain until 1935 (Lousley, 1939, 1944). Its distribution around the south-east of Loch Lomond was mapped in 1967 by Idle (1968), and has not changed markedly in the last 25 years. However, two additional populations have been discovered, one on the west shore of Loch Lomond and the other by the Endrick 10 km upstream of the lake (Mitchell, 1983a, 1993). The known populations of the species do not appear to be threatened, and the relatively recent discovery of the plant in Britain suggests that it may be found elsewhere in northern England or lowland Scotland.

R. aquaticus is a circumboreal species. It has a rather continental distribution in Europe, extending from the arctic to Scotland, central France, the Alps and Bulgaria (Jalas & Suominen, 1979). The species is polymorphic, and several subspecies are recognised. The closely related *R. aquaticiformis* Rech. f. is found in Patagonia.

In Scotland *R. aquaticus* hybridises with *R. obtusifolius*, a terrestrial species. The hybrids tend to occur on drier ground than that normally occupied by *R. aquaticus*. The reduction in seed viability noted in some populations of *R. aquaticus* may be due to hybridity. Detailed accounts of *R. aquaticus*, from which much of the above information has been taken, are provided by Idle (1968) and Mitchell (1983b).

This species grows by still or slowly flowing, base-rich lowland waters, including lakes, slowly flowing rivers and associated ox-bows, canals and ditches. It is a species of eutrophic situations, and flourishes by lakes and ditches where submerged and floating species have been reduced in number or even eliminated by eutrophication. It is often found as scattered plants growing where stands of emergent vegetation join the open water; these emergents can include *Acorus calamus*, *Glyceria maxima*, *Iris pseudacorus*, *Phragmites australis* and *Typha latifolia*. *R. hydrolapathum* is less frequently found as a colonist of bare ground in marshes and fens, where it can temporarily occur in abundance: a 'great expanse' is described by Griffiths (1932) in an area of marshland which had previously been open water but had been partially drained 100 years earlier. However, it fails to persist in closed fen vegetation as established plants are outcompeted by surrounding vegetation and seeds are unable to germinate.

R. hydrolapathum is a wind-pollinated perennial. At Woodwalton Fen a plant of average size produces 16,000 fruits; more than 95% contain viable seed and this viability is not reduced by storage at room temperature for one year. Seeds at this site germinate in spring in areas of bare ground (Duffey, 1968). Seed dispersal is by wind and by water (Lousley & Kent, 1981). Under experimental conditions the germination requirements of *R. hydrolapathum* are similar to those of more terrestrial *Rumex* species: germination and growth is better in freely drained soils and soils where the water table lies 10 cm below the surface than in fully waterlogged conditions (Harper & Chancellor, 1959). Plants do not flower in their first year.

In southern England *R. hydrolapathum* has been lost from some sites because of the drainage of wetlands for agricultural use or for building, but it remains frequent in suitable habitats. In northern England and Scotland it has apparently extended its range in the last 100 years, probably by spread from sites where it was originally planted as an ornamental species. In Northumberland it was not recorded before 1890 but is now locally plentiful and possibly still spreading (Swan, 1993); in Angus it is apparently increasing (Ingram & Noltie, 1981).

R. hydrolapathum is virtually confined to Europe, only occurring elsewhere at sites in NW Anatolia and the Caucasus. In Europe it extends from southern Scandinavia to Sardinia, Italy and the Balkans, but it becomes rare towards the southern limit of its range (Hultén & Fries, 1986, Jalas & Suominen 1979).

This species is the foodplant of the extinct British subspecies of the Large Copper butterfly, and of the closely related Dutch subspecies which has been introduced to Woodwalton Fen. The butterfly lays its eggs on plants which grow in fen vegetation away from the water's edge, but are not hidden by surrounding vegetation. These are not the optimum conditions for *R. hydrolapathum* and suitable conditions for the butterfly can only be maintained by management practises such as cattle grazing or peat cutting (Duffey 1968, 1977).

50. ELATINACEAE

A small family of two genera, *Bergia* and *Elatine*, and 36 species. The genus *Bergia* includes both aquatic and terrestrial species, most of which are robust and conspicuous. They are found in warm-temperate and tropical areas, although *B. capensis* L. is naturalised in Spain.

50/1. *Elatine* L.

This is a small genus of 12 species, all of which are small and inconspicuous. All the species are aquatic in the sense that they grow in sites which are at least seasonally submerged.

E. hexandra can be found at the edge of lakes, reservoirs, ponds and flooded sand and gravel pits. It is usually found on damp mud exposed at the water's edge, or in shallow water less than 0.5 m deep, but it can sometimes be found in water at depths of 2 metres or more (West, 1910). It tolerates a wide range of water chemistry from oligotrophic lakes in the uplands to eutrophic lowland sites; it is, however, absent from highly calcareous waters. This species can grow with the rarer *E. hydropiper*; other associates include *Eleocharis acicularis*, *Littorella uniflora* and (where the water is peaty) *Baldellia ranunculoides* and *Juncus bulbosus*. Most sites are in the lowlands but *E. hexandra* ascends to 425 m at Llyn Gynon; a record from nearly 500 m in the Scottish Highlands (Hooker, 1884) has not been localised.

This species usually behaves as a summer annual, although submerged plants may persist as short-lived perennials. Individuals spread by the growth of the prostrate stem, but most reproduction is by seed. Plants in deep water do not flower, but flowers develop in shallow water and, more freely, on exposed plants. Submerged flowers are cleistogamous and produce fewer seeds than the open but self-fertilised terrestrial flowers. Seeds are dispersed by water and probably also by birds, as when wet they readily adhere to most surfaces. Seed which ripens in summer can germinate immediately, giving rise to a second generation of plants in a single season. Populations of *E. hexandra* vary in size from year to year. When water levels are low and much substrate is exposed enormous numbers of plants can arise from dormant seed: one reservoir pool near Devil's Bridge contained an estimated 12 million plants in 1984. For a detailed account of the reproductive biology of this species, see Salisbury (1967).

The inconspicuousness of *E. hexandra*, coupled with its tendency to vary in numbers from year to year, means that it is easily overlooked. In recent years it has been found at many new sites in Wales, N. England, Scotland and W. Ireland. This almost certainly reflects the increasing amount of systematic fieldwork rather than any increase in the frequency of the plant itself. *E. hexandra* has, however, disappeared from some of its old sites in south-east England; the decline is particularly marked in Sussex (Hall, 1980) but has been offset in other counties by the appearance of new colonies in gravel pits.

E. hexandra is widespread in western and central Europe, from southern Scandinavia south to Portugal, N. Spain and N. Italy. Elsewhere it is only known from N.W. Africa.

This species is found in shallow water (up to 1m deep) at the edges of lowland lakes, reservoirs, ponds and old sand and gravel pits, or on damp mud or silty sand around the water's edge. It is therefore found in the same habitat as *E. hexandra*, with which it often grows, but unlike that species it is virtually restricted to mesotrophic or eutrophic sites. Characteristic associates include *Callitriche hermaphroditica*, *C. stagnalis*, *Eleocharis acicularis*, *Littorella uniflora*, *Lythrum portula* and *Persicaria amphibia*.

The reproductive biology of this species is similar to that of *E. hexandra*. Both submerged and terrestrial plants will flower, but the terrestrial individuals flower and fruit more profusely. Seeds are dispersed by water and by birds: Kerner (1894), working in central Europe, found that *E. hydropiper* was one of the species most frequently found as seeds in mud on the feet of waterside birds. Populations fluctuate greatly in numbers from year to year, being largest in summers where the rainfall is low and much bare mud is exposed.

The history of *E. hydropiper* in Britain is remarkable. It was first recorded in Anglesey in 1830, and subsequently found at a few localities in the Midlands and south-east England. It was, however, last seen in Berkshire in 1917, Staffordshire in 1923, Surrey in 1935 and Sussex in 1935, so that by 1960 it appeared to be restricted to single sites in Worcestershire (Westwood Great Pool) and Anglesey (Llyn Coron). However, the species was found at Loch Lomond in 1968, the first Scottish record (Idle *et al.*, 1970), and it has subsequently been found at a further nine sites in Scotland. *E. hydropiper* has also been discovered since 1960 at additional sites in Worcestershire and North Wales. It is difficult to account for the extinction of this species, but the survival of *E. hexandra*, in southern England. The reason for the apparent spread in Scotland is equally unclear: the species may have been overlooked before 1968 or it may have been spread recently by wildfowl, as Mitchell (1981) suggests. In Ireland the species also appears to have increased in the Lough Neagh area since it was first recorded there in 1837 (Harron, 1986).

E. hydropiper has a more continental distribution than *E. hexandra*, being widespread in northern and central Europe with scattered localities in the mountains further south. It is also recorded in NW Africa, and extends eastwards to E. Asia.

Two taxa are recognised within European *E. hydropiper*, which Uotila (1974) treats as species. The British plant is *E. hydropiper sensu stricto*; *E. orthosperma* Düben has an even more continental distribution than *E. hydropiper*.

62. BRASSICACEAE (CRUCIFERAE)

A large family of some 390 genera and 3000 species. Almost all of these are terrestrial, many of them weeds of cultivated land, waste ground or other open habitats. An excellent identification guide to the British and Irish species is available (Rich 1991). Only c. 9 species in the entire family are aquatic. Aquatic species of *Rorippa* and *Subularia* occur in our area but the third genus which contains aquatics, *Cardamine*; is only represented here by terrestrial taxa.

62/12 *Rorippa* Scop.

A genus of some 70 species, including only four aquatics but a number of other species which grow near water or in seasonally inundated habitats. Most of the species are native to temperate regions.

The British and Irish species of *Rorippa* fall into two groups. One group consists of the white-flowered species which form the *R. nasturtium-aquaticum* aggregate. These are sometimes segregated in the genus *Nasturtium* R. Br. The aggregate contains two closely related species, *R. microphylla* and *R. nasturtium-aquaticum sensu stricto*, and their hybrid, *R. × sterilis*. These taxa occur in similar habitats. In the following text the aggregate species is mapped first, and its ecology and distribution described. The segregates are then mapped separately, with a text which only deals with their particular characteristics. Our knowledge of the distribution and ecology of the segregates is limited because they can only be identified from fruiting material, and many records are therefore only referable to the aggregate. In addition to this unavoidable difficulty, many authors of county floras (especially in southern England) appear to combine records of the aggregate with those of *R. nasturtium-aquaticum sensu stricto*, thus obscuring the relative distribution of the taxa.

The second and larger group of species in our area are the yellow-flowered species in *Rorippa sensu stricto*. The only aquatic species in this group is *R. amphibia*, but the other native plants in this group (*R. islandica*, *R. palustris* and *R. sylvestris*) are usually found in waterside habitats, and can be particularly frequent in sites which are flooded in winter but dry out in summer. *R. amphibia* and its hybrids with *R. palustris* (*R. × erythrocaulis*) and *R. sylvestris* (*R. × anceps*) are treated in the following text. Much of the information in the accounts of these taxa is taken from Jonsell's (1968) masterly account of the north-west European species; Jonsell (1975) is also a useful source of information on *R. × anceps*.

The taxa in this aggregate are plants of wet ground and of shallow water. They are most frequent in or alongside ditches, streams and rivers, occurring in mildly acidic or basic water but in particular abundance in calcareous water (even if this is flowing over base-poor substrates). Their ability to grow terrestrially means that they are well adapted to growth in streams where the water only flows intermittently, including the winterbournes of southern England. Although particularly frequent by running waters, they also grow by lakes, ponds, turloughs, canals and in marshes, where they occur both in open habitats and amongst emergents such as *Glyceria maxima*, *Phalaris arundinacea* and *Sparganium erectum*. They are found over a range of mineral substrates including sands, gravels, silts and clays, but do not grow over peat. *Apium nodiflorum*, *Mentha aquatica*, *Myosotis scorpioides* and *Veronica beccabunga* are characteristic associates. All the taxa in the aggregate are predominantly lowland, only rarely being found above 300m.

These plants are perennials which will flower in their first year. The aggregate contains two fertile species and a sterile hybrid: details of the sexual reproduction are therefore given under the individual taxa. All the taxa reproduce vegetatively by the growth of creeping stems which root at the nodes, and 'detached stem pieces have a remarkable ability to root and form new plants' (Grime, Hodgson & Hunt, 1988). Plants normally overwinter as small individuals, but they will continue to grow through the winter in water which is issuing from chalk springs at a constant temperature.

This aggregate is frequent in lowland Britain and Ireland, and is only absent from the most acidic and oligotrophic areas. It has long been grown for watercress, although it was not cultivated on a large scale until the early nineteenth century. Although all three taxa in the aggregate are undoubtedly native, the extent to which their natural distribution has been modified by the spread of cultivated stock is unknown. There is no evidence that their national distribution has changed in recent years.

R. nasturtium-aquaticum sensu lato is widespread in Europe, north to Scotland and S. Sweden. It extends eastwards through Turkey and Iran to the western edge of the Himalaya. It is widely naturalised in N. America (Green, 1962) and in many parts of the southern hemisphere.

For an account of the ecology of the plants in this aggregate, see Howard & Lyon (1952).

R. microphylla and *R. nasturtium-aquaticum* grow in similar habitats, and sometimes in mixed populations. However, some differences in their ecological requirements are apparent in areas where there is a range of soil types and relief. In Gloucestershire *R. nasturtium-aquaticum* tends to be restricted to calcareous soils (Airy Shaw, 1949). In the Sheffield area *R. nasturtium-aquaticum* is the usual species of low-lying calcareous springs, being replaced by *R. microphylla* or *R. × sterilis* at higher altitudes or on non-calcareous soils (Grime, Hodgson & Hunt, 1988). These preferences have also been noted by Graham (1988) in Co. Durham. *R. nasturtium-aquaticum* appears to be exclusively lowland, and there are no confirmed records above 300m.

This species is a fertile tetraploid ($2n=32$). Although it is normally perennial, it can behave as an annual in sites where the mature individuals are killed by summer drought (Howard & Lyon, 1952). It is self-compatible and regularly sets fruit by self-pollination, although flowers are visited by small insects and some cross-pollination is thought to occur. Freshly shed seeds will float and are capable of germinating immediately. Those which fail to germinate probably retain viability for a period, as Howard & Lyon (1952) obtained 32% germination after seeds had been stored in packets for 5 years. Seedlings have been observed on bare soil, but the species is thought to be incapable of reproducing by seed in closed vegetation.

The differences between this species and *R. microphylla* were set out by Howard & Manton (1946) in a classic cytotaxonomic study. The accounts by Howard & Lyon (1950, 1951) brought the species to the attention of most British and Irish botanists, and provided a provisional assessment of their distribution. The above map is based on records of *R. nasturtium-aquaticum sensu stricto*. The mapped records should be fairly reliable, but the species is almost certainly under-recorded. It is known to be more frequent than *R. microphylla* in southern England, but rarer in north-east England and eastern Scotland. There is little information on the relative frequency of the two in Ireland, although Hackney (1992) comments that they seem to be equally common in the north-east.

R. nasturtium-aquaticum is found throughout the European range of the aggregate, and also extends into western Asia. It is the most frequent segregate in many of the areas where watercress is naturalised, including N. & S. America (Green, 1962) and Australasia (Aston, 1973).

This is one of the members of the aggregate which is grown as watercress. Howard & Lyon (1952) reported that pot-grown plants were considerably less frost-resistant than the those of the other two segregates, and this may be one reason for its more southerly distribution.

Rorippa × sterilis Airy Shaw (*R. nasturtium-aquaticum* (L.) Hayek × *R. microphylla* (Boenn.)
N. Hylander ex A. & D. Löve) Hybrid water-cress

R. × sterilis can sometimes be found growing with both of its parents, but it also occurs in sites where one or both parents are absent. Howard & Lyon (1952) suggest that it may have pH and calcium requirements which are intermediate between those of its parents, but there has been little subsequent research on this. In the Sheffield area the hybrid tends to replace its parents in the uplands, particularly in limestone areas (Grime, Hodgson & Hunt 1988), and nationally it is recorded at a higher altitude than either of its parents, reaching 395 m in flushes E. of Craig Cerrig-Gleisiad.

R. × sterilis is a sterile hexaploid ($2n=48$). Most of the pollen is sterile and the fruits contain only the occasional well-formed seed. Effective reproduction is entirely vegetative.

The characteristics of this hybrid were outlined by Howard & Manton (1946) and Howard & Lyon (1950), and the name *R. × sterilis* was given to it by Airy Shaw (1951). The distribution of the hybrid is still imperfectly known. Populations which occur in the absence of the parents could have originated by vegetative dispersal from naturally occurring clones, or from cultivated stock.

R. × sterilis is 'fairly common' in Europe (Tutin *et al.*, 1993) but its detailed distribution has not been documented. It is also naturalised in north-eastern states of the U.S.A., Japan, New Zealand and almost certainly elsewhere.

Hybrids between *R. microphylla* and *R. nasturtium-aquaticum* and can be produced artificially if *R. microphylla* is the female parent. The hybrid is the plant which is most frequently cultivated as watercress. In cultivation it is more frost resistant than *R. nasturtium-aquaticum* (Howard & Lyon, 1952).

Rorippa microphylla (Boenn.) N. Hylander ex A. & D. Löve Narrow-fruited Water-cress

This species extends into somewhat more acidic sites than *R. nasturtium-aquaticum*. In Gloucestershire and the Sheffield area it is the most common segregate on non-calcareous soils (Airy Shaw, 1949, Grime, Hodgson & Hunt, 1988) and in Co. Durham it is more widespread than that species in acidic water and ascends higher up the dales (Graham, 1988). It is recorded from sea-level to 365 m (Malham Tarn).

R. microphylla is an octoploid ($2n=64$). It is a fertile plant with similar floral biology and germination requirements to *R. nasturtium-aquaticum*.

This species was initially described as *Nasturtium uniseriatum* by Howard & Manton (1946), but Airy Shaw (1947) concluded that the earlier name *Nasturtium microphyllum* was almost certainly based on the octoploid plant, and therefore had priority. The species is almost certainly under-recorded. However, there is no doubt that it is more frequent than *R. nasturtium-aquaticum* in those areas of northern England and eastern Scotland for which reliable records are available. These areas include Durham (Graham, 1988), Northumberland (Swan, 1993), Berwickshire (Braithwaite & Long, 1990), Angus (Ingram & Noltie, 1981) and East Ross (Duncan, 1980).

This species is recorded from much of the native range of the *R. nasturtium-aquaticum* aggregate. In Europe it is commoner than *R. nasturtium-aquaticum* in Denmark and The Netherlands, and extends south and east to Poland and Greece, but the details of its distribution are still imperfectly known (Tutin *et al.*, 1993). It is known to be naturalised in C. & S. Africa, N. America (especially in south-eastern Canada and north-eastern U.S.A.), Australia and New Zealand.

This is the only member of the aggregate in Britain and Ireland which is not commercially cultivated as watercress. It is believed to have evolved following hybridisation between *R. nasturtium-aquaticum* and some other species, the identity of which is not known. Because the seeds of *R. microphylla* tend to occur in one rather than two rows, Howard & Manton (1946) suggested that the other parent is a species of *Cardamine*, but the great similarity of *R. microphylla* to *R. nasturtium-aquaticum* suggests that it is more likely to be an undiscovered member of the *R. nasturtium-aquaticum* aggregate.

Rorippa × *erythrocaulis* Borbás (*R. palustris* (L.) Besser × *R. amphibia* (L.) Besser)
Thames Yellow-cress

This hybrid has been recorded from the banks and artificial embankments of large rivers, ditches near rivers and from mud in a reed bed. It is sometimes found in the absence of one or both parents. It is confined to the lowlands.

This hybrid is a vigorous perennial. The well known population along the Thames is a triploid hybrid between the diploid cytotype of *R. amphibia* ($2n=16$) and *R. palustris*, which is a tetraploid ($2n=32$). It is highly sterile, producing no good pollen, but spreads vegetatively. A plant from a ditch near the R. Avon at Tewkesbury has also been investigated cytologically and has the tetraploid cytotype of *R. amphibia* ($2n=32$) as one parent. This hybrid is much more fertile, with 85% good pollen. As diploid *R. amphibia* is only known from the Thames, hybrids from other localities are likely to involve the tetraploid plant.

This hybrid was first detected in Britain by Britton (1909), who discovered it in several places along the R. Thames between Putney and Richmond, and in particular abundance on the sloping river wall near Hammersmith. Lousley (1976) reported that it was still plentiful by Hammersmith Bridge in 1932, but later became much rarer as a result of the rebuilding of the embankment. Nevertheless, it was still present at Hammersmith Bridge in 1989, growing with *R. amphibia* but not *R. palustris*. There are records of the hybrid from several other localities, but little detailed information on its ecology, distribution or abundance at these sites is available.

According to Rich (1991), the only confirmed records of this hybrid are from Britain and Sweden, although it has been reported from central and eastern Europe. Tutin *et al.* (1993) state that it is fairly frequent in Europe.

Jonsell's (1968) attempts to synthesize the triploid hybrid between *R. amphibia* and *R. palustris* failed. His artificial tetraploid hybrids were similar to the wild plant, but much less fertile.

Rorippa × *anceps* (Wahlenb.) Reichb. (*R. sylvestris* (L.) Besser × *R. amphibia* L.) Hybrid
Yellow-cress

Most of the British records of this hybrid are from river banks; in Ireland it appears to be at least as frequent on the shores of lakes as it is by rivers. Other habitats from which specimens have been collected include ponds, wet ditches, marshes, damp fields and a rubbish dump. The hybrid requires more open habitats than those of *R. amphibia*. All the sites are lowland.

This hybrid is a fertile perennial, and is capable of reproducing by seed as well as by vegetative means. Like the parents, the hybrid is self-incompatible. Some populations have rhizomes derived from *R. sylvestris*, and these assist in local vegetative spread.

Although this hybrid has been recognised at some British and Irish localities for many years, it is almost certainly under-recorded and it may be much more frequent than the map suggests. Jonsell (1968) commented that British records of this hybrid were sparse, but he concluded as a result of his field and herbarium studies that extensive hybridisation had taken place along some river systems. There is also evidence that the hybrids have backcrossed to the parents. All the plants of *R. sylvestris* from the R. Severn and R. Wye seen by Jonsell (1968) showed distinct signs of introgression with *R. amphibia*. Jonsell (1968) also suggests that Irish plants of *R. amphibia* have a distinctive leaf shape which may be attributable to introgression with *R. sylvestris*.

This is a frequent hybrid in Europe, although (like *R. amphibia*) it is rare in the Mediterranean region. The European plants include a series of hybrid derivatives which bridge the morphological divide between the parents. The hybrid also occurs as an introduction in N. America (Stuckey, 1972).

Hybrids in our area include both tetraploid plants, which are derived from crosses between tetraploid *R. amphibia* ($2n=32$) and tetraploid *R. sylvestris* ($2n=32$), and pentaploids, derived from crosses between tetraploid *R. amphibia* and hexaploid *R. sylvestris* ($2n=48$). There is no cytological evidence that diploid *R. amphibia* ($2n=16$) has hybridised with *R. sylvestris*, but records of *R. × anceps* from the Thames at Chertsey and Richmond suggest that it may have done so. Most of our knowledge of its distribution comes from herbarium specimens, and many of the details of its reproductive biology, distribution and habitat requirements need to be established by fieldwork.

This species grows in lowland sites which are flooded in winter, and where shallow water may persist through the summer or recede to leave a damp and often muddy substrate. It often grows amongst the fringe of emergents along the edge of streams or rivers, or on riverside banks of muddy shingle or silty gravel. Other habitats include canals, fenland drains, the sheltered shores of lakes and reservoirs, ditches, ponds (especially on flood plains), turloughs and marshes. *R. amphibia* is usually found where the water is both calcareous and eutrophic. In rivers it is most frequent where calcareous water flows over a clay substrate, as the water level in clay rivers is subject to marked fluctuations, but the substrate is sufficiently deep and stable to allow the development of a fringe of emergents (Holmes, 1983).

R. amphibia is a perennial. Plants are highly self-incompatible, and perhaps for this reason seed-set in the field is often poor. Seeds may become established in areas where the vegetation is open but relatively stable. Seedlings form a vegetative rosette in the first year and flower in subsequent seasons. Established plants spread by the formation of axillary leaf rosettes which develop at the base of flowering shoots towards the end of the season. Vegetative reproduction by fragmentation of the hollow stems and the subsequent dispersal by floods of stem fragments with axillary buds is probably the main method of spread along the edges of lakes and rivers.

R. amphibia is locally frequent in England as far north as the River Tees; there is no evidence that its frequency or abundance have changed appreciably in recent years. Populations in southern Scotland are probably introduced. In Ireland it is now known to be more frequent than the *Atlas of the British Flora* suggests, and it is probably still under-recorded.

This species is native to Europe, N. Africa and Asia. In Europe it is most frequent in the middle latitudes, being rare in the north and in the Mediterranean area. In Asia it is most frequent in the west but it is recorded in scattered localities eastwards to Japan. *R. amphibia* is also recorded as an introduction in N. America, where it was first reported in 1930 (Stuckey, 1972), Argentina and New Zealand.

Two cytotypes of *R. amphibia* are present in the British Isles. A diploid plant ($2n=16$) is only recorded from the Thames valley, where it is apparently the only variant present. The tetraploid ($2n=32$) is recorded from other localities in England and Ireland, and is the only cytotype recorded in Scandinavia. There is a strong sterility barrier between the cytotypes, and attempts to hybridise them have failed, and they appear to be genetically isolated.

62/32 *Subularia* L.

A genus of two species, the widespread *S. aquatica* and the rarer *S. monticola*, which is endemic to the E. African mountains. The species have an isoetid growth form but unlike other isoetids they are annuals or biennials, not perennials. The existence of a genus of isoetids in this predominantly terrestrial family is surprising, and provides a remarkable example of convergent evolution.

S. aquatica is most frequent at the edge of acidic, oligotrophic lakes but it can also grow in outflow streams and, exceptionally, in canals leading from them. It usually grows in water shallower than 1 m, although it can occur down to depths of at least 1.5 m. Plants occur as scattered individuals in open vegetation, with associates such as *Isoetes echinospora*, *I. lacustris*, *Littorella uniflora*, *Lobelia dortmanna*, the aquatic form of *Juncus bulbosus*, *Myriophyllum alterniflorum* and *Potamogeton gramineus*. They are also found amongst stems of *Carex rostrata*, *Eleocharis palustris* or *Equisetum fluviatile* where these emergents form open swamps. Substrates over which *S. aquatica* grows include fine silt, gravel and stones; in some areas it shows a preference for fine gravelly beds. Although it is one of the most reliable indicators of oligotrophic water, it has been found in more eutrophic lakes (Seddon, 1972) but it has not been recorded over base-rich substrates. Plants are able to tolerate short periods of emersion, although terrestrial forms are smaller than those which grow in water. *S. aquatica* is recorded from sea-level to 825 m at Ffynnon Llyffaint.

S. aquatica is more ruderal than the other isoetids (Farmer & Spence, 1986). Most plants are annuals. There is some doubt about the maximum possible longevity, but some individuals can overwinter as rosettes, thus behaving as biennials. Plants flower from June to September. Submersed plants may produce cleistogamous flowers or flowers which open fully; in either case they are self-pollinated while in bud. The flowers of terrestrial plants open fully, and may be insect-pollinated or self-pollinated. Individual plants produce 8-125 seeds, the terrestrial plants producing fewer than the aquatics. The seeds do not float, but germinate readily. *S. aquatica* lacks any means of vegetative reproduction.

The map of *S. aquatica* in the *Atlas of the British Flora* (Perring & Walters, 1962) grossly underestimates its distribution. It is an inconspicuous species, easily overlooked as it usually grows with other isoetids and rarely occurs in abundance. The species is probably still under-recorded in areas which have not been surveyed intensively, but is much less frequent than *Isoetes lacustris*, *Littorella uniflora* or *Lobelia dortmanna*. Woodhead (1951) considered that it was less abundant at the time he was writing than it had been 90 or even 25 years previously. However, little evidence is available to assess trends in the abundance of *Subularia* in the western parts of Britain or Ireland. Like *Isoetes lacustris* and *Lobelia dortmanna*, it has certainly been lost from some sites at the eastern edge of its range because of eutrophication. Its disappearance from Lough Neagh, where it was first recorded in the British Isles in the 1690s and was formerly plentiful, may be attributable to the lowering of the water table in the 19th century (Harron, 1986).

S. aquatica has a more or less circumboreal distribution, although it is rare in Asia (Hultén & Fries, 1986). It is widespread in N. Europe, and although absent from the Alps extends south very locally to the Pyrenees and Bulgaria. American plants have been described as *S. aquatica* subsp. *americana* Mulligan & Calder.

An account of the ecology of *S. aquatica* is given by Woodhead (1951). Few publications since then have dealt with its ecology in any detail, and the species is too scarce to figure prominently in general accounts of aquatic vegetation.

69. PRIMULACEAE

This is a predominantly terrestrial family of 22 genera and 800 species. The only truly aquatic genus in Europe is *Hottonia*, but species of *Anagallis*, *Lysimachia* and *Samolus* can be found in waterside communities, fens and swamps in Britain and Ireland. Some African *Anagallis* species are submerged aquatics.

69/2. *Hottonia* L.

There are two species of *Hottonia*, the Eurasian *H. palustris* and the American *H. inflata*. The American species differs from ours in being an annual, with small autogamous flowers, and in having swollen and bouyant flowering stems.

This species is confined to small, sheltered, lowland water bodies, where it grows submerged in shallow water or as a terrestrial form at the water's edge. Almost all records are from ponds, ditches and fenland drains. *H. palustris* is notably shade-tolerant and can sometimes be found in ponds in woods and plantations. It is also recorded as a colonist of pools in disused brick, gravel and sand pits, and disused canals. It is a plant of mesotrophic or meso-eutrophic, usually calcareous, water. It grows over both organic and mineral substrates but is often particularly frequent over peat. Characteristic associates include *Callitriche obtusangula*, *Elodea canadensis*, *Hippuris vulgaris*, *Myriophyllum verticillatum* and *Potamogeton lucens*.

This species is a shallow-rooted perennial. It remains green throughout the winter, and can survive periods when it is embedded in ice. It flowers in May; the aerial inflorescence arises from, and is supported by, a whorl of leaves just below the surface of the water. *H. palustris* is heterostylous, with 'pin' and 'thrum' flowers. The inflorescences remain above the water until the seeds mature. After the seeds are shed the flowering stems disintegrate and the fragments can become established as new plants. Plant fragments may be dispersed by birds or by machinery used to clear ponds and ditches. The seeds have no innate dormancy; they can germinate under a wide range of environmental conditions or survive at least 15 months desiccation. The seeds sink as soon as they are shed (Ridley, 1930) but most seedlings float for a period after germination in water. Seedlings develop much more rapidly on moist soil than in water. If mature plants are stranded above the water level they persist as a land-form with smaller, more rigid leaves.

H. palustris is a native species in England and Wales. Like many plants found in small water bodies it has decreased in many areas because of the in-filling of ponds, and the mechanical dredging or elimination of drainage ditches. The conversion of grazing marshes to arable land has also had an adverse effect on this species (Palmer, 1986). An isolated Scottish population in the Culbin Forest may have been introduced by waterfowl; it persisted from 1923 until the pond in which it grew dried up in 1958 (McCallum Webster, 1978). In Ireland the species is probably introduced at all its sites. The only area where it might be native is in Co. Down, where it was first recorded in 1810. Here it has declined and is now very rare (Hackney, 1992).

This species is virtually confined to Europe, where it is found from C. Sweden south to S. France, C. Italy and Romania; it is absent from the Mediterranean area. It just extends into W. Asia (Hultén & Fries, 1986).

A detailed account of *Hottonia* is provided by Prankerd (1911), and valuable additional observations on the reproductive biology of *H. palustris* have been published by Fitter & Smith (1979) and Brock, Mielø & Oostermeijer (1989). Both recent authors conclude that *H. palustris* is probably favoured by fluctuating water levels. Emerged stands have a higher biomass than submerged stands; and reproduction by seed is more likely if water levels fall during the late summer, and seedlings are able to grow on newly exposed mud (Fitter & Smith, 1979).

73. CRASSULACEAE

This family is widespread in both temperate and tropical areas. Most of the 33 genera and 1280 species are succulent herbs or shrubs, but the genus *Crassula* includes a few aquatics.

73/1. *Crassula* L.

Only 10 of the 300 species of *Crassula* are aquatics. Two of these occur in our area: *C. aquatica* is apparently native whereas *C. helmsii* is a widespread introduction.

At its Scottish locality *C. aquatica* grows at the side of the R. Shiel, and in a ditch and a shallow scrape created for ducks nearby. In the sheltered shallows of the river it can grow as scattered plants or in dense swards in water up to 25 cm deep, associated with frequent *Glyceria fluitans* and *Alisma plantago-aquatica*, *Callitriche* sp., *Eleocharis palustris*, *Elodea canadensis*, *Hydrocotyle vulgaris*, the aquatic form of *Juncus bulbosus*, *Littorella uniflora*, *Persicaria hydropiper*, *Ranunculus flammula* and *Fontinalis antipyretica*. It also grows terrestrially as scattered plants on moist and rather bare sandy soil, with *Agrostis stolonifera*, *Galium palustre*, *Gnaphalium uliginosum*, *Juncus bulbosus*, *Ranunculus flammula*, *Viola palustris*, *Fossombronia* sp. and *Pellia epiphylla*. In Yorkshire *C. aquatica* grew in shallow water at the edge of an artificial lake, and with *Callitriche stagnalis*, *Limosella aquatica*, *Persicaria hydropiper*, *P. minor* and *Rorippa palustris* on damp mud. Both sites are below 300 m.

C. aquatica is a small annual which presumably germinates in spring and summer. Plants flower and fruit in August and September. Both terrestrial and aquatic plants flower freely. The flowers are inconspicuous and are probably automatically self-pollinated. The number of plants in the Scottish population varies from year to year: the plant was present in 1969 and 1971, for example, but could not be found in 1970 (Sowter *et al.*, 1972).

C. aquatica was first discovered in Britain at Adel Dam in 1921 (Butcher, 1921). It increased in abundance in the years following its discovery, but later declined as the soft mud on which it grew became colonised by dense beds of *Carex rostrata*, *Juncus effusus* and *Typha latifolia* (Sledge, 1945). It was last seen in 1938 and had gone by 1945. The Westernness population was discovered in 1969, when it occupied an area of c. 6 square metres (Sowter, 1971). In 1990 it was present along a length of river at least 200 m long, but the population has not been surveyed sufficiently frequently to establish whether this represents a long-term increase or whether numbers simply fluctuate from season to season.

This species is widespread in the northern hemisphere but has a disjunct distribution. The main concentrations of records are from Europe, E. Asia and both western and eastern N. America, south to Mexico, but it is also recorded at scattered localities elsewhere. In Europe it occurs from Iceland and northern Scandinavia south to Austria.

It is difficult to account for the presence of this species in just two British sites, but their disjunct nature and their northerly location fit in with the European distribution of the species. The tiny seeds may have arrived on the feet of aquatic birds, as Druce (1922) suggests. The Scottish site is a salmon river, and *C. aquatica* could have been brought to this site on the waders of a visiting fisherman.

CHK:Keeley & Morton, *Photosynthetica* 16:546-53, 1982.

This introduced species grows on damp ground or in sheltered, standing or very slowly flowing water up to 3 m deep. In swamps or shallow water it grows as an emergent, and it can be present in dense masses which may exclude competing species. In deeper water the submerged stems grow in more open stands with species such as add list. *C. helmsii* is usually found in ponds but it is also an increasingly frequent colonist of flooded sand and gravel pits; additional habitats include lakes, reservoirs; marl pits, dune slacks, canals, ditches and fenland drains. It grows over a range of soft substrates including clay, coarse and fine silt and peat, and tolerates a wide range of water chemistry from nutrient-poor and acidic to eutrophic and calcareous. It is usually absent from exposed sites with wave-washed gravel substrates and from very soft, easily disturbed silts. It is confined to the lowlands.

C. helmsii is a monoecious perennial which remains green throughout the winter months. Flowers are only produced on the emergent stems; submerged populations persist in a vegetative state. British plants set seed but this may not be viable, as Dawson & Warman's (1987) efforts to germinate it failed. Effective reproduction is by vegetative fragmentation: a portion of stem with only a single node can become established as a new plant. Plant fragments may be inadvertently introduced into ponds when the contents of aquaria are emptied out, or spread on footwear or fishing tackle. Spread by animals such as waterfowl or (in some areas) ponies is thought to be a less important means of dispersal, but this is a difficult subject to study and few direct observations on the method of spread are available.

This species has been sold commercially in Britain since 1927 as an aquatic suitable for outdoor ponds. It was first discovered as a naturalised plant in 1956, when it was found in a pond at Greensted (Laundon, 1961). There were relatively few additional records until the 1970's, when the species began to be reported from scattered sites in southern England. This spread has continued, and the number of recorded sites currently doubles every 2-3 years.

C. helmsii is a native of S.E. Australia, Tasmania and New Zealand. In addition to its localities in our area it has been reported as an introduction in Belgium and Russia.

This account is based on the detailed study of *C. helmsii* by Dawson & Warman (1987). The rapid spread of this species has caused considerable concern because of its ability to outcompete native vegetation in shallow ponds. In areas such as the New Forest *C. helmsii* may represent a threat to the habitat of several rare or scarce plant species (Byfield, 1984). Methods of control are discussed by Dawson & Warman (1987) and in a leaflet published by the Natural Environment Research Council.

75. ROSACEAE

There are 107 genera and 3100 species in the Rosaceae. The family includes both shrubby and herbaceous genera, many of which make an important contribution to the vegetation of temperate regions. Cook (1990) does not classify any members of the family as aquatics, but one species qualifies for inclusion in this work.

75/9. *Potentilla* L.

This is a large genus of 500 species of shrubs and herbs, most of them plants of the north temperate and boreal zones, although a few occur in south temperate regions. The single species considered here is sufficiently different from the others to have been placed by Linnaeus in its own genus, as *Comarum palustre* L. It is now regarded as the sole European (are there any others?) representative of Subgenus *Comarum* (L.) Syme.

This species grows in permanently flooded swamps, and in mires and wet meadows where the water table lies below the soil surface during the summer months. In swamps it usually grows in shallow water (less than 20 cm deep) at the edge of oligotrophic or mesotrophic lakes. It usually occurs amongst open stands of *Carex rostrata*, but it can also be found with *C. vesicaria*, *Equisetum fluviatile*, *Phragmites australis* and *Schoenoplectus lacustris*. *Menyanthes trifoliata* is a characteristic associate. *P. palustris* is also frequent and locally abundant in mires at the edges of lakes, in natural hollows, bog pools, peat cuttings and on floating rafts which extend out over the surface of lakes and pools. It favours sites where the water is nutrient-poor but slightly or moderately base-rich; in very acidic and oligotrophic mires it is confined to areas where there is an inflow of base-rich water. It often grows with *Carex rostrata*, *Equisetum fluviatile*, *Galium palustre* and *Mentha aquatica* and bryophytes such as the more base-tolerant sphagna or, in more calcareous sites, pleurocarpous species such as *Campylium stellatum*, *Calliergon cordifolium*, *C. cuspidatum*, *Plagiomnium* spp. and *Scorpidium scorpidioides*. *P. palustris* grows over a wide range of organic and mineral soils. It will persist in sites which have become partially shaded by the encroachment of willow or alder carr. It ranges from sea-level to 800 m at Tom a'Choinnich (McVean & Ratcliffe, 1962); there is an unlocalised record from 850 m in the Scottish Highlands (Hooker, 1884).

P. palustris is a rhizomatous perennial. The flowers are self-compatible and are visited by a range of insects. Cross-pollination enhances seed-set but in the absence of insect visitors flowers will self-pollinate and produce some seed (Olesen & Warncke, 1992). The seeds will float for long periods (Ridley, 1930), but little is known about the circumstances under which the species reproduces by seed. Established plants spread by growth of the rhizome, and floating rafts of vegetation are often bound together by the rhizomes of *Menyanthes trifoliata* and *P. palustris*.

This distinctive species is still frequent in northern and western parts of Britain and Ireland. Like many species of mires it has decreased in S.E. England, where it is extinct in a number of vice-counties, including Bedfordshire (last recorded in 1969), Cambridgeshire (1886) and Hertfordshire (1919), and in others is confined to a few populations.

P. palustris is a circumboreal species which is found in arctic and boreal regions throughout the northern hemisphere (Hultén & Fries, 1986). In Europe it extends southwards in the mountains to Spain, Italy and Bulgaria.

Further detail of many of the plant communities in which this species grows can be found in Rodwell (1991, in press (swamps)).

Chk Praeger and W-Peacock for floating seeds.

79. HALORAGACEAE

This is a small family of 9 genera and 120 species. All the native European species are members of the largest genus, *Myriophyllum*. The other genera include both terrestrial and aquatic plants, most of which are found in the tropics and the southern hemisphere. One species, *Haloragis micrantha*, was recently discovered naturalised in western Ireland, where it grew in a very wet, peaty heath (Green, 1989); it is often found in water in its native range (Cook, 1990).

79/2. *Myriophyllum* L.

This genus includes some 60 species. All are aquatics, but the genus includes both submerged plants and emergents as well as some species which can be found in seasonally flooded habitats. The genus attains its greatest diversity in Australia, where many new species have been discovered in recent years.

All three native species of *Myriophyllum* have inflorescences in the form of terminal spikes which project above the water level. These bear female flowers in the lower half and male flowers towards the apex; the sexes are often separated by a few hermaphrodite flowers. The flowers are well adapted to wind pollination (Cook, 1988), with petals which are very small or absent.

M. verticillatum grows in still or slowly flowing, calcareous water in lowland lakes, ponds, streams, canals, fenland drains and disused clay and gravel pits. It is a plant of clear or somewhat turbid water which is moderately but not excessively eutrophic: in the Norfolk Broads it increased in abundance when nutrient levels first began to rise but then declined to extinction as eutrophication continued (George, 1992). It can grow in abundance in suitable habitats, where its associates often include *Elodea canadensis*, *Hippuris vulgaris*, *Lemna trisulca*, *Potamogeton crispus*, *P. natans* and *Ranunculus circinatus*. *M. verticillatum* can be found over a range of substrates including both peat and mineral soils. It can persist as a terrestrial form for brief periods if stranded above the water level.

M. verticillatum is a perennial species. Seed is set in Britain but little is known about its subsequent fate. Vegetative spread is probably more important than sexual reproduction. The species overwinters as turions, which develop on the stems in late August and September. Field studies in Michigan have shown that the turions are initially dormant but germinate in the early months of the year, when the water temperature is still 0-4°C. Under experimental conditions their dormancy is broken by cold treatments of 0-4°C. Detached stems initially float and produce turions much earlier than rooted plants. They eventually sink and develop adventitious roots, and can therefore become established as new plants (Weber & Noodén, 1974, 1976).

Fossil evidence suggests that this species may have been present in the British Isles throughout the Pleistocene (Godwin, 1975). The map indicates that in Britain its distribution has contracted in recent years, and this conclusion is supported by detailed local studies (Mountford, 1994). The reasons probably include eutrophication, habitat destruction (the filling in of ponds and ditches) and land-use change (particularly the conversion of pasture to arable). The adverse effects of land use change on this species in coastal grazing marshes was demonstrated by Driscoll (1983, 1985), who found that it had decreased markedly in frequency in an area which was converted to arable in the late 1970s, but remained virtually unchanged in a similar area which was still managed as pasture. The apparent decline in Ireland may be due to under-recording.

M. verticillatum is widespread in the temperate regions of the northern hemisphere. In Europe it extends from northern Scandinavia to the Mediterranean area, but it is rare near the northern and southern edges of its range. Records from S. America are erroneous (Orchard, 1981).

Although both the inflorescences and the turions of *M. verticillatum* are distinctive, the identification of vegetative material is not always as simple as most floras imply. Records of *M. verticillatum* from outside its known range in Britain and Ireland should be treated with caution, as it is sometimes confused with *M. alterniflorum* or *M. aquaticum*. Many of the Welsh records listed by Ellis (1983), for example, have proved to be erroneous.

This introduced species is recorded from shallow, still or very slowly moving water in a range of lowland habitats. Most records are from ponds but *M. aquaticum* has also colonised reservoirs, flooded gravel pits, streams, canals and ditches. There is a single record from the shallows of the R. Wharfe near Otley, but this population may not have persisted. Almost all the water bodies where *M. aquaticum* has become established are eutrophic, but it is difficult to generalise about the ecological requirements of the species from the scattered localities in which it has become established. It is able to persist as a terrestrial plant when ponds dry out, and has even been recorded on the dry bank of a council tip in West Cornwall (Grenfell, 1984).

M. aquaticum is a perennial which, unlike the native species, produces emergent as well as submerged shoots. The species is dioecious, with flowers which are borne in the axils of the upper emergent leaves. Both sexes occur in the native range of the species, but even there female plants very rarely set seed. Only female plants have become naturalised, and introduced populations spread by asexual means. There are no specialised vegetative propagules, but the stems are brittle and small fragments can become established as new colonies.

This species is widely grown in garden ponds in both Britain and Ireland. The first naturalised plants to be discovered were collected from a pond at Lingfield in Surrey in 1960 but misidentified as *Hottonia palustris* (Leslie, 1987). *M. aquaticum* was recorded in E. Sussex in 1969, W. Cornwall in 1972 and Glamorgan in 1975. It was subsequently found in an increasing number of sites in Britain, and it was discovered in clay pits in Ireland in 1990 (Hackney, 1992). It has survived the winter in ponds which became covered with ice during cold spells (Milner, 1979), and has persisted at individual sites for at least 10 years. Most populations probably originate as plants discarded from aquaria or garden ponds. Dawson (1993) noted that *M. aquaticum* is spreading less rapidly than *Crassula helmsii* because it does not produce the numerous small vegetative fragments which act as propagules in that species.

M. aquaticum is a native species of the lowlands of central S. America; its native range is mapped by Orchard (1981). Female plants are naturalised in warm temperate and tropical areas elsewhere in S. America and in Africa, Asia, Australia, New Zealand, N. & C. America and Hawaii. In mainland Europe it is naturalised in France and it is also recorded from Austria.

M. spicatum usually grows in water which is both calcareous and meso-eutrophic or eutrophic. It is found at depths of 0.5-3 m in lakes, ponds, rivers, streams, canals, major ditches and fenland drains, and in flooded quarries and clay, sand and gravel pits. It grows in both sluggish and rapidly flowing rivers, where it roots in a range of substrates but is perhaps more frequent over sand and gravel rather than over fine clay or silt. Like *Potamogeton pectinatus* and *Zannichellia palustris*, it often persists in highly eutrophic water from which other macrophytes have disappeared. *M. spicatum* can also be found with these species in brackish water, and it even grows in rocky cliff-top pools in western Scotland. Although normally found in eutrophic sites, it also occurs in abundance in highly calcareous but nutrient-poor limestone lochs. It is a primarily lowland species, which reaches 380 m at Malham Tarn and 520 m in Conny Pot Beck.

M. spicatum is a perennial which dies back to the roots in winter. Populations usually flower and set seed freely, unless they grow in deep or turbulent water. The seed can float for a few hours or a day. They exhibit prolonged dormancy, which can be broken mechanical or chemical treatments which rupture or erode the stony endocarp (Patten, 1955). Over 30% seeds dried and stored for seven years by Davis *et al.* (1973-CHK) germinated when rewetted. The seeds of *Myriophyllum* are eaten by wildfowl, including Pochard and Teal (Olney 1963, 1968), and these might act as dispersal agents. Reproduction by seed may be rare: in N. America seedlings have not even been found in lakes where an estimated 4 million seeds are set per hectare (Aiken *et al.*, 1979). Plants can regenerate vegetatively from axillary buds, which are easily detached, and from fragments of stem, which are shed naturally during the growing season as well as broken off by disturbance (Guppy, 1894; Aiken *et al.*, 1979). Turions have not been seen in British or Irish material, and have only rarely been reported from mainland Europe (Orchard, 1981). Plants survive periods of emersion in a terrestrial form.

Like *M. verticillatum*, this species may have been present in the British Isles throughout the Pleistocene (Godwin, 1975). It is still frequent in suitable habitats in Britain and Ireland. It may have increased in abundance in the last 150 years in some areas of grazing marsh (Mountford, 1994) and it has also invaded newly available habitats such as sand and gravel pits. These gains more than offset losses in other areas caused by the conversion of grazing marshes to arable land (Driscoll, 1983).

M. spicatum sensu lato is widespread in boreal and temperate regions of the northern hemisphere, extending south to N. Africa, the Himalaya and Japan. The native American populations differ morphologically from most of those in Eurasia, and regularly produce turions. Some authors treat them as a separate species, *M. exalbescens* Fernald, but Orchard (1981) concluded that they are best recognised as a variety of the Eurasian plant. The Eurasian taxon has been introduced into North America, where it behaves as an extremely aggressive aquatic weed, 'hampering fishing, boating, and swimming...choking out water plants, providing mosquito breeding habitats, and lowering real estate values' (Blackburn & Weldon, 1967).

For a more detailed account of the biology of this species, based on research in North America, see Aiken *et al.* (1979).

Myriophyllum verrucosum Lindley

This introduced species was formerly naturalised in a large, disused gravel pit at Eaton Socon. Here it grew in deep water in large pools in the gravel pit, and in a dwarfed terrestrial state on wet gravel. In its native range it is typically found in stagnant or slowly flowing water 30-60 cm deep, but it is also found in the relatively deep water of fast-flowing rivers and on damp mud (Orchard, 1985).

M. verrucosum is a perennial species. Brenan & Simpson (1949) described the flowers of the naturalised material as hermaphrodite; Australian plants are also monoecious but usually have male flowers at the top of the spike, female flowers below and hermaphrodites restricted to a zone between them (Orchard, 1985). The British plant flowered only sparingly when growing in water, but both flowers and fruits were produced in abundance in terrestrial habitats. In Australia it is an opportunistic species which can flower at any time of year. Plants in deep water do not flower but flowering is probably triggered by falling water levels, and terrestrial populations flower and fruit profusely (Orchard, 1985).

M. verrucosum was first collected in Bedfordshire in 1944, but initially identified as *M. verticillatum*. It was thoroughly naturalised by 1946, when its correct identity was established, but it failed to survive the severe winter of 1946-47. It was almost certainly introduced to Britain as seeds in Australian wool-shoddy, which was then extensively used by farmers and market gardeners as a manure and water-retaining agent. A number of other alien species of Australian origin were recorded in the gravel pit at Eaton Socon. For a detailed account of the Bedfordshire plant, see Brenan & Chapple (1949).

This species is a native of Australia, where it is the most widely distributed *Myriophyllum* species. It grows 'almost throughout the mainland wherever there is semi-permanent water available', and has spread into the arid regions by colonising stock watering facilities (Orchard, 1985). The British records are the only known occurrences outside Australia.

This species has a wide ecological amplitude, as it grows in standing waters, including lakes and pools, and in slowly or rapidly flowing streams and rivers. In addition to these natural habitats, it also colonises flooded quarries and gravel pits. In southern England and Wales it is confined to acidic and mesotrophic or oligotrophic water. In Scotland and Ireland it is most often found in such habitats, and it is one of the few macrophytes which are frequent in the acidic, peat-stained streams and rivers of the north and west. However, it can also grow in highly calcareous water, as in the lochs on the Durness limestone, although it is absent from sites which are both calcareous and eutrophic. It is found over a wide range of nutrient-poor substrates from fine sand, peat and marl to stones and boulders. It is usually found at depths of 0.3-3 m, but it can grow in a terrestrial state if exposed above the water level, and it descends to depths of 4.5 m in Loch Ness (West, 1905). It is frequent in both lowland and upland waters, ascending to 730 m at Carn a'Chuillin.

M. alterniflorum is a perennial species. Viable seed is set in Britain but little is known about the frequency with which new plants are established from seed. The species lacks specialised turions, but it can regenerate from short lengths of shoot. In north-west Scotland the species has proved to be very variable genetically, both within and between populations (Harris *et al.* 1992).

The fossil record of *M. alterniflorum* demonstrates that it has certainly persisted in the British Isles since the middle of the last glacial period, and it may have been continuously present for much longer (Godwin, 1975). It is frequent and locally abundant in the acidic areas of the north and west. Like many calcifuges, it has declined in the south and east where acidic habitats are infrequent and have often been destroyed. It was, for example, last recorded in Essex in the second half of the 19th century (Jermyn, 1974), and became extinct in Cambridgeshire, Hertfordshire and Leicestershire in the first half of the 20th (Perring *et al.*, 1964, Dony, 1967, Primavesi & Evans, 1988).

This species is found in the boreal and temperate zones of the northern hemisphere. In Europe it is most frequent in the north and west but extends south to Sicily. It is also recorded from N. Africa, eastern and western N. America and Greenland.

Pugsley (1937-CHK) drew attention to the presence of plants with very short leaves in shallow water in Lough Neagh and Lough Beg. He considered that these were similar to the normal variant of the species in N. America, and therefore named them *var. americanum*. They have now become very rare in these loughs, which have undergone eutrophication (Harron, 1986). However, similar plants have been reported from elsewhere in Ireland (Praeger 1937-CHK, Hackney, 1992) and also occur in the Hebrides. They may simply be compact, shallow-water phenotypes, but the problem requires reinvestigation.

Myriophyllum heterophyllum Michaux

This introduced species was formerly naturalised in a lowland canal between Halifax and Salterhebble. It grew in some quantity in a stretch of canal which also contained the alien aquatics *Potamogeton epihydrus* and *Vallisneria spiralis*.

M. heterophyllum is a monoecious perennial. The reproductive biology of the naturalised population does not appear to have been studied.

This plant was first discovered in its British locality in 1941 (Walsh, 1944). It persisted there until the drainage of the canal in ??? (Lavin & Wilmore, 1994).

M. heterophyllum is a native of N. America, where it extends from S.W. Quebec, Ontario and N. Dakota south to Florida and New Mexico. In its native range its habitats include ponds, lakes, streams, ditches, canals, swamps, sloughs and borrow pits (Godfrey & Wooten, 1981).

Look at Murgatroyd, 1991, Botanical Report (pp.1-12), in Natural History in Calderdale. Halifax Scientific Society.

Any more on American reproductive behaviour, habitats etc.?

81. LYTHRACEAE

Most of the 30 genera and 580 species in the Lythraceae are herbs, but the family also includes some trees and shrubs. Eight of the genera contain aquatic plants. The distribution of the family is primarily tropical, and only the most widespread genus, *Lythrum*, occurs as a native in western Europe.

81/1. *Lythrum* L.

This genus includes 38 species which range from robust perennial herbs to small annuals. Both these extremes are represented in the British Isles: *L. salicaria* is a perennial with a spectacular inflorescence and *L. portula* is an inconspicuous annual. The contrast is so great that *L. portula* was placed in the separate genus *Peplis* by Linnaeus, where it remained until Webb (1967) pointed out that the two species were linked by intermediates. The only aquatic species in our area is *L. portula*, but *L. salicaria* is frequent in fens and *L. hyssopifolia* is a rare species of seasonally flooded ground.

Two subspecies of *L. portula* are recognised in the British Isles. There is no evidence to suggest that they differ in their ecology, so the text accompanying the maps simply deals with their distribution and taxonomy.

L. portula is found in water and on damp ground by the water's edge. It is sometimes found in dense masses in shallow ditches, pools and sheltered lakes, occasionally occurring in water as deep as 1 m (West, 1910). However, it is much more frequently found in habitats which are flooded in winter but dry out in summer. Typical sites include the stony, gravelly or muddy margins of ponds, lakes and reservoirs, springs, flushes and moist streamsides, dried up pools and ditches, depressions in heaths and sand dunes, damp areas in sand and gravel workings and rutted tracks and woodland rides. It is a distinct calcifuge, which is typically found over base-poor mineral soils (including sands, gravels and clay) but avoids the most acidic and nutrient-poor soils and is rarely found over peat. The occurrence of a large population on limestone by Coole Lough in the Burren is exceptional, and an example of the anomalous behaviour of normally calcifuge species in western Ireland (Webb & Scannell, 1983). *L. portula* is a primarily lowland species, which ascends to 460 m at the source of the River Teme (Wilson, 1956).

Most plants of *L. portula* are prostrate, and easily root at the nodes, although erect variants sometimes occur (Salisbury, 1970). The species behaves as an annual in most sites but plants can persist as short-lived perennials, regrowing from the rooted stems in spring (Briggs, 1880). The flowers are usually self-pollinated (Knuth, 1911). Plants which grow in water fruit less readily than terrestrial individuals (Allen, 1954). The seeds are small and have no obvious adaptation to dispersal, but they somehow reach isolated sites such as disused gravel pits. The seeds require light for germination. A substantial proportion of the fresh seeds sown by Salisbury (1970) at the end of August germinated within 6 days, with further seeds appearing sporadically or in flushes thereafter. If seeds do not germinate they can probably remain dormant for many years, as plants can reappear at a site after long intervals (Croft, 1994). The stems of *L. portula* are brittle and the species may also spread vegetatively within a water body (Arber, 1920).

L. portula has decreased in some areas, especially in the eastern part of its British range. Many of the ponds on commons and heaths where *L. portula* once grew in south-east England are now overgrown or drained, and formerly rutted tracks are now surfaced and quite unsuitable. Nevertheless, the species is able to persist on woodland rides, and occasionally colonises newly available habitats. This may explain why it has not undergone the severe decline shown by some other species of seasonally flooded habitats.

This is primarily a European species, extending from Scandinavia to southern Europe (Hultén & Fries, 1986). It also occurs in N. Africa and W. Asia and, as an introduction, in California, C. & S. America and New Zealand.

CHK: California, New Zealand.

Lythrum portula subsp. *portula*

The infraspecific taxa currently recognised in *L. portula* were defined by D.E. Allen (1954). The records of subsp. *portula* plotted on the map are based on herbarium specimens determined by Allen and by F.H. Perring (Perring & Sell, 1968), with some later additions. Only material with mature fruits can be determined to subspecific level, and this limits the number of records which can be obtained from herbaria. The preponderance of pre-1950 records is a reflection of the period when most specimens were collected, and does not indicate that the subspecies has declined. The subspecies of *L. portula* have not been recorded systematically by field botanists, and their distribution is imperfectly known.

Subsp. *portula* is widespread in Europe, and extends south to Italy, Sardinia and Corsica (Allen, 1954).

L. portula shows considerable variation in the length of the epicalyx segments. In some plants these are almost obsolete, whereas in others they can be up to 2 mm long. In the British Isles there is a cline from west to east, with the plants with the longer segments growing in the west (Allen, 1954). The extremes of variation are recognised as distinct taxa, which are defined somewhat arbitrarily. Subsp. *portula* includes plants with segments up to 0.5 mm long, whereas subsp. *longidentata* has segments 1.5-2 mm long. The subspecies are linked by a series of intermediates, and some populations of the species include both intermediates and plants referable to subsp. *portula*. The taxa are perhaps best treated as varieties, as Allen (1954) suggests, rather than as subspecies.

Lythrum portula subsp. *longidentata* (Gay) Sell

The records plotted on the map are based on those listed by Allen (1954), with some later additions. As with subsp. *portula*, the preponderance of pre-1950 records simply reflects the fact that most records are based on herbarium specimens.

Subsp. *longidentata* is found in western Europe and the Mediterranean region, being recorded from France, Portugal, Spain, Algeria and the Azores.

84. ONAGRACEAE

There are 24 genera and 650 species in the Onagraceae; most of the species are herbs or shrubs but some are trees. The family has a cosmopolitan distribution but the species are most numerous in N. and S. America. The largest genus in Britain and Ireland is *Epilobium*, which contains a number of species which grow in damp habitats (e.g. *E. hirsutum*, *E. palustre*). Two genera contain aquatics, the widespread *Ludwigia* and the American *Biosduvalia*.

84/3. *Ludwigia* L.

This is a genus of 75 species, including 15 aquatics. Only a single species, *L. palustris*, occurs as a native in Europe but two South American species are naturalised in France and Spain. The species which occur in the Old World have been monographed by Raven (1963).

In the New Forest this species grows as an emergent in shallow water [depth?] in ponds, streams, ditches and old gravel, sand and clay pits, and as a terrestrial plant on mud at the edge of ponds, the dried-up beds of ponds and streams and damp ground in marshy hollows. In shallow water at the edge of ponds can it can be the dominant macrophyte, and some stands cover hundreds of square metres. All/most sites are on grazed common land over acidic soils derived from [add list]. Characteristic associates include *Apium inundatum*, *Eleogiton fluitans*, *Hydrocotyle vulgaris*, *Hypericum elodes*, *Juncus bulbosus*, *Mentha aquatica*, *Pilularia globulifera* and *Potamogeton polygonifolius*; the nationally rare *Galium debile* and *Mentha pulegium* also grow with it at some sites. Outside the New Forest, the only recent record of *L. palustris* as a native species is from Epping Forest, where it grows on mud at the edge of a pond over acidic sands and gravels. It appeared in 1989 in a garden pond at Tonbridge, where it was not planted deliberately. In 1991 it was found in a dew pond at Seaford Head, where it also seems likely to be an introduction although one can only speculate about the circumstances in which it arrived.

L. palustris is an annual or a short-lived perennial. Terrestrial plants flower and fruit freely; aquatic plants tend to flower less freely but are more likely to perennate. The fruits are indehiscent and mature fruits float; they are therefore likely to be dispersed locally by water movement. Like other species of similar habitats *L. palustris* seeds require light for germination, but desiccation does not enhance germination. If seeds are removed from the fresh capsules they show 'quasi-simultaneous' germination, with some germinating rapidly but the majority remaining dormant. Seeds can germinate within the fruits, emerging through the fruit wall. For further details of the reproductive biology of this species, see Salisbury (1972). Populations of *L. palustris* can vary in size from year to year: one at Brockenhurst reappeared in the dry autumn of 1969 after a long absence (Salisbury, 1972) and the species was discovered at Epping Forest in the dry summer of 1976, growing on mud which is normally under water.

L. palustris was formerly more widespread as a native plant than it is today, but it has been lost from at least four localities. It became extinct during the nineteenth century at two outlying sites: Petersfield Heath, where the marshy areas in which it grew dried out (Townsend, 1883), and a pit near Buxted, which became completely overgrown with scrub (Wolley Dod, 1937). In Jersey *L. palustris* was known from two areas of marshland: it disappeared from one when the area was drained in the 1870s and was last seen in the other in 1920 (Le Sueur, 1984). In the New Forest it was formerly regarded as an extreme rarity, only being known to Townsend (1883 ?2nd ed.) from a single site, but it is now known from several localities. These areas are often species-rich and are therefore designated as Sites of Special Scientific Interest. The future of the species appears to be secure, although there has been some concern that it may be threatened by the spread of *Crassula helmsii* (Byfield, 1984). Essex?

This is a plant with a rather southerly distribution. It is found in W., C. and S. Europe northwards to England and The Netherlands; it appears to be most frequent in the south-west, and in Portugal it is common near the coast (Raven, 1963). Elsewhere it is found in N. Africa, Asia east to Iran and in temperate N. America. It is established as an introduced species in southern Africa, Hawaii and New Zealand; in the North Island of New Zealand it spread

explosively following the first record in 1929 (Raven, 1963).

Salisbury (1972) points out that the indehiscent capsules of *L. palustris* are likely to limit its powers of dispersal, and suggests that this might partly explain its limited distribution in southern England. The recent records of plants which have presumably become established from horticultural sources are therefore particularly noteworthy, and it will be interesting to see if the species becomes more widespread as a result of such introductions.

107. APIACEAE (UMBELLIFERAE)

A large family of 420 genera and over 3,000 species. The family has a cosmopolitan distribution, but attains its greatest diversity in the temperate regions of the northern hemisphere. Most members of the family are herbs but there are some woody species. The Apiaceae is closely related to the Araliaceae, a smaller and predominantly tropical family in which most species are woody. There is little or no scientific justification for separating these two families (Mabberley, 1987), but they are kept apart by tradition. An illustrated account of the British and Irish members of the Apiaceae is given by Tutin (1980). Our plants include representatives of all three subfamilies which are recognised in the family: Hydrocotyloideae, Saniculoideae and Apioideae.

Cook (1990) classifies 15 genera and 70 species as aquatics, but many of these are only seasonally submerged. In addition to the species considered below, *Carum verticillatum*, *Cicuta virosa*, *Hydrocotyle vulgaris* and *Sium latifolium* occur in fens or seasonally flooded habitats in our area, and are included within Cook's broader definition of an aquatic.

107/1. *Hydrocotyle* L.

Most of the species in the subfamily Hydrocotyloideae occur in the temperate regions of the southern hemisphere, particularly in S. America. The only genus which reaches our area is *Hydrocotyle*, with one native and three naturalised species. The aquatic *H. ranunculoides* was only discovered in Britain in recent years, and is not listed by Stace (1991) or Kent (1992), but it is now sufficiently well naturalised to be considered here.

This robust species grows as a rooted plant on mud or in free-floating colonies on the surface of still or slowly moving water. The floating colonies can be quite large: the most extensive patch so far recorded covered an area of 24 m². *H. ranunculoides* is naturalised in the R. Chelmer and the Chelmer & Blackwater Navigation canal, and has also become established in artificial lakes, ponds, streams, a drainage ditch and a flooded gravel pit.

Plants growing on mud flower and set seed. Floating plants do not flower, but reproduce vegetatively. The stems root at the nodes and are brittle. Fragments are easily broken off and can float to new localities, where they become established.

H. ranunculoides is sold in aquatic plant nurseries, often as 'marsh pennywort', the English name of *H. vulgaris*. It was first recorded as a naturalised alien in 1990, when M. Heywood discovered the population in the R. Chelmer at Chelmsford. By 1992 it had been recorded in the Chelmer & Blackwater Navigation up to 12 km downstream of Chelmsford, and in 1993 it was found in lakes, ponds and streams elsewhere in Essex. It is also known from a lake near Milton Keynes. On the basis of its behaviour in Essex, Payne (1994) suggests that it may spread to become a common species.

This species is a native of N. America, where it is widespread from Washington state and Pennsylvania southwards. Godfrey & Wooton (1981) describe it as growing 'in dense mats on mucky shores, in shallow water near shores, or in floating mats'. It is naturalised to the south of its native range in C. & S. America, and in some areas it is a serious weed. In the Old World it is recorded from S. Europe (Italy, Sardinia, Spain) and Africa (Ethiopia). Tutin *et al.* (1968) consider that it is possibly native in Italy and Sardinia, but this seems unlikely.

For further information about this plant in Britain, see Payne (1994). The above notes are based on this account and on information collated and supplied by K.J. Adams.

Update!

107/16. *Berula* Besser ex Koch

This is a small genus containing two species, the widespread *B. erecta* and the African *B. thunbergii*.

B. erecta can grow as a submerged aquatic or as an emergent species in shallow water or seasonally flooded ground. Completely submerged leafy clumps are frequent in clear, calcareous streams and the upper reaches of rivers, where the flow of water is rapid but stable and the substrate is a coarse gravel. In this habitat *B. erecta* is often associated with *Ranunculus penicillatus* subsp. *pseudofluitans*, and it frequently grows immediately upstream of a patch of *Ranunculus*, in the zone where the flow of water is reduced (Haslam, 1978). As an emergent *B. erecta* grows at the edge of lakes, ponds, streams, rivers, canals, ditches and in marshes. It is also associated with calcareous, mesotrophic water in these habitats, but it usually grows on substrates such as fine silt or mud. *Apium nodiflorum*, *Mentha aquatica*, *Rorippa nasturtium-aquaticum*, *Veronica anagallis-aquatica* and *V. beccabunga* often grow with it. *B. erecta* is confined to the lowlands.

The submerged leaves of this species remain green throughout the winter, and clumps spread in early spring by the growth of short-lived stolons or rhizomes. Sediment often accumulates around the shoots and the clumps become raised above the surface of the substrate, until they become vulnerable to erosion and are washed away. The entire cycle from establishment to erosion can take less than a year (Haslam, 1978). The species can become established from vegetative fragments. Submerged clumps often fail to flower, but terrestrial plants flower more freely. Little is known about the frequency with which they reproduce by seed.

B. erecta is sometimes overlooked because of the similarity of its leaves to those of *Apium nodiflorum*. The differences were not clearly set out by successive editions of Clapham *et al.* (1952), but they were described by Haslam *et al.* (1975) and Wigginton & Graham (1981) and are now widely known; the mapped distribution should therefore be fairly accurate. The overall distribution of the species appears to be fairly stable, but the plant has declined in frequency in some areas, including Essex (Tarpey & Heath, 1990) and Gloucestershire (Holland, 1986), probably because of habitat destruction. The most northerly population in our area, in a limestone valley in Shetland, was greatly reduced in quantity in 1986, when the stream in which it grew was widened and deepened to facilitate drainage (Scott & Palmer, 1987).

B. erecta is found in Europe from southern Scandinavia southwards, although it is rare in the Mediterranean region. It extends eastwards to C. Asia, and it is also widespread in temperate N. America. It is also recorded as an introduction in Africa and Australia (not listed by Aston- chk Australia).

107/19. *Oenanthe* L.

A genus of 40 species, most of which are found in wetland habitats in the temperate N. hemisphere. The genus is not a critical one, but the species are more difficult to identify than those in other genera of the Apiaceae in our area. Three of the seven British and Irish species are considered below; in addition *O. silaifolia* is a plant of unimproved, seasonally flooded meadows.

This plant occupies a range of moist or wet habitats in the lowlands. It is usually found in places which are flooded for at least part of the winter but where the summer water table lies at or below the surface. These include meadows and pastures on the flood plain of rivers, marshes and fens with a species-rich sward which is not dominated by the tall reedswamp species and in the fringing vegetation at the edge of lakes, ponds, rivers, streams, canals and ditches. However, plants can also be found growing as emergents in shallow water, particularly in grazing marsh ditches.

O. fistulosa is a perennial with tuberous roots. Both terrestrial and emergent plants flower and fruit freely. Swards of seedlings can be found in moist, open vegetation in the summer and autumn. The species has no specialised means of vegetative reproduction.

In areas such as the Somerset Levels where grazing marshes provide much suitable habitat this is a frequent species, but elsewhere it is rather uncommon. It is able to persist at the edge of ditches or in winter-flooded hollows in fields where the grassland has been improved for agriculture, but it has undoubtedly decreased in abundance in regions where low-lying pastoral land has been converted to arable. Its decline has been documented in Bedfordshire (Dony, 1976) and Essex (Tarpey & Heath, 1990).

O. fistulosa is a predominantly European species, occurring from Scotland and southern Scandinavia southwards, and in adjacent parts of N. Africa and S.W. Asia.

This is the most robust member of the genus in our area. It grows in shallow water in streams, on the banks of rivers, streams, lakes, ponds and canals, in marshes and wet woodland, in crevices in waterside masonry, amongst flushed stones and boulders at the top of beaches and on dripping or flushed sea cliffs. It is one of the few macrophytes which will grow in small, rocky coastal streams in western Britain, where its roots lodge firmly in rock crevices. However, the largest plants are found in muddy swamps, especially where these are enriched by run-off from nearby farmyards. *O. crocata* is most frequent in or by acidic water, or where calcareous waters flow over acidic substrates, but it also occurs in calcareous habitats throughout its British and Irish range. These include wetlands in the Burren (Webb and Scannell, 1983) and the classic chalk rivers of south-east England (Holmes, 1983). It is tolerant of a variable water level, and is therefore able to grow at the edge of rivers over clay. In the Isles of Scilly it extends into drier places than is usual on the mainland, and it can even be found on wall-tops (Lousley, 1971). It is a distinctly lowland species, which is only rarely recorded above 300 m; it occurs up to 320 m on The Paps in Co. Kerry (Scully, 1916-CHK).

This is a perennial with tuberous roots and leaves which remain green through the winter. The reproductive biology of the species does not appear to have been studied in any detail. Plants flower in early summer and after flowering the stout but hollow flowering stems often collapse. They lack specialised means of vegetative dispersal and spread, although the tuberous roots of riverside plants could conceivably be washed out of the substrate and become established downstream. Reproduction is usually by seed.

O. crocata is frequent and often abundant within its rather sharply delimited British and Irish range. It is highly poisonous to both man and his animals, but it is rarely persecuted by farmers who perhaps consider that the effort to control such a frequent species would be wasted. However, Marquand (1901) suggested that the disappearance of the plant from Alderney may have been caused by deliberate eradication. The only indication that the species is declining comes from the London area, at the very edge of its range; even here it is still frequent by the Thames (Burton, 1983).

This species has an Atlantic distribution, extending from Belgium and Britain south to Spain, Portugal and Morocco; it extends into the western Mediterranean region as far as Italy.

O. fluviatilis is most frequent in the crystal-clear, meso-eutrophic water of calcareous streams and rivers, where it can often form large beds. It is also found in canals, fenland lodes and ditches, but only rarely grows in ponds. It occurs in both still or sluggish water and in streams where the flow is more rapid, and at a range of water depths, from shallow water in streams where the flow is sufficiently constant to protect the plant from desiccation to water at least 1.5 m deep in fenland lodes. It is often found over sands and gravel, or in places where these substrates are mixed with clay; it avoids deep, fine silt. *Ranunculus penicillatus* subsp. *pseudofluitans* is an almost constant associate; other species which often grow with *O. fluviatilis* include *Callitriche obtusangula*, *Nuphar lutea*, *Sagittaria sagittifolia* and *Zannichellia palustris*. **CHK against CDP notes.** *O. fluviatilis* is confined to the lowlands.

This is a perennial species with leaves which remain green throughout the winter. In rapidly flowing water the prostrate stems root at the nodes and form large vegetative clumps which rarely flower; reproduction of these colonies is by vegetative fragmentation. Plants in still or sluggish water flower more freely. If the flowering stems are not broken off or dragged down below the water level by the current they produce viable seed, but the frequency with which the species reproduces from seed is unknown.

This species was first described as *O. phellandrium* var. *fluviatilis* by Babington (1843); it had previously been confused with *O. aquatica* (*O. phellandrium*). The differences between the two species were clarified by W.H. Coleman (1844, 1849), who recognised that *O. fluviatilis* deserved specific rank. There is little doubt that *O. fluviatilis* has declined since its discovery some 150 years ago, as rivers have become very eutrophic or have suffered from deep dredging and channel 'improvement' or greatly increased boat traffic. Rivers in which it is now much less frequent than it was, or from which it has disappeared, include the Thames in Berkshire (Bowen, 1968) and the London area (Lousley, 1976; Burton, 1983), the Blackwater and the Stour in Essex (Tarpey & Heath, 1990) and the Welland in Leicestershire (Primavesi & Evans, 1988). The species may, however, be somewhat under-recorded. Its vegetative clumps, once known, could scarcely be mistaken for anything else, but a surprising number of botanists manage to overlook them.

O. fluviatilis is endemic to W. Europe; its world distribution is mapped by Cook (1983). On the European mainland it is known from Denmark and from a rather compact area between the Seine and the Rhine in Belgium, France and Germany. It is declining in N.W. France (Meriaux, 1981) and is apparently extinct in Germany (Haeupler & Schönfelder, 1988).

Unlike the closely related *O. aquatica*, this is found in lowland sites where the water is still or slowly flowing, and subject to marked fluctuations in depth. It is most frequent in shallow ponds and ditches, where it often grows on deep, silty and often eutrophic substrates in areas where the vegetation is kept open by trampling cattle. It is also found in open vegetation at the edge of sheltered lakes, reservoirs, canals, sluggish streams and rivers, in marshes and in seasonally flooded depressions. It can persist in moderate shade in ponds which are surrounded by trees, but is rarely found in closed vegetation in reedswamps. In many areas it is particularly frequent on clay soils, but it is not confined to them.

The seeds of *O. aquatica* will germinate soon after they are shed, but germination is enhanced by a period of stratification under water and then favoured by light, aerobic conditions and moderately high temperatures. Swards of seedlings can therefore be found in summer on ground from which water has receded. Once seedlings have become established they continue to grow terrestrially or, if the water level rises, as aquatics with more finely divided leaves. Plants may behave as winter annuals, germinating in autumn and flowering the next summer, or as summer annuals, flowering in the same year that they germinate. The winter annuals tend to grow into larger plants which produce more seeds. The seeds can float for some hours after they are shed; seedlings which sink may germinate and give rise to seedlings which then float. The number of plants at a site may vary greatly from year to year, depending on the fluctuations in water level.

This is an uncommon species throughout much of its British and Irish range. It has undoubtedly decreased in some areas of eastern Britain, including Berwickshire (Braithwaite & Long, 1990), Berkshire (Bowen, 1968), Essex (Jermyn, 1974; Tarpey & Heath, 1990) and Leicestershire (Primavesi & Evans, 1988). In Suffolk it was 'formerly frequent and generally distributed, now rare and disappearing, as its habitats have been rapidly destroyed in recent years' (Simpson, 1982).

O. aquatica is widespread in Europe and western Asia, especially in the middle latitudes; it extends north to southern Scandinavia. It is also known in a few scattered sites in central Asia and, as an introduction, in New Zealand.

See Hroudová *et al.* (19??) for a detailed account of the reproductive biology of this species in Czechoslovakia; the details of its germination and establishment are taken from this as there has been little research in Britain or Ireland.

107/28. *Apium* L.

A genus of 30 annual or perennial species which are confined, as natives, to the Old World. Four of these are aquatic, including two which occur in our area.

A. nodiflorum can be found in shallow water in marshes, springs, streams and ditches, where it may form dense, pure stands, and at the edges of rivers, lakes, ponds and canals. It is usually emergent but can also form submerged patches. It characteristically grows in fertile sites where the growth of taller species is restricted by erosion or by ditch clearance or other disturbance (Grime *et al.*, 1988). Although it can be particularly abundant in rapidly flowing, calcareous streams, including winterbournes which dry out in summer, it is also found in non-calcareous habitats. It is a highly palatable species which can be eliminated by grazing. It has a predominantly lowland distribution, reaching 335 m at Harley Dingle.

A. nodiflorum is a perennial with shoots which die back over winter and regrow in spring. Plants flower and fruit freely. Seeds germinate from early spring to autumn on damp substrates or in shallow water. Seedlings which become established in open vegetation may reach maturity but those which arise in or near established stands of the species tend to be outcompeted by mature plants (Thommen & Westlake, 1981). Vegetative reproduction and spread takes place by the regeneration of detached shoots, which can develop new roots within 2 days under laboratory conditions (Grime *et al.*, 1988).

This species is still frequent throughout much of its British and Irish range, and no decline is apparent at the scale of the map. Even in the London area it is still frequent outside the most heavily built-up areas (Burton, 1983; Kent, 1975).

W., C. & S. Europe, most frequent in the west and reaching its northern limit in Scotland. It also occurs in S.W. Asia and N. Africa, and as a naturalised and spreading alien in N. & S. America (Cook, 1990).

A. nodiflorum is ecologically very similar to *Rorippa nasturtium-aquaticum sensu lato*. *A. nodiflorum* is at a selective advantages in sites which dry out in summer, as its roots penetrate more deeply into the substrate. It replaced *R. nasturtium-aquaticum* as the dominant species at some sites in Dorset after the 1976 drought. *R. nasturtium-aquaticum* is favoured where the water is deeper than 40 cm, and its superior ability to regenerate from fragments also leads to its dominance in heavily grazed or disturbed situations (Thommen & Westlake, 1988). *Berula erecta* differs from *A. nodiflorum* in being restricted to calcareous sites, and is more frequently found as submerged plants.

NB Check mapped northern records, esp. Berwicks-see Braithwaite & Long- and N coast

A. inundatum is a heterophyllous species which can grow as an aquatic with finely divided submerged leaves or as a terrestrial plant with broader leaves. It grows in sites where the water level fluctuates and which are subject to periodic desiccation: these include the edges of lakes and reservoirs, pools and dune slacks. It is able to colonise freshly created habitats, including new ponds and, in one area, scrapes dug for natterjack toads. It can also be found in more permanent shallow water in streams, ditches, canals, the backwaters of rivers and marshes. It is confined to oligotrophic or mesotrophic habitats, occurring over a wide range of substrates including sand, silt, gravelly stones and peat, but it appears to avoid the least fertile sites. Most of its sites are base-poor, but it can also grow in highly calcareous water where the nutrient levels are sufficiently low. Characteristic associates include *Baldellia ranunculoides*, *Callitriche hamulata*, *Eleogiton fluitans*, the aquatic form of *Juncus bulbosus*, *Littorella uniflora*, *Myriophyllum alterniflorum* and, in western Ireland, *Eriocaulon aquaticum*. *A. inundatum* is a primarily lowland species, which reaches 450 m at Rhyd Galed and 500 m on Cronkley Fell.

A. inundatum flowers and fruits freely in both terrestrial habitats and in shallow water. Pollination? Reproduction is by seed. It fluctuates in abundance in response to changes in water level, and it can be the most abundant species in shallow ponds.

This species appears to be declining throughout eastern Britain: the decrease has been documented in numerous areas including S. England (Bowen, 1968), East Anglia (Perring *et al.*, 1964; Simpson, 1982), N. England (Graham, 1988; Swan, 1993) and Scotland (Ingram & Noltie, 1981). Like many species of shallow water, it has suffered from the destruction of its habitats by drainage. It may also have been lost from sites which are now overgrown, following cessation of grazing, or which have become eutrophic. By contrast, Allen (1984) draws attention to the numerous recent records from the Isle of Man and Galloway, and suggests that they may represent an increase in the plant rather than more adequate recording of this inconspicuous species. There are insufficient data to assess trends in Ireland.

A suboceanic species, found in W. and C. Europe from Britain, S. Scandinavia and Poland south to the Iberian peninsula and Sicily. It is listed as 'vulnerable' in The Netherlands (ref to Gorteria 1990 paper) and appears to be declining in Germany (Haeupler & Schönfelder, 1988). It also occurs in N. Africa.

The sterile hybrid between *A. inundatum* and *A. nodiflorum*, *A. × moorei*, is a very local plant in Britain, but is widespread in Ireland; it is not known on the European mainland (Perring & Sell, 1968; Tutin, 1975). It grows in marshes and at the side of lakes, rivers, streams and canals.

113. MENYANTHACEAE

This small family contains five genera and about 40 species. All the species are submerged, floating or emergent aquatics. The family was once thought to be closely allied to the Gentianaceae, but it is now placed in the Solanales rather than the Gentianales.

113/1. *Menyanthes* L.

This is a monotypic genus which contains the familiar Bogbean, *Menyanthes trifoliata*. This differs from other members of the family in having trifoliolate rather than entire leaves.

M. trifoliata grows at the fringe of lakes or slowly flowing rivers, and in pools and wet flushes. At the edge of lakes pure stands of this species are often found where the emergent zone gives way to open water. At their landward edge pure stands usually grade into mixed communities of *Carex rostrata*, *M. trifoliata* and *Potentilla palustris* in shallower water, and then to carpets of *Calliergon cuspidatum* or *Sphagnum* spp. where the water table lies near the surface of the soil. In these fen communities *M. trifoliata* can be accompanied by a wide range of other herbs. It may also grow in bog pools or flooded peat cuttings, where *Eriophorum angustifolium*, *Sphagnum auriculatum* and *Utricularia minor* are frequent associates. It is also found, often as dwarf shoots, in the wettest parts of flushes dominated by small sedge species and in dune slacks. It occurs over both organic and inorganic substrates, in calcareous and acidic waters and over a wide range of nutrient levels. It is recorded from sea level to 700m on Glaramara and Glyder Fawr (Wilson 1956) and 927m in the Breadalbanes (White 1898).

M. trifoliata is a rhizomatous, deciduous perennial. Established colonies spread by growth of the rhizome, and in open water they can occupy many square metres. The flowers are heterostylous and self-incompatible, and 'pin' and 'thrum' clones do not tend to grow intermixed. They are pollinated by insects. The pollen of thrum plants is less viable than that of pin plants, and the number of seeds set per flower is often low (Hewett, 1964; Nic Lughadha & Parnell, 1989). The seeds are buoyant and under experimental conditions may remain floating for 15 months. The seed coat is hard and germination will not take place until it is ruptured. See Ridley on duck dispersal. Reproduction by seed appears to be rare (Hewett, 1964).

The fossil record of *M. trifoliata* in our area is remarkably complete: it has been found in deposits from the last four interglacials. It may have persisted through the last glacial period, and Godwin (1975) suggests that it was a characteristic species of the aquatic communities which developed after the melting of the ice-sheets. It is still a frequent plant in northern and western Britain and Ireland, especially in peatland areas. However, it has decreased in almost all the counties of southern and eastern England because of the drainage of wetland habitats in historic and recent times. It is an ornamental species which is sometimes planted out in the wild, and several of the extant populations in the London area, for example, are believed to originate from such introductions (Burton, 1983).

M. trifoliata occurs in boreal and temperate regions throughout the northern hemisphere.

Add uses.

113/2. *Nymphoides* Séguier

There are 20 species in this genus, all of which have the 'water-lily' growth form with floating leaves and aerial flowers; the flowers of many species are insect-pollinated. The genus includes both annual and perennial species. Although the genus has a world-wide distribution, only a single species, *N. peltata*, is native to Europe.

Some species of *Nymphoides*, including *N. peltata*, are heterostylous, with a weak incompatibility mechanism between the 'pin' and 'thrum' forms. Other species in the genus have a strong incompatibility mechanism (e.g. *N. humboltiana*, *N. indica*) or are dioecious (e.g. *N. cordata*). Ornduff (1966) suggests that both the strongly incompatible and the dioecious species have evolved from weakly incompatible ancestors, under selection pressures that favoured outbreeding.

Within the area in which it is thought to be native, *N. peltata* is a plant of lowland, calcareous and eutrophic water over inorganic substrates at the edge of lakes, slowly flowing rivers and fenland lodes. In these sites it often grows in dense masses in water 0.5-2 metres deep. The species is also grown as an ornamental plant, and it is thoroughly naturalised in ponds, natural and ornamental lakes, flooded gravel pits, claypits and quarries and in rivers, canals and ditches.

N. peltata is a rhizomatous perennial. It is heterostylous, individual plants having 'pin' or 'thrum' flowers. Each flower lasts for only one day, but plants flower over a long period. The flowers appear patterned to organisms with vision which extends into the ultraviolet wavelengths, and are visited by a range of insects (van der Velde & van der Heijden, 1981). The fruits develop under water. More seed is set from crosses between pin and thrum plants than if both parents have the same floral morphology, and the viability of seeds and vigour of the seedlings is greater (Ornduff, 1966). The seeds float and may be dispersed by water. They are completely digested when eaten by waterfowl, but they are tolerant of desiccation and may be carried on the feathers of birds (Cook, 1990b; Smits *et al.*, 1989). The seeds require a short cold treatment before germination. In The Netherlands they will germinate in quantity in spring in aerobic conditions on exposed mud flats or in very shallow water; in anaerobic situations they remain dormant in a persistent seed bank (Smits *et al.*, 1990). Plants may reproduce vegetatively from rhizomatous spread or fragmentation of the stems.

N. peltata is thought to be native in the Thames valley, where it was recorded as frequent in the R. Thames about London in 1570 (Kent, 1975), and in East Anglia, where Ray (1660) found it 'in many rivers about the Fens in great plenty' [CHK]. The native range has, however, been obscured by the spread of plants which have been deliberately introduced into the wild or have spread from cultivated stock, and it cannot now be delimited with certainty. The species has decreased in its native sites in the Thames valley (Bowen, 1968; Burton, 1983), but it continues to be introduced and spread both within the area in which it also occurs as a native and elsewhere.

As a native plant *N. peltata* is widespread in Europe from England and the Baltic southwards, and extends eastwards through Asia to Japan. It is naturalised in North America (Stuckey, 1974).

All the native plants in East Anglia appear to be the pin morphotype; in the Thames valley both forms occur. Many introduced populations consist of either pin or thrum plants, suggesting that they may be spreading clonally.

116. BORAGINACEAE

This is a large but predominantly terrestrial family, which contains 156 genera and 2,500 species of herbs, shrubs or trees. All the European representatives are herbs or dwarf shrubs. In the British Isles 8 genera and 23 species occur as natives, and there are numerous introduced taxa. Cook (1990a) does not list any aquatic Boraginaceae, but a single species is sufficiently aquatic in our area to be mapped in this book.

116/15. *Myosotis* L.

Five of the ten native species of *Myosotis* in the British Isles belong to Series *Palustres* M. Pop. They are closely related ecologically as well as taxonomically, as they all grow in seasonally flooded or permanently damp or wet habitats. Only *M. scorpioides* can regularly be found growing in water, but *M. caespitosa* subsp. *laxa* and *M. secunda* often occur at the water's edge. *M. stolonifera* is a scarce species of upland springs, flushes and other waterside habitats (Stewart *et al.*, 1994), and *M. sicula* is confined to a single poolside in Jersey (Le Sueur, 1984). A taxonomic account of the European species in Series *Palustres* has been given by Schuster (1967), but some of his conclusions have not been adopted by later authors. Useful notes on the identification of our species are given by Welch (1961).

M. scorpioides grows in a range of open or shaded, wet or damp habitats. It can be found as an aquatic, forming submerged patches or floating rafts at the edge of lakes, rivers, streams, canals and ditches. It is, however, more frequent above the water level, usually growing at the edge of still and flowing water in situations where the growth of more robust species is restricted by the disturbance associated with winter flooding (Grime *et al.*, 1988). It is usually found in fertile sites over calcareous or mildly acidic soils. It is a predominantly lowland plant, ascending to about 450 metres in Wales and northern England.

M. scorpioides is a rhizomatous perennial which overwinters as leafy shoots. Submersed patches may not flower, but emergent and terrestrial stands flower freely. The species is gynodioecious, with female and hermaphrodite plants (CHK Kay?). The incompatibility system of *M. scorpioides* is controlled by several genes and the degree of self-incompatibility differs from plant to plant: some hermaphrodite individuals are completely self-incompatible whereas in others 95% of self-fertilised ovules may develop into seeds (Varopoulos, 1979). The seeds do not float (Ridley, 1930-CHK). Plants also reproduce vegetatively: stems are broken off by flowing water and the resulting fragments can regenerate. Vegetative reproduction is probably more important than reproduction by seed (Grime *et al.*, 1988).

This species is frequent in suitable habitats throughout Britain and Ireland. There is no evidence that it is declining, except in totally urban areas where its habitat has been eliminated.

M. scorpioides is a variable species which is widely distributed in temperate Eurasia. It also occurs as an alien in N. & S. America and New Zealand.

Botanists sometimes confused this species with *M. secunda*, which replaces it in areas where the soils are infertile and base-poor. The third frequent taxon in Series *Palustres*, *M. laxa* subsp. *caespitosa*, is an annual of disturbed, waterside habitats. The hybrid between *M. laxa* and *M. scorpioides*, *M. × suzae*, is a vigorous and partially fertile perennial which is known from a few localities in England and Wales, growing in sites where both parents occur (Benoit, 1975). It is probably under-recorded.

CHK Fritsch, Ber. Deutsch. Bot. Ges. 18:472-480 for 'gynodioecie'

Grau, Mitt. Bot. Staatssamml. Munch. 5: 675-688; 6:517-530; 7:17-100; 8:127-136.

119. HIPPURIDACEAE

This family contains a single genus, *Hippuris*. The relationships of the family, like those of many families with highly reduced flowers, are uncertain.

119/1. *Hippuris* L.

This is a small genus, treated by some authors as monotypic although others recognise two or more closely related species. The genus has given its name to the '*Hippuris* syndrome', used to describe plants with erect, unbranched stems with simple, elongate leaves borne in symmetrical whorls. This character-complex has evolved in several unrelated flowering plant families, all of them dicots, including Elatinaceae (*Elatine alsinastrum*), Haloragaceae (*Myriophyllum elatinoides*, *M. hippuroides*), Lythraceae (*Rotala hippuris*), Ranunculaceae (*Ranunculus polyphyllus*) and Scrophulariaceae (*Hydrotriche hottoniiflora*, *Limnophila hippuridoides*). It is also found in some cryptogams, including *Chara* and *Equisetum*. The syndrome was described by Cook (1978), who suggested that it represents one way in which aquatic plants can increase the surface area of their assimilating organs.

This is a heterophyllous species which may occur as an aquatic with submerged or emergent shoots or as a terrestrial plant. As an aquatic it is found in still or sluggish water of lakes, ponds, flooded gravel pits, rivers, streams, canals and ditches. Aquatic plants are usually found in clear, base-rich water, and are abundant in the limestone lakes of Lismore and the Durness area of Sutherland. As an emergent or terrestrial plant *Hippuris* grows at the edge of standing waters, and in swamps, marshes and upland flushes. Terrestrial plants are most vigorous on soft, eutrophic substrates, and *H. vulgaris* is one of the few species to persist in the nutrient-enriched Norfolk Broads. However, small scattered shoots of *H. vulgaris* can be found over mesotrophic or meso-oligotrophic substrates. *H. vulgaris* is a predominantly lowland species, rarely found above 400 metres but ascending to 900 metres in bryophyte-dominated springs on Moine Mhor.

H. vulgaris is a rhizomatous perennial which can form large stands in favourable habitats. It has bisexual or unisexual flowers. There appears to be little information on its reproductive biology. It is able to colonise newly available habitats such as freshly dug ponds and bird scrapes and abandoned clay, gravel and sand pits.

Palynological studies suggest that *H. vulgaris* may have been present in our area throughout the Pleistocene period (Godwin, 1975). Its fruits are abundant in deposits of Early, Middle and Late Weichselian age, suggesting that it was a frequent plant in periglacial vegetation. Currently, there do not appear to be any marked trends in its distribution. It is reported to be declining in some areas, including Essex (Tarpey & Heath, 1990) and Suffolk (Simpson, 1982), but increasing in others, such as Gloucestershire (Holland, 1986). It may be spread by deliberate introduction to some sites: Sykes (1993) comments that in the North York Moors it is 'often planted in new fish-ponds and ornamental lakes'.

H. vulgaris is widespread in arctic, boreal and temperate regions of the northern hemisphere, and also occurs as a native species in southern S. America.

The submerged-type of shoot differs greatly from the aerial-type, and intermediates do not occur. The switch from submerged to aerial shoots is triggered by high light intensities, and only takes place at temperatures above 10°C. Although the transition normally takes place as shoots emerge from the water, aerial-type shoots can also be formed under very clear water (Bodkin *et al.*, 1980).

120. CALLITRICHACEAE

A small family which contains a single genus, *Callitriche*.

120/1. *Callitriche* L.

This is a genus of at least 25 species, most of which are aquatics with submerged or submerged and floating leaves. Some species grow in damp, terrestrial habitats.

The genus is taxonomically difficult, as the species are very variable in vegetative morphology, often having both aquatic and terrestrial forms, and the flowers are very reduced. Ripe fruits are often needed for identification. The species have been studied intensively by H.D. Schotsman. Her account in *Flora Europaea* (Tutin *et al.*, 1972), and more detailed studies of the species in Bavaria, Belgium, France, the Netherlands and Portugal (Schotsman, 1954, 1958a, 1961a,b, 1967, 1972, Duvigneaud & Schotsman, 1977) are particularly useful to British and Irish botanists. For southern European taxa the *Flora Europaea* account is now rather outdated, and it should be read in conjunction with Schotsman's later papers (e.g. 1977, 1982).

Schotsman's early account of the Dutch species was summarised by David (1958). Unfortunately British and Irish botanists have continued to neglect the genus, which in our area still retains its 'somewhat shady reputation' (Schotsman, 1954). The few critical studies of our taxa include Savidge's (1960) outline of his work on the experimental taxonomy of the European species, and Lewis-Jones & Kay's (1977) survey of the genus in West Glamorgan. Most field botanists do not attempt critical identifications of the plants they find, and there are no experts in our area who will identify material. As a result of this neglect the distribution of our more difficult species is still imperfectly known, and the distribution maps of these taxa remain 'patchy and discontinuous' (Lewis-Jones & Kay, 1977).

C. hermaphroditica and *C. truncata* differ from the other species in our area in having translucent submerged leaves; they both lack floating leaves and never produce modified terrestrial variants. One would not expect them to be confused with other species, but examination of the voucher specimens has revealed that many of the records of *C. hermaphroditica* reported by McCallum Webster (1978) are erroneous, and other botanists may have made the same mistake. We have attempted to eliminate dubious records of this species from the map. Although *C. hermaphroditica* is similar to *C. truncata*, their British and Irish distributions are virtually vicarious and confusion between them is therefore unlikely. Of the other species, *C. obtusangula* is a distinct species, identifiable in the field or (in cases of doubt) by microscopic examination of the pollen grains. This leaves two pairs of similar species: *C. platycarpa* and *C. stagnalis* are very difficult to separate, as are *C. brutia* and *C. hamulata*. The degree to which these species are under-recorded is discussed in the accounts of the species.

Plants of *Callitriche* are monoecious, with male and female flowers borne on the same stem. There are three pollination syndromes in the British and Irish species (Schotsman, 1982). The pollination of the totally submerged *C. hermaphroditica* and *C. truncata* occurs under water. Male and female flowers are initially enveloped in several pairs of imbricate young leaves. The pollen is released into this closed space and adheres to the long stigmas. In three species

(*C. obtusangula*, *C. platycarpa*, *C. stagnalis*) the flowers only develop in the axils of the floating rosette leaves. The stamens project above the surface of the water, and the emergent stigmas are fertilised by wind-blown pollen, or perhaps by pollen which falls onto the surface of the water and floats amongst the rosette leaves. As the stem grows, the developing fruit gradually becomes submerged. The male flowers of the terrestrial forms also release their pollen into the air. Self-pollination of these species is usual, but cross-pollination may occur. Finally, *C. brutia* and *C. hamulata* have flowers which (in aquatic forms) are borne under water in the axils of the submerged linear leaves or the rosette leaves. There is usually a male flower in one axil of a pair of leaves and a female flower in the other. The single stamen of the male flower usually bends towards the two stigmas of the female. The pollen germinates in the anther and the pollen tubes grow towards the stigma. In terrestrial forms pollination is similar, but the anthers only dehisce when moistened by a drop of rainwater or dew in the leaf axils. These species have fewer pollen grains in the anther than the wind-pollinated taxa. Their mechanism of self-pollination is very effective and results in good fruit set.

The species lack specialised means of vegetative reproduction, but detached fragments root freely at the nodes and may become established as new plants in water and (if the species grows terrestrially) on moist soil.

No *Callitriche* hybrids are known in our area. In mainland Europe sterile hybrids are known from several sites: all are probably crosses between *C. platycarpa* and *C. cophocarpa*.

In addition to the species treated below, Stace (1991) lists *C. palustris* L. as a British plant, apparently on the basis of a single specimen in the Herbarium Delessert, Geneva, which was collected at Petersham, Surrey, in 1877 and listed by Schotsman (1954). R.D. Meikle, N.Y. Sandwith and J.P. Savidge examined the only specimen from Petersham in this herbarium, collected by C.B. Clarke on 2 September 1877, and were in no doubt that it was a terrestrial form of *C. stagnalis* (Meikle & Sandwith, 1956). Unless further evidence comes to light, it seems best to delete *C. palustris* from the British list.

This species typically grows submerged on silty substrates in mesotrophic or eutrophic lakes. It can be found in shallow water at the edge of sheltered lakes, but in more exposed sites it is confined to deeper water, and sometimes descends to depths of five or six metres. In addition to lakes, it occasionally grows in deep, eutrophic streams and also occurs as a colonist of canals and flooded gravel pits. In mesotrophic waters characteristic associates include *Myriophyllum alterniflorum*, *Potamogeton gramineus*, *P. × nitens* and *Nitella flexilis*, and it often grows with the scarce *Najas flexilis*. In more eutrophic sites it can be found in abundance, growing with *Potamogeton crispus*, *P. pusillus* and *Zannichellia palustris*. It is a predominantly lowland species, which is found up to 350 metres at Kingside Loch and was formerly recorded at 380 metres in Malham Tarn.

C. hermaphroditica is a shallow-rooted, self-pollinated annual. Plants usually fruit prolifically, and plants laden with fruit are often uprooted and dispersed by autumn gales. Little is known about its germination requirements.

The presence of fossil fruits of *C. hermaphroditica* in late glacial deposits in Cornwall, Co. Wexford and Co. Louth suggests that it was widespread at that period but has since contracted to a predominantly northerly distribution. Its current distribution was under-recorded in both Britain and Ireland in the *Atlas of the British Flora* (Perring & Walters, 1962). It is therefore difficult to assess any recent changes. There is no evidence to suggest that it is declining, and the recent discovery of plants in gravel pits in Lincolnshire suggests that it may even be extending its British range.

C. hermaphroditica has a circumboreal distribution. In Europe it has a predominantly northern distribution, extending south to the British Isles, northern Germany and Rumania. It is absent from the Alps.

Populations of *C. hermaphroditica* differ in fruit morphology. In Britain two variants have been reported by Savidge (1958) and Schotsman (1958b); one has fruits c. 1.5 mm in diameter and is known from canals in England and Wales, whereas the other has more broadly winged fruits c. 3 mm in diameter and is more common in Scotland and Ireland, although it also occurs in Anglesey. The Anglesey plants have been described as var. *macrocarpa* by Hegelmaier (1867-chk ref). A recent study of Swedish material has confirmed the existence of two variants there, a small-fruited plant in the south and a large-fruited plant in the north (Martinsson, 1991). More detailed studies of the variation of this species in Britain and Ireland are required.

C. truncata is a pioneer species which colonises newly created lowland habitats, or areas which have been disturbed by major management operations. It can be found in abundance in lakes, reservoirs, ponds, rivers, canals, ditches and flooded gravel pits. It is usually found in base-rich, mesotrophic or somewhat eutrophic waters; in Ireland it is found in brackish ditches. It is found in both shaded and unshaded sites, and grows over a wide range of substrates from pebbles and stones to soft organic sediments. It usually grows in shallow water, but can descend to depths of 1.5 metres. Plants are most vigorous in clear, still or very slowly flowing water but are occasionally found in sites where the water flows steadily but rather more rapidly, or in turbid conditions. *Elodea canadensis* is a frequent associate.

C. truncata is an annual, although plants which break up in autumn and float to the surface can overwinter as vegetative fragments. Recent observations indicate that it fruits freely at most of its British sites (Barry & Wade, 1986); these contrast with the traditional view (e.g. Pearsall, 1935; David, 1958) that the British populations rarely set seed. Dispersal of seed is by water or possibly by wildfowl: seed fed to ducks has germinated when recovered from the faeces. The seeds have no innate dormancy, but in the wild seeds shed in autumn do not germinate until spring. The species may reappear in a stretch of water after a long absence (Lousley, 1937), presumably germinating from dormant seed.

It is difficult to account for the very restricted distribution of *C. truncata*. In recent years it has apparently become extinct in Guernsey (last seen in 1968), Sussex (1966) and Kent (1971). Some of its sites have been destroyed in Guernsey, but there is no obvious reason for its disappearance from the other localities. It has, however, been recorded in new localities in recent years: Barry & Wade (1986) had records from 12 water bodies since 1980 whereas it is now known from 28. The recent discovery of plants in a fishing lake and a reservoir in S. Essex in 1988 (Adams, 1988), and a reservoir in N. Essex in 1991, represent a significant extension to the species' range. *C. truncata* is an inconspicuous plant which may be refound at some of its old localities, or discovered elsewhere.

C. truncata has a Mediterranean-Atlantic distribution. The western European plant is subsp. *occidentalis*, which occurs in Malta, Spain, Portugal, France, Belgium and the British Isles. It is replaced by subsp. *truncata* in the central and eastern Mediterranean region, and in N. Africa, and by subsp. *imbriata* in S. Russia.

Much of the information in the above account is taken from Barry & Wade's (1986) detailed account of the ecology of this species.

C. stagnalis grows as an aquatic in shallow water or as a terrestrial species on open ground. As an aquatic it is found in a wide range of oligotrophic, mesotrophic or eutrophic waters. It is most frequent on non-calcareous soils (Grime *et al.*, 1988), but it is absent from the most acidic and nutrient-poor localities. It usually grows over fine organic or inorganic substrates and occurs in both shaded and open situations. Typical habitats include the sheltered bays of lakes, the quiet edges or backwaters of rivers, and in pools, streams or ditches. Terrestrial plants grow on seasonally flooded or moist, disturbed ground and can typically be found at the edge of lakes or reservoirs, in ditches and dune slacks which dry up in summer, on tracks and woodland rides and occasionally in arable fields. There are confirmed records of *C. stagnalis* up to altitudes of 475 metres (Llyn y Figyn), and probable although unconfirmed records up to 890 metres (Foel Grach, Carnedd Llewelyn).

Aquatic plants of *C. stagnalis* are winter-green perennials. The submerged leaves are broadly elliptical rather than linear. Terrestrial plants are annuals with short internodes: flowers are borne at most nodes and such plants usually fruit copiously. Little information is available about seed dormancy and the conditions required for germination, but Grime *et al.* (1988) suggest that the species may have a persistent seed bank and probably germinates in spring.

C. stagnalis is widespread in Britain and Ireland, and its distribution appears to be stable. All records attributed to *C. stagnalis sensu lato* (an aggregate comprising *C. platycarpa* and *C. stagnalis*) are shown on the map. This probably gives a reasonable picture of the distribution of *C. stagnalis sensu stricto*, but may overestimate its occurrence in south-east England where some records may be referable to *C. platycarpa* or even *C. obtusangula*.

C. stagnalis is found throughout Europe, where it is represented by a number of different chromosome races (Schotsman, 1961c, 1967). It is so frequent in the western Mediterranean that it is sometimes eaten (with *C. brutia*) as a salad (Schotsman, 1961a). It is also found in Macaronesia, N. Africa and W. Asia, and occurs as an introduction in N. America, Australasia and perhaps elsewhere.

In some western areas (e.g. Donegal) *C. stagnalis* is much more frequent as a terrestrial annual than as an aquatic. Unlike the species with linear submerged leaves (*C. hamulata*, *C. obtusangula*, *C. platycarpa*), it is rarely found in deep water.

This species is recorded from a wide range of aquatic habitats, including slow-flowing rivers and streams, canals, ditches, lakes, ponds, turloughs, dune slacks and flooded gravel pits. It is also found as a terrestrial form on damp peat or mud. It has a wide ecological tolerance, growing in both open and partially shaded sites and at a range of water chemistries from acidic and oligotrophic to calcareous and eutrophic. In lowland, basic rivers it often grows with *C. obtusangula*. The ecological distinction between *C. platycarpa* and *C. stagnalis* is not clear-cut, or it has been obscured by the lack of systematic recording of these species. However, *C. platycarpa* appears to favour deeper or more rapidly flowing water. It is a predominantly lowland species, although it ascends to 520 metres at Llynoedd Ieuan.

Like *C. stagnalis*, aquatic forms of *C. platycarpa* are perennial. They overwinter as plants with submerged, linear leaves, and plants growing in deep water may persist in this state throughout the summer. However, floating rosettes develop if the stems reach the surface. Although plants of *C. platycarpa* with floating leaves flower freely, the pollen is variable and characteristically contains a proportion of sterile grains. There is some evidence that this may be the result of irregular meiosis (Schotsman & Haldimann, 1981). Plants of *C. platycarpa* set fruit much less freely than those of *C. stagnalis*, and certain populations appear to be virtually sterile (David 1958, Savidge, 1967). Terrestrial forms are annual and are also wind pollinated (Schotsman, 1982); they may fruit somewhat more freely.

This species is grossly under-recorded. Even those botanists who attempt to identify *Callitriche* species are frequently unable to find the fruiting plants which they need to confirm the identification of *C. platycarpa*. Lewis-Jones & Kay (1977) concluded that the two species could not be separated unequivocally even on the basis of fruit morphology, and found that a chromosome count was the most rapid and reliable way to distinguish them. There is little or no evidence about trends in the distribution or abundance of this species. However, its tolerance of eutrophic water suggests that it is unlikely to be decreasing in south-east England.

C. platycarpa is widespread in temperate parts of Europe, and it is also recorded from a few localities in the Mediterranean region. Its distribution extends into S.W. Asia. It is particularly frequent in western Europe; towards the east it tends to be replaced by *C. cophocarpa* (Schotsman, 1967; Cook, 1983). In Belgium, as in Britain and Ireland, it has a very wide habitat range (Duvigneaud & Schotsman, 1977).

Savidge (1960) suggests that *C. platycarpa* ($2n=20$) is an allopolyploid derived from a hybrid between *C. stagnalis* ($2n=10$) and *C. cophocarpa* ($2n=10$), a European species which is not known from Britain or Ireland. Schotsman (1967) regards his evidence as far from conclusive. Further cytological work is required to establish the origin of the species and investigate its apparent partial sterility.

C. obtusangula usually grows in still or slowly flowing water in lowland rivers, streams, canals, ditches, ponds and turloughs. It is found in both mesotrophic and eutrophic water, and in open habitats and partial shade. It is most frequent in calcareous waters over both peat and inorganic substrates. In calcareous ditches it can be present in large masses in the summer months, often associated with *Elodea canadensis*, *Hippuris vulgaris*, *Lemna minor*, *L. trisulca*, *Myriophyllum verticillatum*, *Potamogeton crispus*, *P. natans*, *Ranunculus circinatus* and *Zannichellia palustris*. In chalk streams and rivers it avoids the central channel where the water velocity is greatest, but grows on unstable silt in quieter reaches (Holmes, 1983). *C. obtusangula* is also found in brackish water, typically in ditches in coastal grazing marshes. Terrestrial forms can be found on damp mud at the water's edge. It is a strictly lowland species.

Aquatic forms of *C. obtusangula* are perennial, with a life-form similar to that of *C. platycarpa*: plants overwinter as shoots with linear leaves and in spring and summer the stems which reach the surface of the water develop floating rosettes. *C. obtusangula* may be more sensitive to winter cold than either *C. platycarpa* or *C. stagnalis* (Schotsman, 1954). In ditches *C. obtusangula* may be present in large masses in the summer months. Plants in flowing water may fail to fruit, but those in still water or on land fruit freely (David, 1958). Seeds of *C. obtusangula* from coastal populations will germinate in water with a greater salt content than will those of other *Callitriche* species, or those of inland populations of *C. obtusangula* (Schotsman, 1954).

Although *C. obtusangula* is a distinctive species, it is almost certainly under-recorded. There is no evidence to suggest that the species has undergone any major changes in its distribution or abundance, although assessing such changes is hampered by the lack of reliable historical records and the patchiness of the modern survey data.

C. obtusangula is a species of the Atlantic and Mediterranean regions of Europe, found from the British Isles, Spain and Portugal eastwards to Greece; there are also outlying localities in central Europe (Schotsman, 1961a; Cook, 1983). It is also known from N. Africa. Although all populations studied have the same chromosome number ($2n=10$), the species consists of a number of cytological races with different caryotypes (Schotsman, 1961c, 1977).

This species is usually found growing terrestrially on the bed of dried-up ponds or on exposed mud above the water-level; if conditions are suitable it can be present in abundance. It has also been recorded from damp hollows in sand dunes, sand and gravel pits and woodland rides, and from ditches, the edge of reservoirs, dried-up river meanders, rutted tracks and the moat of Caerphilly Castle. It also grows in shallow water. It is a calcifuge, which is restricted to base-poor and rather infertile sites. Species with which it may be associated include *Apium inundatum*, *Baldellia ranunculoides*, *Persicaria minor* and *Ranunculus trichophyllus*. Most records are from the lowlands, but there are confirmed records up to 425 metres (Llyn Egnant).

C. brutia is a self-pollinated annual. Fruiting plants have been recorded from mid April to early September. The ripening fruits sometimes become buried in the substrate as their stalks lengthen (Schotsman, 1961a). Like many self-pollinated annuals, individual populations may be characterised by minor morphological traits, which are maintained in cultivation (Schotsman, 1977).

Although variants of *Callitriche hamulata* with pedunculate fruits have been known to British and Irish botanists for well over a century, they have until recently been treated as an environmental modification (David, 1958), a variety (Pearsall 1935) or a subspecies (Clapham *et al.*, 1952) of that species, or have been ignored completely (Savidge, 1967). It is only in recent years that they have been recognised at specific rank, as *C. brutia* (Clapham *et al.*, 1987; Stace, 1991), and recorded systematically. The map almost certainly seriously underestimates its distribution.

C. brutia is known from southern and western Europe, and reaches its northern limit in southern Scandinavia; it is frequent in the western Mediterranean region. It is also known from N. Africa and extends eastwards in Asia to Iran. It grows in brackish water in Norway, and Naustdal (1974) suggests that it might have been transported to these sites on the sinking-stones, anchors, grapnels, ropes and hauling-lines of Vikings returning from expeditions to Britain.

C. brutia ($2n=28$) differs from *C. hamulata* ($2n=38$) in chromosome number. Terrestrial plants of these species are not difficult to separate, as the fruits of *C. brutia* are pedunculate. However, Schotsman (1967) comments, rather disconcertingly, that terrestrial forms of *C. hamulata* may sometimes be found with pedunculate fruits, and that these are nearly impossible to determine. Aquatic forms of both species can have more or less sessile fruits (Schotsman, 1961a), and can only be identified using much more subtle characters (Schotsman, 1967). Few, if any, British or Irish botanists would be prepared to name aquatic material, and this might not only provide a further reason why the species is under-recorded but also bias the map towards areas where it grows terrestrially. Schotsman (1967) regards *C. brutia* as a plant of shallow water; populations of the aggregate in deeper water are likely to be referable to *C. hamulata*.

This species is found in a wide range of acidic waters, including lakes, reservoirs, pools, rivers, streams, canals, ditches, and flooded clay, sand and gravel pits. It is found in both shaded and unshaded sites, and from shallow water to depths of over 3 metres in clear, oligotrophic water. It also grows in upland flushes and, as a terrestrial form, on damp mud. It is the most frequent species of *Callitriche* in the acidic areas of the north and west, where it not only occurs in lakes and pools but also in rocky streams and rivers where few other macrophytes except *Myriophyllum alterniflorum* and the aquatic form of *Juncus bulbosus* will grow. Although it normally behaves as a calcifuge, it sometimes appears to benefit from nutrient-enrichment of acidic waters (e.g. by nesting gulls) and it can occasionally be found in base-rich localities (Seddon, 1972). It is frequent in both lowland and upland areas, ascending to 825 metres (Carnedd Llewelyn); a plant reported as *C. hermaphroditica* from 915 metres (Sgurr na Lapaich) by McCallum Webster (1978) is probably referable to this species.

Aquatic plants of *C. hamulata* are perennial. They have a similar life-form to *C. obtusangula* and *C. platycarpa*, with linear lower leaves and a floating rosette of leaves on the surface of the water. Plants in deep or rapidly flowing water may persist throughout the year in the linear-leaved state. The species is self-pollinated and fruits freely. Little is known of its germination requirements.

The map shows all records attributed to *C. hamulata sensu lato*, an aggregate which includes *C. brutia*. Like all the species in this genus, *C. hamulata* is under-recorded in some areas but the map accurately reflects the abundance of the species in areas where acidic waters predominate, and its scarcity elsewhere. Many calcifuge species have declined in south-east England, but few local floras suggest that this is true of *C. hamulata*, perhaps because authors do not have sufficient reliable data to assess historical trends in the distribution of the species.

C. hamulata is a species of western, northern and central Europe, extending from Iceland and Scandinavia south to the Pyrenees, N. Italy and Rumania. It is also recorded from Greenland and plants referable to *C. hamulata sensu lato* have also been introduced to Australia and New Zealand (cf. Orchard, 1980).

121. PLANTAGINACEAE

This is a small family of only three genera, one of which is aquatic.

121/2. *Littorella* P. Bergius

Littorella is a genus of three species, all of which are aquatic. Only one species is known in Europe, *L. uniflora*.

L. uniflora is a plant of isoetid growth habit, found in shallow, oligotrophic or mesotrophic waters. It grows in lakes, reservoirs, rivers, streams, ponds and winter-flooded dune slacks, occurring over a wide range of substrates including stones, gravel, sand, peat, marl and soft mud. Although it usually grows in oligotrophic or mesotrophic waters, it can be abundant in lakes such as Esthwaite Water which have become eutrophic. It tolerates emersion and can form a dense band in the draw-down zone around lakes and reservoirs. Sheep will graze on exposed plants (West, 1910). In deeper water *L. uniflora* grows in open *Eleocharis palustris* and *Equisetum fluviatile* swamps on exposed shores, and below these zones in a carpet on the bottom of lakes, where it is often associated with *Isoetes lacustris* and *Lobelia dortmanna*. It descends to a depth of 3 or 4 m (West, 1905, 1910). In Scotland and Ireland it is most frequent in areas of base-poor rocks and waters, but it can grow in base-rich habitats such as the clear limestone lakes of Lismore, streams and turloughs in the Burren and even in pools on limestone pavement on Inishmore (Webb & Scannell, 1983). In S.E. England, however, it is only found in acidic habitats. It is recorded from sea-level to 825 m at Ffynnon Llyffaint.

Littorella uniflora only flowers when emersed; the male flowers are stalked and the pollen is dispersed by wind. The germination ecology has recently been studied experimentally by Arts & van der Heijden (1990). Seeds are produced in small quantity, each plant producing a maximum of c. 20 per annum. They require light in order to germinate. Desiccation for 2 or 4 weeks stimulates germination, not only increasing the final number of seeds which germinate once they are rewetted but also causing a rapid and nearly synchronous germination. *Littorella* has a large seed bank, and the seeds remain viable for decades. In addition to sexual reproduction, *Littorella* also has very effective vegetative propagation which allows colonies to persist even if permanently submerged. Established plants send out stolons bearing new rosettes, and this lateral spread can lead to the development of a dense carpet of plants. In conditions of heavy silt deposition the stolons grow upwards, and by this means plants have survived deposition rates of 2 cm of sand per month under experimental conditions (Spence, 1982).

In historical times *L. uniflora* has always been scarce in S.E. England. The map shows that it has decreased, primarily as a result of the drainage of the damp, acidic habitat it favours. Elsewhere it is still a frequent plant, and its tolerance of mesotrophic water has enabled it to survive in areas where other isoetids have declined. Experimental studies show that it is able to exploit increases in nutrients to greater effect than *Lobelia dortmanna*, but much less effectively than *Mentha aquatica* (Farmer & Spence, 1986). At Esthwaite Water, Robe & Griffiths (1992) concluded that *L. uniflora* can adjust well to eutrophic conditions, despite the fact that plants become shaded in summer and autumn by algal blooms and a layer of epiphytes on their leaves. In The Netherlands *Littorella uniflora* has decreased markedly since 1950, being replaced in many sites by the aquatic form of *Juncus bulbosus* and *Sphagnum* spp. These changes are attributed to acidification following increased inputs of ammonium (Roelofs & Schuurkes, 1983 - add additional refs).

L. uniflora is widespread in W., C. and N. Europe, becoming rare in the south but extending to Spain, Portugal and Sardinia (Hultén & Fries, 1986). It is also recorded from N. Africa. A closely related taxon which occurs at similar latitudes in E. North America is treated by

some authors as a separate species (*L. americana* Fernald) and by others as a variety of *L. uniflora*.

L. uniflora differs from the other isoetids in Britain and Ireland in its wider habitat range; it is the only species which grows in calcareous substrates. It is less exclusively aquatic than the other species, often being found above the water level and only flowering when it grows terrestrially.

124. SCROPHULARIACEAE

A large family of 222 genera and some 4,500 species, although Mabberley (1987) comments that despite its size, the family is 'of little consequence to mankind'. Most of the species are herbs but there are also some trees and shrubs. Some 18 genera and perhaps 200 species are aquatics, although it is even more difficult than usual in this family to draw the line between aquatic and terrestrial species (Cook, 1990). The only genus with aquatic species in Britain and Ireland is *Veronica*, although other genera occur in waterside habitats (*Mimulus*, *Scrophularia*) or on damp mud in seasonally flooded sites (*Limosella*).

124/16. *Veronica* L.

Most of the 250 species of *Veronica* are found in the temperate regions of the northern hemisphere, although some extend southwards to mountains in the tropics or to the southern hemisphere. Closely allied shrubby plants in the southern hemisphere are placed in the genus *Hebe*. All the aquatic species of *Veronica* are in Section *Beccabunga* Dumort., which contains 12 species, although *V. scutellata* of Section *Veronica* can be found in fens.

Two subsections of *Veronica* Section *Beccabunga* are recognised, both of which are represented in Britain and Ireland. Subsection *Beccabunga* (CHK nomenclature-Fischer gives this as *Eubeccabunga* Keller) includes the *V. beccabunga* and the non-European *V. americana*, and poses no difficult taxonomic problems. Subsection *Anagallides* J. Keller comprises the species closely related to *V. anagallis-aquatica*, which at a world scale 'is an extremely confusing complex of several species and subspecies intimately connected to each other, with abundant hybridisation' (Öztürk & Fischer, 1982). Even in our area the two species in this Subsection, *V. anagallis-aquatica* and *V. catenata*, are very similar morphologically and hybridise to give *V. × lackschewitzii*. The experimental taxonomy of these taxa has been studied by N.G. Marchant (Marchant, 1970; Walters, 1975).

In the British Isles *V. beccabunga* is diploid ($2n=18$) whereas *V. anagallis-aquatica* and *V. catenata* are both tetraploid ($2n=36$).

This low-growing species is frequent in very shallow water or on damp ground at the edges of streams and rivers. It is confined to sites where the growth of more vigorous plants is restricted by erosion during floods or by other disturbances. It can usually be found, for example, on muddy ground at those places along a riverbank where cattle come to drink, but is often absent from the intervening stretches where emergents form a continuous sward. In shallow chalk streams it may grow across the entire channel (Haslam, 1978). Other habitats include shallow ditches, marshy hollows in pastures, damp woodland rides, open flushes and on disturbed areas by lakes, ponds and canals or in fens. It is found over a range of substrates from fine silt to stones and rocks, and in both calcareous and non-calcareous sites, but it is absent from very infertile substrates such as acidic peat. It often grows with *Apium nodiflorum*, *Glyceria fluitans*, *Ranunculus flammula*, *R. sceleratus* and *Rorippa nasturtium-aquaticum sensu lato*. It is frequent in the lowlands, and ascends to 730 metres (Knock Fell); Wilson (1956) cites an unlocalised record from 850 metres in the Scottish Highlands.

V. beccabunga is a winter-green perennial. It flowers freely, and the flowers may be self-pollinated or cross-pollinated by insects (CTW-presumably from Knuth?). Plants set many seeds which germinate readily; there is also a persistent seed bank in the soil (Grime *et al.*, 1988). The seeds are not buoyant, and therefore rarely occur in floating plant debris. However, they produce a mucilaginous coat when exposed to water and might therefore be dispersed by animals (Guppy, 1906-CHK ALL THIS). Fragments of stems root readily, and the plant frequently spreads vegetatively along streams (Grime *et al.*, 1988-CHK Ridley). The species is shallow rooted and in floods entire plants may be swept away (Haslam, 1978).

This species is still frequent throughout much of Britain and Ireland, and there is no evidence for any decline at the scale of the map. Few authors of county floras regard it as a decreasing species, except in the most heavily built-up areas (Kent, 1975; Graham, 1988).

V. beccabunga is widespread in temperate regions of Eurasia, and also occurs in N. Africa. It is naturalised in N. America, where it was probably introduced initially with ships' ballast. Its spread in N. America has been less rapid than that of some other alien aquatics, perhaps because many suitable habitats there are already occupied by the closely allied *V. americana* (Les & Stuckey, 1985).

The unusual epithet *beccabunga* is derived from the Low German 'beckbunge': 'beck-' is cognate with our word beck and means stream but the meaning of '-bunge' is not clear (Gilbert-Carter, 1964). Add names in Grigson.

This species is found as submerged stands in shallow water, and as an emergent or terrestrial species in swamps and on disturbed ground at the water's edge. It grows by a wide range of water bodies, including rivers, streams, ditches, lakes, ponds and flooded clay and gravel pits. It is found on fertile substrates, whether acidic or calcareous. It is primarily a lowland plant, which reaches 380 metres at Malham Tarn (Sinker, 1960).

Young plants of *V. anagallis-aquatica* soon develop stolon-like lateral branches from their base, which send out numerous adventitious roots (Marchant, 1970). The vegetative vigour and reproductive performance of the species varies greatly with habitat conditions. In flowing water it may persist as submerged vegetative stands. Plants on fertile silt by streams and rivers are much larger than those which grow in disturbed and rather dry terrestrial habitats. Individual plants are self-compatible. Although their inflorescences are usually aerial, plants which are made to flower under water in experimental conditions produce flowers which do not open but which nevertheless set seed (Combes, 1965). The fruits of *V. anagallis-aquatica*, like those of *V. catenata* and their hybrid, are often galled by the weevil *Gymnetron villosulum*. Submerged stands fragment when streams are in spate (Haslam, 1978), and the stems can root and become established as new plants.

The two related species *V. anagallis-aquatica* and *V. catenata* were not separated by British botanists until the differences were set out by Druce (1911, 1912); a more detailed account was provided by Britton (1928) and the correct nomenclature established by Burnett (1950). Historical records cannot be attributed to one or other species unless they are supported by herbarium specimens. Both species may still be somewhat under-recorded in some areas as they can only be identified in flower or fruit; in other areas where the hybrid *V. × lackschewitzii* is frequent, *V. anagallis-aquatica* may be over-recorded (Crackles, 1990). There is no evidence to suggest that the distribution or abundance of *V. anagallis-aquatica* has changed markedly since it was first recognised in our area.

V. anagallis-aquatica is a native of the temperate and mediterranean regions of Eurasia and N. Africa, which extends north in Europe to central Scandinavia. However, it has been introduced to C. & S. Africa, N. & S. America and New Zealand, and so now has an almost cosmopolitan distribution. The species is taxonomically complex, with both diploid and tetraploid subspecies (Öztürk & Fischer, 1982).

Veronica × *lackschewitzii* J. Keller (*V. anagallis-aquatica* L. × *V. catenata* Pennell)

This hybrid is found in a similar range of habitats to *V. anagallis-aquatica*. Some populations are completely submerged in flowing water over 50 cm deep; these rarely if ever flower in the wild. The most conspicuous plants grow in shallow water in lakeside swamps, ditches or at the edge of streams and rivers. Some riverside plants accumulate mounds of silt around their roots and therefore rise above the water level. In terrestrial habitats *V. × lackschewitzii* can be found on muddy cattle-trampled ground at the edge of streams and rivers, on crumbling riverbanks, on moist mud at the edge of reservoirs and on damp sand or gravel in disused mineral workings. The hybrid can often be found with both parents, but it can also occur in the absence of one or both parents. In Hampshire it appears to replace both parents over a large area (ref. to Fl. Hants. when published). The hybrid is confined to the lowlands.

In favourable habitats *V. × lackschewitzii* can be a very robust perennial: clumps with 70 flowering stems 1.2 metres high have been recorded. F1 hybrids are normally highly sterile, and continue flowering long after the parents have set fruit, the racemes becoming longer and longer. Such hybrids are thought to be at a selective advantage in flowing water because of their vegetative vigour (Walters, 1975). However, F2 and later generations can be more fertile. Many populations of the hybrid consist of highly sterile plants, and may represent a single clone, but some wild populations with a range of fertility are known (Walters, 1975). The stems root readily at the nodes, even high up on the inflorescence (Wells, 1968) and the hybrid reproduces and spreads vegetatively after fragmentation in floods or as a result of other disturbance. Large populations can develop in rivers which are regularly cleared out. The hybrid can be very persistent: it was still present in 1991, for example, by the R. Piddle at Chamberlayne's Mill, a site where it was first collected in 1921.

The first British record of this hybrid was made by Williams (1929), soon after Britton (1928) clarified the distinction between the parental species. Earlier specimens have since been discovered in herbaria. The highly floriferous but sterile F1 hybrids are distinctive. Nevertheless, many botanists are still unaware of the plant and it is almost certainly under-recorded, especially in Ireland. Submerged plants which persist in the vegetative state can only be identified by bringing them into cultivation.

This hybrid is widespread in mainland Europe. It is also recorded from N. America, where *V. catenata* is native but *V. anagallis-aquatica* is a naturalised alien (Brooks, 1976; Heckard & Rubtzoff, 1977).

This species grows in shallow water in streams and ditches, in flushes, on mud at the edge of lakes, reservoirs, ponds, rivers and streams and on moist ground in sand dunes or disused sand, gravel, clay and chalk pits. It has also been recorded from riverside rocks. Although it can be found on fertile, acidic soils, it tends to be much more frequent in calcareous regions. It also occurs in coastal areas which are occasionally flooded by brackish water. Although it often grows with *V. anagallis-aquatica*, it has a more restricted habitat range than that species, occurring more frequently on exposed mud at the edge of standing waters. Characteristic associates in such habitats include *Alisma plantago-aquatica*, *Lycopus europaeus*, *Ranunculus sceleratus*, *Rorippa nasturtium-aquaticum sensu lato* and *Rumex maritimus* (Sinker *et al.*, 1985). *V. catenata* is confined to the lowlands.

Unlike *V. anagallis-aquatica*, young plants of *V. catenata* develop basal branches which grow into flowering stems rather than stolon-like stems which spread vegetatively (Marchant, 1970). The species is a perennial, but tiny plants in disturbed terrestrial habitats may be annuals. There is little detailed information on its reproductive biology, and the extent to which it spreads vegetatively.

This species was not recognised in Britain and Ireland until 1911, having previously been confused with *V. anagallis-aquatica*. Even after Druce (1911, 1912) had outlined the differences, the aggregate continued to be recorded for some time. Botanists in Somerset, for example, began to distinguish the segregates in the 1930s (Roe, 1981) and in Gloucestershire the distribution of the two taxa has not yet been worked out (Holland, 1986). *V. catenata* may therefore be somewhat under-recorded.

V. catenata is widespread in the temperate regions of the northern hemisphere, and in Europe extends north to southern Scandinavia. It occurs as an introduction in C. Africa and Australia.

128. LENTIBULARIACEAE

This small family contains three genera and 275 species of carnivorous plants. Members of the genus *Pinguicula* are rooted herbs which trap animals on their viscid leaves. All the species are terrestrial. The other two genera, *Genlisea* and *Utricularia*, are rootless, although the plants may be anchored by buried stolons or rhizoids. They possess specialised animal-catching traps. *Genlisea* is a small tropical genus of mostly terrestrial species. *Utricularia* is a much larger genus with a cosmopolitan distribution, although most species are found in the tropics.

128/2. *Utricularia* L.

There are 214 species of *Utricularia*, most of which are terrestrial; 3 of them are sometimes segregated in the genus *Polypompholyx*. They have recently been the subject of a superb monograph (Taylor, 1989). The morphology of this genus is unlike that of other flowering plants. Stems are absent or very reduced, and are replaced by stolons. There is much variation within the genus (Sculthorpe, 1967). The largest species is *U. humboldtii*, which grows in pools of water in the leaf axils of South American bromeliads; the most spectacular are perhaps the species in Section *Orchidioides*; which have large white, lilac or orange-red flowers and grow on mossy banks or tree branches in the montane rain forests of Central and South America. At the other extreme are plants such as *U. neottioides* which form low mats on rocks in swiftly flowing water, to which they are affixed by numerous rhizoids. Excluding these rheophytes, ?? species of *Utricularia* are aquatics. The aquatic species may be free-floating plants with green stolons or may be anchored by additional colourless stolons buried in the substrate. The 8 native European species, all of which are aquatics, are closely related members of Section *Utricularia*.

Utricularia is a taxonomically troublesome genus on a world scale, partly because it is difficult to collect adequate specimens. Even in Europe there are still unresolved taxonomic problems: Taylor (1989) refers to the 'extraordinary amount of often contradictory written matter' devoted to these few species. One of the major problems in our area is that floral characters are important for identification, but many populations persist and spread vegetatively, and rarely flower. All the European species reproduce by turions, which are only found in the aquatic species of Section *Utricularia* which grow outside the tropics. The turions, like those of *Myriophyllum verticillatum*, are made up of morphologically reduced, concave, overlapping leaves and they are borne at the apices of the stems and the main lateral branches. They are usually formed in autumn, although they may be produced earlier on plants which are droughted or starved of nutrients (Sculthorpe, 1967).

Flowering plants of *U. australis* and *U. vulgaris* are easily recognised, but vegetative distinctions between the two species are slight and perhaps too variable to give an absolutely certain identification. A map of the aggregate is provided here, followed by maps of the two segregates.

There are more difficult taxonomic problems concerning *U. intermedia sensu lato*. Taylor (1989) suggests that most British material is *U. ochroleuca*, and that the evidence for the presence of *U. intermedia sensu stricto* is not conclusive. Stace (1991), basing his taxonomy on work by Thor (1988) which was not published in time for Taylor to evaluate, recognised

three species in our area, *U. intermedia*, *U. ochroleuca* and the newly described *U. stygia*. Only the aggregate is mapped, as data on the distribution of the segregates is very incomplete.

The final species, *U. minor*, is the only one which is relatively free of taxonomic complications. We may, however, be overlooking *U. bremii*, a Central European species which closely resembles *U. minor*. An old herbarium specimen from [? Loch Spynie], Morayshire 'could well be this species' (Taylor, 1989).

The 'bladders', of *Utricularia* were initially thought to be flotation devices, or reservoirs of air. It was not until the middle of the 19th century that they were recognised as animal-catching traps. These reports attracted the attention of Darwin (1875), who made the first thorough study of their morphology. He accurately described the traps, and understood the way in which the bristles around the entrance provide a funnel leading to the trapdoor. However, he thought that small invertebrates pushed their way past the trapdoor, which then prevented their escape. It was not until 1911 that the true mechanism was discovered. There is a negative pressure inside the bladders. The trapdoor opens when animals touch the bristles at the lower margin of the trapdoor, and the victim is sucked inside (Meyers, 1982).

Utricularia vulgaris sensu lato

The floating stolons of *U. vulgaris sensu lato* grow in nutrient-poor, still or very slowly flowing water. They can be found both in acidic and in basic, highly calcareous water over a range of inorganic or peaty substrates, but do not grow in eutrophic conditions. Characteristic habitats include the sheltered bays of lakes, pools and marl pits, swamps, ditches in bogs, fens and grazing marshes, disused peat diggings and flooded clay pits. Plants in this aggregate are shade-tolerant, and can be found in stands of lakeside emergents such as *Carex rostrata* and *Phragmites australis*. Although they are often found in shallow water, they can grow at greater depths in lakes with clear water, and descend to 4 metres in the limestone lakes of Lismore (?ref to West). Although predominantly lowland, the aggregate is recorded at 500 metres in Llyn Anafon; there is an unlocalised record from 640 metres in Perthshire (White, 1898).

For details of the flowering and fruiting behaviour of the species in this aggregate, see under *U. australis* and *U. vulgaris*. Effective reproduction of both species is by turions, which develop on the apex of the shoots from July onwards.

As the map shows, these species have declined in lowland Britain. The marked decline in S. Lancashire was caused by the drainage of the extensive 'mosses' in the early 19th century, and many smaller sites have been lost elsewhere as lowland peatlands have been drained and taken into agricultural use. Other sites have been adversely affected by eutrophication, and *U. vulgaris sens. lat.* is now a local plant in most parts of Britain. It remains plentiful only in the north and west, where acid soils predominate, and in a few areas where calcareous waters are still unpolluted. The map suggests that the plant has undergone a similar decline in Ireland, but this needs to be confirmed by further fieldwork.

U. vulgaris sensu lato is widespread in Europe, extending north to scattered localities in northern Scandinavia. The aggregate has a wide distribution outside Europe, occurring in temperate and tropical Asia, throughout Africa and in Australia and New Zealand.

For individual treatments of the two species in this aggregate, *U. australis* and *U. vulgaris*, see the following accounts.

This is a species of base-rich waters. Typical habitats include shallow, sheltered bays in limestone lakes, pools and ditches in calcareous fens, ditches in grazing marshes, fenland lodes and flooded clay and marl pits. It has also been recorded as a colonist of flooded gravel pits. It can be found in oligotrophic and mesotrophic waters: it increased in abundance in the Broads as the input of nutrients increased in the first half of this century, only to decline again as the levels of nutrients continued to increase (George, 1992). *U. vulgaris* is apparently confined to the lowlands.

It is not unusual to find flowering plants of *U. vulgaris* in the southern part of its British and Irish range, and at some sites flowers can be found every year. There is considerable variation from year to year, and flowering may be particularly prolific in hot summers. Gurney (1922) suggests that the temperature when flower buds are initiated in spring may be as important as the temperature at the time of flowering, but the precise factors which govern flowering have not been studied critically. In northern England and Scotland plants flower much less regularly. Unlike many aquatics, the fruits mature in air. Fruiting plants have been found north to Lincoln, although the frequency with which seed is set is unknown. The usual form of reproduction is by turions, which sink to the bottom of the water in autumn. They may survive periods of freezing (Sculthorpe, 1967), and in East Anglia they begin to grow in late March or early April (Clarke & Gurney, 1921; Friday, 1989).

The map is based on records of flowering plants, to which records of vegetative material determined by P. Taylor have been added. Both the historical and recent range of the species must be seriously underestimated. This under-recording makes it almost impossible to demonstrate trends in the distribution of the species, but there is little doubt that its range has retracted in southern and eastern England because of habitat destruction and eutrophication.

U. vulgaris is widespread in Europe, although it is rare both in the Mediterranean region and towards its northern limit in northern Scandinavia. It is also known from N. Africa and temperate Asia east to Siberia and Tibet.

Detailed studies of a population of *U. vulgaris* at Wicken Fen have shown that the traps account for about half the biomass of a *Utricularia* plant. An individual plant has a mixture of large traps on the mid-line of each leaf lobe, and smaller traps on the finer segments. The youngest traps are the most effective: after six days their ability to catch prey declines rapidly, and most traps are lost from the leaves within 32 days. New leaves bearing young traps develop continually. In a single season an average plant may produce a total of 15,000 traps, and catch 230,000 crustaceans, midge larvae and oligochaete worms (Friday, 1988, 1989, 1991, 1992).

It is difficult to obtain precise information about the ecological requirements of *U. australis*, and the extent to which they differ from those of *U. vulgaris*, because the confirmed records of *U. australis* are so few, and are not necessarily representative of the majority of its populations. It is generally agreed that *U. australis* differs from *U. vulgaris* in its preference for base-poor water. It is found in acidic water in lakes, reservoirs, ponds, canals, ditches, and swamps over inorganic or peaty substrates. The two British sites from which both *U. australis* and *U. vulgaris* have been recorded were acid bogs at the foot of calcareous hills, and there is no evidence that the two species actually grew together (Taylor, 1989). However, *U. australis* is recorded from some moderately calcareous sites in Ireland, such as a pond on sand dunes on Cruit Island where it grows with abundant *Chara hispida*. There are no confirmed records of *U. australis* above 300 metres, but plants growing at 500 metres in Llyn Anafon are probably referable to this segregate.

U. australis appears to flower much more frequently in the southern part of its British range than in more northerly localities, although flowering plants have been found as far north as the Culbin Forest. There is no evidence that the British and Irish populations set seed, and reproduction appears to be entirely by turions. Despite its extensive world range, mature fruit of *U. australis* is only known from China and Japan (Taylor, 1989) and the species apparently reproduces vegetatively almost everywhere. **Chk chromosome paper.**

The map is based on records of flowering plants of *U. australis*, to which records of vegetative material determined by P. Taylor have been added. It must greatly under-estimate both the historical and the current distribution of this segregate, and the fact that bladderworts flower more frequently in the southern part of their range must give it an unduly southern bias. The records are also inadequate to provide an accurate estimate of changes in its distribution. However, *U. australis* has almost certainly decreased in southern and eastern England, but is probably still frequent in those areas of Wales, northern Scotland and western Ireland where the aggregate is recorded.

U. australis is widespread in Europe, north to central Scandinavia. It is found in temperate and tropical regions throughout the Old World, and also in Australia and New Zealand.

Utricularia intermedia sensu lato

U. intermedia usually grows in shallow, oligotrophic water, where buried, colourless and trap-bearing stolons anchor it to the substrate. It is most frequent in acidic and peaty sites, including the shallow edges of lakes (where it sometimes grows in stands of emergents such as *Menyanthes trifoliata* and *Phragmites australis*), pools, wet flushes, slow-flowing streams and ditches. Characteristic associates in these habitats include *Carex nigra*, *Drosera intermedia*, *Juncus bulbosus*, *Potamogeton polygonifolius*, *Ranunculus flammula*, *Chara virgata*, *Sphagnum* spp. and, in western sites, *Hypericum elodes*. *U. intermedia* also grows in highly calcareous but nutrient-poor lakes, fens and flushes over peaty substrates. It was, for example, one of the species which grew in the clear water of the Broads in their pristine state (George, 1992). It is recorded from sea-level to 655 metres at Loch na Stairne (West, 1905-CHK).

Members of the *U. intermedia* aggregate flower much less frequently than either *U. vulgaris sensu lato* or *U. minor*. The populations which flower most frequently are those in Dorset (Hall, 1939), and even here Taylor's (1989) attempts to see flowering plants were 'thwarted by a succession of cool summers'. Reproduction is by turions, which usually begin to develop on the green stolons in late July or August. They can, however, develop earlier, sometimes on plants in pools which are drying out (Gurney, 1922). They begin to grow when temperatures rise in the spring: in Norfolk Clarke & Gurney (1921) found that they could be grown in an indoor aquarium in December, but in the wild they began to elongate in late April.

This species had a more restricted distribution in eastern Britain than the other bladderworts. [Ask DAP if any decrease in Dorset/Hants]. It has decreased in East Anglia and eastern Scotland for the same reasons that *U. vulgaris sensu lato* has declined: the destruction of many lowland peatlands and the eutrophication of the remaining lakes, pools and ditches. It remains frequent in its strongholds in the north and west.

U. intermedia sensu lato has a circumboreal distribution. In Europe it is frequent in the boreal zone and extends south in scattered localities to S. France and N. Italy.

Three segregates of *U. intermedia* are thought to occur in Britain: *U. intermedia sensu stricto* (Intermediate Bladderwort), *U. ochroleuca* R. Hartman (Pale Bladderwort) and *U. stygia* (Nordic Bladderwort). The differences between them are outlined by Thor (1979, 1987, 1988). As yet only a few records of these segregates are available, and their distribution in Britain and Ireland needs to be worked out.

U. minor is most frequently found in peat-stained, acidic and oligotrophic water, where it is often anchored to the substrate by colourless stolons. Its habitats include bog pools and old peat cuttings, where it can sometimes occur in abundance, shallow water at the edge of lakes, ditches and wet flushes. It often grows in shallow water in stands of emergent *Menyanthes trifoliata*. Other associates include *Carex nigra*, *Drosera intermedia*, *Juncus bulbosus*, *Menyanthes trifoliata*, *Potamogeton polygonifolius*, *Utricularia intermedia sens. lat.*, *Sphagnum auriculatum* and *S. cuspidatum*. Although *U. minor* is found in base-poor habitats to a greater degree than our other bladderworts, it can also grow in nutrient-poor but base-rich water, as it does in fens and ditches on the Burren limestone near Mullaghmore. It is recorded from sea level to 600 metres (Haystacks Tarn), and Wilson (1956) cites an unlocalised record from 690 metres in Scotland.

U. minor flowers occasionally throughout much of its British and Irish range. In some years plants flower freely in S.E. England: 1910 was a good flowering year in Norfolk, for example, and populations also flowered freely in the hot summer of 1921 in those sites where its pools did not dry out (Clarke & Gurney, 1921; Gurney, 1922). *U. minor* flowers much more frequently in Scotland than the other members of the genus. Nevertheless, reproduction is usually by turions, which are formed at the end of the green stolons from late July onwards. These will germinate in winter if kept at room temperature; in the wild growth begins in Norfolk in early April (Clarke & Gurney, 1921).

This species has suffered a marked decline in the eastern part of its British range. The major cause is the destruction of lowland peat bogs, but shading and scrub encroachment on remaining bogs may also have contributed, and perhaps eutrophication in those sites (e.g. Wicken Fen) where it appears to have grown in calcareous habitats. *U. minor* is apparently extinct in numerous counties or vice-counties including Sussex (last recorded 1963), Kent (1966), Cambridgeshire (1951), Lincolnshire (1961), S.E. Yorkshire (before 1902), Northumberland (1959) and Berwickshire (1974). The map suggests a similar decline in S.E. Ireland, but detailed local studies are needed to confirm this. *U. minor* remains frequent in the peatlands of the north and west, and as the smallest member of the genus it may be somewhat under-recorded in these areas.

U. minor has a circumboreal distribution, extending south to the Himalaya, Burma, Japan and California and also found at high altitudes in Papua New Guinea. In Europe it occurs from Iceland and northern Scandinavia southwards, but it is rare in the Mediterranean region.

129. CAMPANULACEAE

The only native European aquatic genus in this family is *Lobelia*, which is often placed in the segregate family Lobeliaceae.

129/7. *Lobelia* L.

Only two native species are known in our area, the aquatic *L. dortmanna* and the terrestrial *L. urens*, a rare species of S. England. The familiar garden 'Lobelia', *L. erinus*, is also recorded as an escape from cultivation.

Lobelia dortmanna is one of the most characteristic, and one of the most attractive, species of oligotrophic lakes in Britain and Ireland. Like other isoetids, it is a slow-growing perennial of low competitive ability. It is virtually confined to lakes, but it can sometimes be found in their outflow streams. It grows in shallow water less than 2 m deep over a wide range of substrates from coarse sand to highly organic silts. In exposed sites it is found in open communities, where it is often accompanied by *Eleocharis palustris*, the aquatic form of *Juncus bulbosus*, *Littorella uniflora*, *Myriophyllum alterniflorum* and *Ranunculus flammula*. As the vegetation cover increases with depth additional associates include species such as *Callitriche hermaphroditica*, *Potamogeton gramineus* and *P. natans*. *L. dortmanna* also grows in open stands of emergents such as *Carex rostrata*, *Equisetum fluviatile* and *Schoenoplectus lacustris*. Although it is tolerant of exposure, the most luxuriant plants are found in more sheltered sites. It is confined to shallow water because it is intolerant of shade, and thus unable to persist at low light intensities. It is only found over acidic substrates, but it can be found in base-rich but nutrient-poor water where the substrate is siliceous (Webb & Scannell, 1983). *L. dortmanna* may be excluded from marl lochs by an inability to tolerate the deposition of marl on the leaves, and from mesotrophic water by the shading effect of epiphytes (Farmer and Spence, 1986; Farmer, 1989). Small colonies of compact plants can very occasionally be found growing terrestrially (Farmer, 1987). The species grows from sea-level to 745 m at Llyn Glas Bach.

L. dortmanna flowers from May to October. Aerial flowers are probably self-pollinated (they do not seem to be visited by insects), and almost all set seed. Flowers which develop under water also set seed. After liberation from the capsule the seeds sink rapidly. They require a cold pretreatment of 1-3° C for one month before they will germinate, and they only germinate in the light. Seeds will, however, germinate at light levels which are too low to sustain seedling growth. *Lobelia* populations have a persistent seed bank, and seeds can remain viable for 30 years (Arts & van der Heijden, 1990). New rosettes are formed vegetatively at the base of the old flower stalk by the growth of axillary buds. There are no specialised vegetative propagules, and long-distance dispersal is dependant on the spread of seed. A detailed account of the reproduction of *L. dortmanna* is given by Farmer & Spence (1987).

This 'singular and elegant plant' (Wade, 1802) is distinctive when in flower or fruit, and the vegetative rosettes would only be overlooked by inexperienced recorders. The map in the *Atlas of the British Flora* (Perring & Walters, 1962) consequently gave a much truer picture of its distribution than those of other isoetids such as *Isoetes lacustris* and *Subularia aquatica*. Although *L. dortmanna* is still frequent in much of western Britain and Ireland it is vulnerable to eutrophication and the map clearly indicates that sites have been lost at the eastern edge of its range, where human population densities are greatest and agriculture more intensive. It is, for example, extinct in the Shropshire meres (Sinker *et al.*, 1985), in several lochs in S.E. Scotland including Loch Leven (Farmer & Spence, 1986) and at Lough Neagh, where it was first recorded in Ireland by W. Sherard in 1694 (Harron, 1986; Hackney, 1992).

L. dortmanna is an amphi-atlantic species, widespread in Northern Europe, extending south very locally to S.W. France, and in N. America.

For a detailed account of the ecology of *L. dortmanna*, from which much of the above information is drawn, see Farmer (1989).

136. BUTOMACEAE

The monotypic genus *Butomus* is the only member of this family, which is allied to the Alismataceae and the non-European Limnocharitaceae.

136/1. *Butomus* L.

The distinctive and highly attractive *Butomus umbellatus* is the only species in this genus.

B. umbellatus grows as a submerged or emergent aquatic, or as a terrestrial species near the water's edge. It is usually found where the water is calcareous and eutrophic, and it can persist, even as a submerged aquatic, in highly managed and very eutrophic rivers. Submerged plants are usually found in sluggish rivers, streams and fenland lodes, where they often grow with *Sagittaria sagittifolia* and *Sparganium emersum*, two other species with strap-like leaves. Emergent or terrestrial plants are found at the edge of lakes, reservoirs, rivers, streams, canals and ditches. They often occur as individual clumps, but extensive *B. umbellatus* swamps sometimes develop, notably in the Lough Neagh basin. The species is also planted by ornamental lakes, village ponds and disused gravel pits. It is confined to the lowlands.

This is a rhizomatous perennial. Plants spread by lateral buds which develop on the rhizome (Hroudová, 1989). These are easily detached when plants are uprooted by floods, disturbed by waterfowl or damaged in dredging operations. They float on water and readily give rise to new plants. The flowers are insect pollinated and self-incompatible. Both diploid and triploid cytotypes are known in Europe; the triploids are sterile and their sole means of reproduction is vegetative spread (see Love Feddes Rep. 62, 136-148, 1960?). Little is known of the cytology and fertility of the British or Irish plants. Variants with bulbils in the inflorescence are known from Scandinavia and Belgium (Lohammar, 1954; Jans, 1989), but not from Britain or Ireland. The bulbils do not drop off individually, but remain attached to the inflorescence.

B. umbellatus is almost certainly native to Britain (Godwin, 1975). In England losses caused by habitat destruction have been balanced by its spread along canals and its deliberate introduction as an ornamental plant to new sites. The species is believed to reach its northern limit as a native British plant in Co. Durham, where it is now extinct. However, there are thriving populations in natural habitats further north, which are apparently the result of recent spread. It is locally frequent by the Tweed and its tributaries, for example, but was not recorded there until 1956 (Braithwaite & Long, 1990; Swan, 1993). It may have spread from planted stock. In Ireland it is also thought to be native in some areas, including Co. Clare (Webb & Scannell, 1983). However, the large populations round L. Neagh and L. Beg were not known to Stewart & Corry (1888) but the plant subsequently spread rapidly, perhaps originating from cultivated material (Harron, 1986; Hackney, 1992).

B. umbellatus is widespread in temperate Eurasia, extending north in Europe to northern Scandinavia; it also occurs in N. Africa. It has spread as a naturalised alien in N. America, particularly in the Great Lakes and St Lawrence River regions (Anderson *et al.*, 1974).

The southerly distribution of *B. umbellatus* in Britain is surprising in view its presence here in the last full glacial period, and its occurrence in northern Scandinavia (Godwin, 1975). Its apparent ability to spread from introduced plants north of its native range suggests that it might have been limited by its powers of dispersal.

CHK paper in Can. J. Bot. 57:2353-2373 (1979).

137. ALISMATACEAE

This is a family of 11 genera and some 95 species, all of which are aquatic. The family has a cosmopolitan distribution.

The Alismataceae and the Butomaceae are members of the Order Alismatales. It has often been suggested that these are the most primitive monocots. Their similarity to dicot families such as the Nymphaeaceae has led to the suggestion that the ancestral monocots arose from ancestors which were not unlike the modern Nymphaeales (Cronquist, 1981). Recent authors have viewed this theory rather sceptically, or rejected it completely (Tomlinson, 1982; Mabberley, 1987), and Dahlgren *et al.* (1985) suggest that the similarity between the two orders is probably the result of convergent evolution in aquatic habitats. However, support for the traditional view has come from studies of chloroplast DNA, which have revealed similarities between the monocots and a group of 'palaeoherbs', including the Nymphaeaceae (Chase *et al.*, 1993). Further work along these lines ought to throw new light on the vexed question of the origin of the monocots.

Many important aquatic families are included with the Alismatales in the Subclass Alismatidae, one of the major subdivisions of the monocots. Those with representatives in our area include the Hydrocharitaceae, Aponogetonaceae, Potamogetonaceae, Ruppiaceae, Najadaceae and Zannichelliaceae, and the marine Zosteraceae. Many of these families appear to have been derived from ancestors similar to the modern Alismatales, but often have very reduced vegetative and floral parts.

137/1. *Sagittaria* L.

Sagittaria is one of the larger genera in the Alismataceae, with 20 species. There are two relatively recent monographs of the genus (Bogin, 1955; Rataj, 1972a,b) but, as Cook (1990) comments, 'neither of these revisions have found general acceptance'. Two species are native to Europe, one of which occurs in Britain and Ireland. Most of the species are found in the New World and three of these are established in our area, although none of them are widely naturalised.

This is a plant of lowland, shallow, still or slowly flowing water in sheltered lakes and ponds, rivers, streams, ditches and canals. In many areas it is restricted to the major water scours and their associated streams and ditches. It grows in calcareous and eutrophic (but not brackish) water over a range of fine substrates, including clay, sand and silt. *Nuphar lutea* and *Sparganium emersum* are frequent associates in managed rivers; in grazing marsh ditches there is often a richer flora which may include [list]. *S. sagittifolia* very rarely colonises newly available aquatic habitats in sand, gravel and clay pits. It is confined to the lowlands.

S. sagittifolia has broad, strap-shaped submerged leaves as well as the familiar arrow-shaped emergent leaves. In the central channel of streams and rivers only submerged leaves may develop. Elsewhere, plants produce emergent leaves and flower freely. Female flowers are borne below male flowers on the same peduncle, and are insect-pollinated. The peduncle with its globose fruiting heads falls into the water. The seeds have a waxy coat and may float until this is damaged by frost. Little is known about the extent to which plants in our area become established from seed: in Central Europe seeds germinate in spring at temperatures above 13°C, often in anaerobic, submerged sediments (Hroudová *et al.*, 1988). In autumn mature plants die down, perennating by tubers which develop on stolons in the leaf axils. These also provide a means of vegetative dispersal.

Fossil evidence suggests that *S. sagittifolia* is a native British plant: it is even known from late glacial sediments in Cumberland and Skye, north of its current native range. It colonised the canal network in both Britain and Ireland, even becoming established as an introduction in the Forth & Clyde Canal, where it was first recorded in 1889 (Hennedy, 1891). In recent years it has decreased in ditches in river valleys, sometimes becoming restricted to the rivers themselves (Tarpey & Heath, 1990). It has also decreased in some grazing marshes (Mountford, 1994). Its ability to persist in eutrophic, canalised and highly managed rivers has probably prevented a more serious decline.

S. sagittifolia is a variable species which, if broadly interpreted to include *S. trifolia* L., is widespread in boreal, temperate and tropical regions of Eurasia. In Europe it is rare in the Mediterranean region, and extends north to northern Scandinavia [Godwin says that it is only found as non-flowering submerged plants in Arctic circle: any ref with more details?] It is replaced by the closely related *S. latifolia* in N. America.

This alien species is recorded from shallow water in lowland lakes and ponds, roadside ditches and at the edge of streams and rivers. In one pond it grows with *Menyanthes trifoliata*. In most cases it has become established in the area where it was originally planted, but it may be spreading along the R. Wey, where isolated patches up to 3 metres in diameter have been recorded in recent years.

Like *S. sagittifolia*, *S. latifolia* dies down in the autumn to tubers which are borne on stolons in the leaf axils. They act as a means of perennation and vegetative spread. The species flowers in Britain, but there are no published observations on the occurrence of ripe seed or seedlings. In America some populations consist of monoecious plants and others of dioecious individuals; the dioecious plants usually reproduce vegetatively (Wooten, 1971). Exposed mud is required for successful seedling establishment. Germination occurs once the seed coat has been eroded or ruptured, which usually happens during the winter. In suitable conditions seedlings may be very abundant in spring and early summer (Kaul, 1985).

This species was first recorded in 1941 in a pond on Epsom Common, where it survived until the pond was filled in in 1956. It is now known from several other localities in Surrey (Lousley, 1976). It was found in an overgrown pool in Jersey in 1961, and it still persists there, having survived the clearing out of the pool some years after its discovery (Le Sueur, 1984). It was discovered in Hampshire in 1962-check this-and in Sussex in 1976. It may be overlooked elsewhere because of its similarity to *S. sagittifolia*.

S. latifolia is an American species which is naturalised in several European countries. It is the commonest and most widespread species of *Sagittaria* in N. America, found in temperate and subtropical wetlands throughout the continent and extending south to C. America, Colombia, Ecuador and Venezuela. Its native distribution is mapped by Bogin (1955). It is also naturalised in the West Indies and Hawaii.

The starchy tubers of this species were formerly used as food by the North American Indians, and by Chinese and Japanese immigrants in California (Bogin, 1955). They are, however, too large and too deeply buried to be of much use to wildfowl (ref to Martin book).

S. rigida is recorded as a naturalised alien in the R. Exe in the Exeter area, and from the nearby Exeter Canal. In the Exe was recorded along the edge of the river, and plants were exposed above the water when water levels dropped in hot weather. In the canal it is also found close to the bank as an emergent, associated with *Carex acutiformis*, *C. riparia*, *Lycopus europaeus*, *Oenanthe aquatica*, *Schoenoplectus lacustris* and *Scrophularia auriculata*.

This is a stoloniferous perennial. Both monoecious and dioecious plants occur in Britain (Hiern, 1908). The inflorescences of the female plants are shorter than those of the male, and have very few whorls of flowers. The monoecious plants have male flowers in the upper whorls of the inflorescence and female flowers below. Hiern (1908) noted that the early flowering plants tended to be dioecious, and the later ones monoecious. Ripe fruit is set in Britain, and the species also reproduces by tubers produced in autumn on the stolons.

S. rigida was first recorded from the R. Exe by Hiern (1908), who found it in considerable quantity in and near Exeter. Soon afterwards it was found in the Exeter Canal (Druce, 1910, *J. Bot.* p. 116 - CHK). In Keble Martin & Fraser (1939) described it as well established in the river and canal, but it was last recorded in the river in 1952 [Check card for this NMW record]. It was still present in the canal in 1975, when two groups of plants were recorded, but it has not been seen in more recent surveys. It is too earlier to conclude that it is extinct, but confirmation of its continued presence is required.

This species is a native of S.E. Canada and the eastern United States, where it grows in inland, calcareous waters and fresh or brackish tidal creeks. Its native distribution is mapped by Bogin (1955). There are no confirmed records of the species as an established alien elsewhere in Europe (Tutin *et al.*, 1980).

Sagittaria subulata (L.) Buchenau

Narrow-leaved Arrowhead

This species is naturalised in a single lowland pond. It grows in abundance in shallow, acidic water, accompanied by *Elodea canadensis* and *Potamogeton natans*.

S. subulata has submerged and floating but no emergent leaves. The unisexual flowers open at the surface of the water, as in *Luronium natans*, and only a single flower on each inflorescence opens at any one time. It has a long flowering period in Britain, from June to October. The British population sets ripe fruit, and also reproduces vegetatively by tubers which are produced on stolons in the mud.

This species was discovered at Shortheath Pond by Mr & Mrs D.N. Turner in 1962; in 1983 it was 'still abundant and obviously established' (Grenfell, 1984). It is occasionally sold as an aquarium plant, and was probably introduced into Shortheath Pond with discarded material from an aquarium.

S. subulata is a native of N. & S. America, where it is found in the coastal plain from Massachusetts south to Alabama, and in Venezuela and Colombia. The N. American distribution is mapped by Bogin (1955). In this area it grows in tidal waters, small, slow-flowing streams and occasionally in ponds. It is a variable plant, divided by Bogin (1955) into three varieties. Plants of var. *kurziana* in warm streams in Florida may have leaves that reach 15 metres in length, and flowering scapes up to 90 cm. *S. subulata* is recorded as a probable introduction from the highlands of New Guinea (Rataj, 1972a), but the British station is the only one known in Europe (Tutin *et al.*, 1980).

The information on the habitat and reproductive biology of this species in Britain is taken from Brewis (1975).

137/2. *Baldellia* Parl.

There are two species of *Baldellia*, one widespread in Europe (*B. ranunculoides*) and the other endemic to the mountains of the Iberian peninsula (*B. alpestris*). *Baldellia* is one of several small genera in the Alismataceae related to the larger and predominantly tropical genus *Echinodorus*. Their generic limits are not very well defined, and Cook (1990) suggests that *Baldellia* 'is very close to and should perhaps be united with *Echinodorus*'.

Although Tutin *et al.* (1980) do not subdivide European *B. ranunculoides*, some authors recognise two subspecies, subsp. *ranunculoides* and subsp. *repens* (Lam.) Löve & Löve (e.g. Vuille, 1988) and others even treat subsp. *repens* at specific rank (e.g. Lindblad & Ståhl, 1990). Subsp. *repens* differs from subsp. *ranunculoides* 'by having runners, fewer flowers per umbel, slender and curved pedicels, larger petals, fewer carpels, smaller anthers, a poorer fruit-set, and smaller, papillose fruits' (Lindblad & Ståhl, 1990). Vuille (1988) found that populations of subsp. *ranunculoides* were self-compatible whereas subsp. *repens* was strongly self-incompatible and did not set seed when artificially self-pollinated. The British and Irish populations are treated below as a single taxon, but both subspecies may be present. Scully (1916) reports 'a profusely stoloniferous form' as 'rather common on the shores of some of the larger Kerry lakes'. A study of the variation within our *B. ranunculoides* might be worthwhile.

B. ranunculoides is found in habitats where the competition from more robust species is restricted by a variable water level and a low level of nutrients. These include the edges of lakes and reservoirs, pools, streams and ditches, canals, flooded quarries, abandoned peat cuttings, marshes and flushes on sea cliffs. Although it is sometimes found in acidic waters, it is more frequent in sites which are at least slightly basic. These range from those which receive some enrichment from nearby calcareous or ultrabasic rocks, or from dune sand, to highly calcareous waters over chalk or limestone. It can also occur in brackish sites. It grows over a range of organic and inorganic substrates including peat, sand and fine calcareous marl. It is sometimes found in sites where the competing vegetation is restricted by cattle poaching, or as a colonist of newly constructed bird 'scrapes' or recently cleared ditches. It is a lowland species which ascends to 320 metres W. of Libanus.

This is a phenotypically variable species which may persist in relatively deep water as vegetative plants with submerged leaves. These spread by stems which root at the nodes, producing new plants. Plants in shallow water or on mud exposed above the water level produce aerial leaves and flower freely. Their flowers are pollinated by insects and usually give rise to numerous fruits. Field observations indicate that plants which flower under water may also be capable of fruiting, suggesting that the flowers are self-compatible and capable of self-fertilisation. Plants sometimes reappears in abundance in newly cleared ditches, suggesting the presence of a persistent seed bank. Established individuals may reproduce vegetatively by division of the basal rootstock, and Vuille (1988) reports pseudovivipary, with plantlets developing from vegetative buds within the inflorescence.

As the map suggests, *B. ranunculoides* has decreased greatly in England and eastern Scotland in the historical period. It is now extinct in several counties, and has decreased in many others. Many sites were on commons which were formerly important for watering stock but have now been filled in or become overgrown. Others were ditches which have disappeared with agricultural improvement, or are now managed unsympathetically, or canals which have become disused and dried out. Some sites have been lost through eutrophication. Although *B. ranunculoides* may reappear in areas where it was thought extinct, as it did in Middlesex in 1988, there is no doubt that it continues to decrease in many areas. There is less evidence of a decline in Ireland, where it is still frequent in shallow, calcareous water in many areas.

B. ranunculoides is found in W., C. & S. Europe, north to S. Norway and E. to Greece; it also occurs in N. Africa. It is most frequent in the western part of its range. **CHK Cook paper.**

137/3. *Luronium* Raf.

This is a monotypic genus which, like *Baldellia*, is of rather doubtful validity. The only species, *L. natans*, is found in both Britain and Ireland. For a detailed study of the British plant see Willby & Eaton (1993); Rich *et al.* (in press) have recently reviewed the Irish records.

The most frequent natural habitat for *L. natans* is acidic and oligotrophic lakes, where it grows in water up to 2 metres deep, with species such as *Callitriche hamulata*, *Isoetes lacustris*, *Littorella uniflora* and *Lobelia dortmanna*, or on bare mud exposed by falling water levels. It also grows in a slow-flowing, mesotrophic stretch of the Afon Teifi, and it was found in the past from a variety of other habitats including streams, ditches, lowland lakes and pools. At least one of the lakes in which it has been recorded, Lough Leane, was calcareous but nutrient-poor. *L. natans* is also established in the canal system, where it grows in circumneutral or slightly basic, mesotrophic water, often with *Elodea nuttallii*, *Lemna minor*, *Sparganium emersum* and *Potamogeton* spp. In canals it apparently relies for its survival on periodic disturbance, which can be provided by light boat traffic in navigable waters or by periodic dredging or the control of marginal vegetation elsewhere (Willby & Eaton, 1993). The introduced populations in Broadland grow in ditches (Driscoll, 1985), and the Argyll plants are at the edge of a loch (Slack, 1964). *L. natans* is found from near sea-level to 450 metres (Bugeilyn).

L. natans is a stoloniferous perennial. In flowing or deep water, or in sites that are shaded or turbid, it can persist as rosettes of submerged leaves, which spread vegetatively. In shallow water or on wet mud it produces floating or terrestrial leaves and flowers. The flowers are entomophilous and fruit freely. Populations in natural habitats appear to be greatest when water levels are low and much bare mud is exposed, but when levels are high many plants may be present as inconspicuous, submerged rosettes. In canals plants are most numerous after disturbance.

Although flowering *L. natans* is very distinct, the vegetative plant can be confused with other members of the Alismataceae and has probably been overlooked in some sites and recorded in error at others. A number of outlying records mapped by Perring & Walters (1962) are now known or suspected to be errors. In Britain the populations in oligotrophic, upland lakes appear to be stable, but the plant has disappeared from many of its lowland, mesotrophic localities because of habitat destruction or eutrophication. During the nineteenth century the species colonised the canal system, but the canal populations have decreased since 1970 as recreational boat traffic has increased. Although *L. natans* was first recorded in Ireland in 1801, the records have long been dismissed as errors and have only recently been reinstated following the discovery of the species in Connemara (Rich *et al.*, in press). The plant may be more frequent in Ireland than the map suggests.

L. natans is endemic to W. and C. Europe, where it extends from S. Norway to N. Spain and eastwards to Bulgaria. It is most frequent in the western part of its range, in Britain, France and N. Germany; in N. Spain, where it has been confused with *Baldellia alpestris*, it is rare (Rodriguez-Oubiña & Ortiz, 1991). **Trends?**

137/4. *Alisma* L.

This genus of 9 species is found throughout the northern hemisphere. Detailed studies of the taxonomy, cytology, reproductive biology and ecology of the European species have been published by Björkqvist (1967, 1968), from which much of the information below has been taken.

There is a wide range of leaf form in the European species of *Alisma*. Plants may have strap-shaped submerged leaves, floating, emergent or terrestrial leaves; the emergent and terrestrial leaves are very similar. The type of leaf produced varies from species to species and, within a species, with environmental conditions. This plasticity enables plants to adapt to changes in water level in the marginal habitats in which they grow. Seedlings of *A. plantago-aquatica* with submerged leaves or immature plants with floating leaves often puzzle botanists who are unfamiliar with the variability of this common species.

Alisma plants are perennials which die down in winter, regrowing from a terminal bud on the rootstock. The individual flowers are ephemeral, but the more robust species have large, branched inflorescences and a long flowering period. Although the flowers are often cross-pollinated by insects in the field, all species are self-compatible and are capable of self-fertilisation, and fruit set is usually very high. The seeds will float for long periods (up to 128 hours in Björkqvist's (1967) experiments, and may be dispersed by water. They have a hard seed coat and may still be viable after passing through the intestines of birds. See Ridley: **plumage & clothing**. The seeds may remain dormant for long periods, as germination occurs once the seed coat has been broken. Seeds will germinate on land or in shallow water. A limited amount of asexual reproduction may occur by the growth of side shoots on the rootstock or by the uprooting of plants in floods. All the species are poor competitors, usually found in open vegetation or on bare mud. They favour water which is at least moderately eutrophic.

There are confirmed records of three of the four European species in our area, *A. gramineum*, *A. lanceolatum* and *A. plantago-aquatica*. The fourth species, *A. wahlenbergii*, is a Baltic endemic closely related to *A. gramineum* and sometimes treated as a subspecies of that species. *A. wahlenbergii* was reported as occurring with *A. gramineum* in Norfolk (Swann, 1975) but the identity of these plants requires reassessment.

Alisma gramineum ($2n=14$) and *A. plantago-aquatica* ($2n=14$) are diploids, whereas *A. lanceolatum* is a tetraploid with two morphologically indistinguishable cytotypes ($2n=26, 28$). *A. lanceolatum* seems likely to have evolved by polyploidy from *A. plantago-aquatica* or an extinct species with a similar karyotype. It is apparently an ancient species; tetraploid plants of *A. plantago-aquatica* which were artificially synthesized by Björkqvist (1968) did not have the morphology of *A. lanceolatum*. Hybrids between *A. lanceolatum* and *A. plantago-aquaticum* are known from The Netherlands, Poland and Sweden; they were described as *A. × rhinocarpum* by Schotsman (ref). Björkqvist (1968) and Pogan (1971) confirmed the identity of the hybrid cytologically and both Schotsman and Björkqvist synthesized the hybrids artificially without difficulty. Although the hybrids are intermediate between the parents, they tend to have a rather greater resemblance to *A. lanceolatum* than to *A. plantago-aquatica*. The hybrids are partially sterile, but the degree of sterility varies. Both Polish and Swedish hybrids grew in disturbed habitats, and the hybrid was replaced by its parents in one

Swedish site once the disturbance ceased. Hybrids between *A. gramineum* and both the other species have been obtained artificially, but are unknown in the wild. They set very little seed.

There is some doubt whether the hybrid *A. × rhinocarpum* occurs in Britain and Ireland. It is recorded from both countries, and Allen (1984) considers that in the Isle of Man it is commoner than its parents, and more tolerant of the repeated clearing out of drainage ditches. However, Stace (1991) suggests that all records require confirmation. This could be obtained by a study of the microscopic characters which separate the parents (e.g. stomatal length) and the cytology of the putative hybrids.

This species is found in shallow water or exposed mud at the edges of a wide range of water bodies, including lakes, reservoirs, pools, slow flowing rivers, streams and ditches, and in marshes and swamps. It usually grows in open habitats, including shallow water where cattle congregate, but it can be found amongst open stands of emergents such *Glyceria maxima*, *Phragmites australis*, *Sparganium erectum* and *Typha latifolia*. It is found in both mesotrophic and eutrophic water and usually grows on fine-grained, nutrient-rich substrates; plants on shallow water over eutrophic mud can be very robust. It often appears in abundance in newly cleared ditches and is a frequent colonist of newly available habitats such as gravel pits, and even deep wheel ruts where water lies in winter (Tarpey & Heath, 1990). It may also be planted around new ponds and lakes (Swan, 1993; Sykes, 1993). It is virtually confined to the lowlands, but reaches 403 metres at Dock Tarn (Stokoe, 1983).

Plants of *A. plantago-aquatica* in water deeper than c.65 cm persist as plants with submerged leaves but fail to flower. In shallower water the plants flower and fruit freely. Clapham *et al.* (1952) suggest that *A. lanceolatum* flowers in the morning whereas *A. plantago-aquatica* flowers in the afternoon. This view is supported by Perring *et al.* (1964), who describe the differences as surprisingly constant, but has been questioned by other observers (e.g. Percy, 1962; Morton, 1966). Plants of *A. plantago-aquatica* cultivated by Björkqvist (1967) opened their flowers later than those of *A. lanceolatum*, but there was then a broad overlap in flowering time. In addition to insect pollination, plants may be wind-pollinated (Daumann, 1965-CHK). The seed may remain viable for at least 10 years if stored at room temperature. *A. plantago-aquatica* reproduces freely by seed, and swards of seedlings can sometimes be seen in shallow water.

Fossil evidence suggests that this species is a long-established native which has persisted in our area through both glacial and interglacial stages. It is still frequent in suitable habitats in both Britain and Ireland, although it is apparently extinct in North Aberdeenshire, near the northern edge of its British range (Welch, 1993). Its ability to exploit eutrophic waters and colonise new sites doubtless explain why it has survived in areas where some other members of the family have declined.

This species occurs as a native throughout most of Europe (north to the Arctic Circle) and Asia, and all round the Mediterranean; it also occurs in the mountains of E. Africa. It has been introduced to S. Africa, S. America, Australia and New Zealand. Despite its large range, there is little evidence of geographical variation within the species.

This species occurs in shallow water or on damp mud in a similar range of habitats to *A. plantago-aquatica*, with which it often grows. It is found at the edges of lakes, reservoirs, ponds, slowly flowing rivers, canals, fenland lodes and ditches, and in marshes and swamps. It is also found as a colonist of flooded quarries and sand, gravel and clay pits, and even occasionally of seasonally flooded hollows in arable fields. It usually grows in eutrophic water which is often, though not invariably, calcareous. It is most frequent over fine-grained substrates, although it will grow on sand. It is confined to the lowlands.

A. lanceolatum usually has emergent or terrestrial leaves; submerged and floating leaves rarely, if ever, develop. Plants in shallow water flower and fruit freely. The seeds have a less resistant coat than those of *A. plantago-aquatica*: in experiments a greater proportion of untreated seeds germinate and relatively mild pretreatments such as a short period of frost will enhance their germination to a much greater degree.

This is a rarer species than *A. plantago-aquatica* throughout its British and Irish range. In many counties the largest or even the only populations are found in canals. For many years British and Irish botanists did not recognise it as a distinct taxon, or treated it as a variety of the commoner species. Druce (1932), for example, simply notes under *A. plantago-aquatica* that 'narrow leaved (*lanceolatum*) and broad leaved (*latifolium*) plants occur'. It is difficult to assess trends in the distribution of *A. lanceolatum* because of the absence of reliable historical records in many areas and it may still be overlooked for the commoner species. In eastern England Simpson (1982) and Tarpey & Heath (1990) suggest that the species must have declined greatly if the older records can be trusted. *A. lanceolatum* is occasionally found as an introduction, and it is established in a burn in Skye, north of its native range (Murray, 1980).

A. lanceolatum is widespread in Europe, N. Africa and W. Asia. It is the commonest species in the genus in the Mediterranean area and Asia Minor, and has a more southerly limit in Europe than *A. plantago-aquatica*, only reaching S. Sweden. The species becomes distinctly calcicolous towards the northern edge of its range.

Björkqvist (1967, 1968) found that the cytotype of *A. lanceolatum* with $2n=26$ was widespread in W. & C. Europe, but that with $2n=28$ was much rarer, being found in Sweden, Denmark and Poland. He did not examine any British or Irish material, but $2n=28$ has been reported from the Cambridge area by Priestley (1953).

A. gramineum is recorded from shallow, eutrophic water at the edge of lowland lakes and rivers; or in fenland drains. At Westwood Great Pool it usually grows amongst stands of emergents in water less than 10 centimetres deep, although it sometimes grows in open water or on recently exposed mud. Lousley (1957) found it with abundant *Eleocharis palustris* but in recent years most plants have grown amongst *Typha latifolia*. In Lincolnshire it formerly grew in water 0.7-1.3 metres deep over a soft, muddy substrate in the R. Glen and its associated drains. It has only been seen recently in a single ditch in this area, where it appeared in 1991 and 1992 after clearance, but did not survive once *Phragmites australis* recolonised the site. The other British records are from a fenland ditch in Cambridgeshire (Libbey & Swann, 1973) and Langmere in Breckland (Swann, 1975).

In the shallow water in which it usually grows *A. gramineum* forms rosettes of numerous submerged leaves. Plants with submerged leaves may flower, but mature plants may also develop floating and emergent leaves. The observation in Clapham *et al.* (1952) that the flowers open between 6 and 7.15 a.m. is totally fictitious: in the wild British plants flower throughout the day and in cultivation Björkqvist (1967) found that the flowers of this species remained open for 13-15.5 hours, longer than those of the other species he studied. Cleistocarpous flowers may develop and set seed under water. Seed set is good in the wild, and reproduction by seed occurs although the number of seeds which germinate at Westwood varies greatly from year to year. Many plants in Britain are annuals, but some persist as short-lived perennials.

This species was first discovered in Britain in 1920 at an artificial lake, Westwood Great Pool, but it was initially confused with *A. lanceolatum*. It still persists in this site, where the population size is usually small but can exceed 150 flowering plants in a favourable year. The reason for the fluctuations is unknown. It was discovered in the R. Glen and nearby ditches in 1955, but is now much less frequent in this area. At its other sites it does not appear to have persisted for long, although it may survive as buried seed. It is an inconspicuous species which could be overlooked elsewhere. It has been suggested that the East Anglian populations may be derived from seed carried by wildfowl arriving from Denmark or the Baltic (Libbey & Swann, 1973), but *A. gramineum sensu stricto* is replaced by *A. wahlenbergii* in the Baltic.

A. gramineum is widespread in temperate latitudes in Europe, Asia (except the Far East) and N. America. In Europe it is absent the Iberian peninsula and the Mediterranean region; it now reaches its northern limit in Denmark, having become extinct in Sweden. In mainland Europe it is uncommon throughout its range, and it is normally found as small populations (Björkqvist, 1967). It is difficult to account for its rarity in western Europe. Its sporadic appearance and apparent dependence on disturbance make it a difficult plant to conserve. By contrast, it has spread along the St Lawrence River in N. America, where it has been described as a 'pesky weed' (Raymond & Kucyniak, 1948; Countryman, 1968).

137/5. *Damasonium* Miller.

This small genus has a remarkably disjunct distribution, occurring in the Mediterranean region in the Old World, and in mediterranean climates in western N. America (*D. californicum*) and Australia (*D. minus*). Vuille (1987) recognises three species in Europe, the tetraploid *D. alisma* and the diploids *D. bougeai* and *D. polyspermum*. Other authorities (e.g. Tutin *et al.*, 1980) treat all the European plants as a single, variable species, *D. alisma*. *D. alisma sensu stricto* is intermediate in its breeding system between the *D. californicum*, which is adapted to cross-pollination, and *D. minus*, which is usually autogamous and can be pollinated when still in bud. In *D. alisma* the stamens are spread at the start of anthesis, exposing the stigma, but self-pollination may occur if cross-pollination fails (Vulille, 1987).

For detailed accounts of the ecology and conservation of *D. alisma* in Britain see Birkinshaw (1994) and Marren & Rich (1993).

D. alisma is a plant of shallow water or exposed mud in lowland ponds, where it grows on acidic substrates which are disturbed and sparsely vegetated. Many of its British sites were ponds on grazed commons, where fluctuating water levels and disturbance by stock ensured that the marginal vegetation remained open. The surviving populations rely on disturbance by trampling by dogs and people, or deliberate management by conservationists. It is found amongst sparse emergents such as *Glyceria fluitans* or *Sparganium erectum* at these sites; other associates include *Apium inundatum*, *Callitriche* spp., *Juncus articulatus*, *J. effusus*, *Potamogeton natans*, *Ranunculus peltatus*, *R. repens* and *Solanum dulcamara*. Although almost all British records are from ponds, there were isolated occurrences at the edge of lakes and rivers, and in canals and ditches.

D. alisma is an annual in the wild, although it can be cultivated as a short-lived perennial. Its seeds will only germinate under water; a high proportion of fresh seed is dormant, and the germination of additional seeds is stimulated by drying followed by resubmergence. Seeds usually germinate in early winter and develop into small, submerged plants with linear leaves. In spring floating leaves develop, and (if water levels fall) terrestrial leaves. Plants with floating leaves and those with terrestrial leaves will flower. Although the species will complete its life cycle in water, it eventually becomes outcompeted by aquatic plants unless the habitat dries out occasionally. Plants vary greatly in size depending on environmental conditions, and exposed plants will continue to flower only while the substrate remains moist. The individual flowers are ephemeral and one or two seeds, one much larger than the other, develop in the conspicuous follicles. The seeds are larger and the seed output less than that of many commoner species that grow on exposed mud (Salisbury, 1970). The smaller seed is released in water once the fruits are resubmerged, but the larger seed remains in the follicle. Plants may reappear at particular sites after long intervals, suggesting that the seeds may remain dormant for many years.

This southern species was, very surprisingly, present in Britain in the last glacial period (Godwin, 1975). In historical times it was never common, but this century it has suffered a catastrophic decline. Some of the ponds in which it grew have been filled in, but most are still present, but lack suitable habitat. Some are no longer visited by stock and have become overgrown or surrounded by woodland; others have a stable water level which is artificially regulated for fishing or are infested by large flocks of wildfowl. Pond restoration has resulted in the reappearance of this species in at least two sites in recent years, and deliberate management of its sites will probably save this species from extinction.

D. alisma has a Mediterranean-Atlantic distribution, occurring in S. Europe, S.W. Asia and N. Africa and extending north along the Atlantic coast to England.

138. HYDROCHARITACEAE

A family of 19 rather small genera, all of which are aquatics found in freshwater or marine habitats. The members of the family are very variable in both vegetative and floral parts, even in our area. Many species are dioecious, and male and female plants of the same species can have different distributions at both the local and the world scale. It is not, therefore, surprising that for many species vegetative propagation is the main means of reproduction. Detailed accounts of many of the freshwater genera have been published by C.D.K. Cook and his colleagues in recent years.

138/1. *Hydrocharis* L.

There are three species of *Hydrocharis*: *H. chevalieri* (found in tropical Africa), *H. dubia* (S. & E. Asia, Australia) and *H. morsus-ranae* (discussed below). For an account of the genus, including a summary of the morphology, ecology and distribution of all three species, see Cook & Lüönd (1982b).

The floating rosettes of this species are normally found in shallow water in the sheltered bays of lowland lakes (where they often grow amongst the scattered stems of emergents), ponds, canals and drainage ditches. It favours calcareous, mesotrophic or meso-eutrophic water and occurs in water bodies over both peat and mineral soils. It is a characteristic species of freshwater ditches in grazing marshes, where it tends to grow in narrow gavity-drained ditches in water less than 1 m deep. Here emergent species are kept in check by grazing and the water is too shallow to support more vigorous competitors such as *Nuphar lutea* and *Nymphaea alba*. In such localities *Hydrocharis* is often associated with other floating species, including *Lemna gibba*, *L. minor*, *Spirodela polyrhiza* and *Wolffia arrhiza*. Sometimes, as in the Somerset Levels, associated submerged species are few - *Lemna trisulca* and *Ceratophyllum demersum* being the most frequent - but in the Pevensey Levels and Broadland there is a richer submerged community. The smaller emergents, such as *Alisma plantago-aquatica* and *Oenanthe fistulosa*, are frequent associates. *Hydrocharis* has successfully colonised some canals. If exposed to terrestrial conditions by falling water levels it is only able to survive for short periods.

The proportion of *Hydrocharis* plants in a population which flower varies from season to season. Populations in southern England can flower freely in warm summers, but fewer flowers are produced in cooler conditions and some populations in northern and western sites appear to flower very sparingly. Individual rosettes bear either male or female flowers, but it is not certain whether all plants of the same genetic individual are the same sex. Ripe seed is rarely reported from Britain and Ireland, but in the hot summer of 1947 a large proportion of flowers set viable seed in Norfolk (Gurney, 1949). British botanists may have overlooked fruiting plants in more recent hot summers, as the peduncle elongates and bends over after fertilization and the fruit matures under water. Seedlings do not appear to have been reported in Britain. For a detailed account of sexual reproduction of the species in Canada, see Scribailo & Posluszny (1984, 1985). Plants multiply by vegetative reproduction, new rosettes developing on the end of stolons. They over-winter as winter-buds which develop on stolons in the late summer and autumn, and germinate in spring. Most winter buds require 2 weeks at temperatures approaching 15°C for germination (Richards & Blakemore, 1975).

Hydrocharis is still almost ubiquitous in the Somerset Levels, but has decreased markedly in some of its former strongholds in recent years. In Cambridgeshire it was described as 'rather common throughout the fens' by Perring, Sell & Walters (1964) but it has since decreased dramatically and is now restricted to a few sites (Payne, 1989). A similar decline has been documented in Romney Marsh by Mountford & Sheail (1989). The main cause has been the conversion of grazing land to arable, after which those small ditches which have not been completely eliminated become overgrown with emergents. *Hydrocharis* only survives in such areas in the small fragments of pasture which survive, or in Cambridgeshire in grassland maintained as washland and with an internal drainage system. Even in areas of Broadland which are still managed as grazing marsh, *H. morsus-ranae* has declined. Some 26% of ditch samples which in 1972-74 had meso-eutrophic species-rich plant communities dominated by *H. morsus-ranae* and *Stratiotes* had other communities in 1988-89 (Doarks, 1990). Many ditches which formerly supported *H. morsus-ranae* are now dominated by *Lemna minor*, *L. trisulca* and filamentous algae, a community characteristic of more eutrophic sites.

Hydrocharis is occasionally found as an introduction and has become well established in the Forth and Clyde Canal, well beyond the northern limit of its native distribution.

H. morsus-ranae is widespread in W. and C. Europe, extending north to S. Sweden and S. Finland and south to N. Italy. It occurs at scattered localities in E. Europe and Asia, extending to the S. shore of the Caspian Sea; there are also reports from C. Asia. Its native distribution is mapped by Cook & Lüönd (1982b). The species also occurs as an alien in N. America, where it escaped from a botanic garden at Ottawa into an adjacent canal in 1939 and has since spread over much of S.E. Ontario, S. Quebec and New York State (Dore, 1986; Catling & Dore, 1982). Seed set is apparently poor throughout the range of the species, perhaps because of the local separation of the sexes.

138/2. *Stratiotes* L.

Stratiotes has a fossil record dating back 48 million years. A number of species have been described from fossil material, including some from Tertiary freshwater deposits in Hampshire and the Isle of Wight. Today only a single species survives, *S. aloides*. For a review of the fossil members of the genus and a detailed account of *S. aloides*, from which much of the information below has been taken, see Cook & Urm-König (1983).

The unmistakable rosettes of *Stratiotes* float on the surface of still or slowly flowing water. In the low-lying fenland areas where it appears to be native *Stratiotes* grows in calcareous, meso-eutrophic water; it was formerly found in lakes and slow-flowing rivers but is now virtually confined to drainage ditches. In Broadland it occurs in the most species-rich grazing marsh ditches, where its associates include *Hydrocharis morsus-ranae*. It is intolerant of brackish conditions and it is also unable to grow on mud, and is therefore absent from sites where there are marked fluctuations in water level. *Stratiotes* is also found as an alien in lakes, ponds, canals, ditches, gravel, clay and marl pits. Most introduced populations are probably derived from material discarded by gardeners. At some sites it has increased rapidly to cover the water surface - this happened in the Basingstoke Canal in the 1950s (Lonsby, 1976) and the Lancaster Canal in the 1960s (Greenwood, ?1974). Although some alien populations become well established, others are only transient.

Plants overwinter as rosettes on the bottom of the water. In spring new leaves with gas-filled intercellular spaces develop and the rosettes rise to the surface. In deeper water, or in cool summers in some northern localities, they may remain on the bottom of the water. The flowers are showy and apparently have an unpleasant smell like that of carrion. All British and Irish plants are female (although the female flowers have staminodes which are usually sterile but sometimes produce pollen). Reproduction here is entirely vegetative: new rosettes (sometimes open, sometimes almost bud-like) are produced on lateral shoots throughout the summer. Parthenocarpic fruits often develop, but contain unripe ovules; the fruits reported from Britain by Geldart (1906) and Crackles (1982) were presumably of this sort as the authors were unable to detect ripe seeds. In autumn plants become weighed down by dead, waterlogged leaves and sink to the bottom of the water. The species apparently lacks a means of long-distance dispersal over land.

Stratiotes was known to 17th century botanists in Cambridgeshire, Lincolnshire, S. Yorkshire and Holderness (Gerarde, 1633; Ray, 1660); it therefore seems likely that it is native in Eastern England and perhaps also in Cheshire. Cook and Urmi-König (1983) argue that the absence from Britain of the dragonfly *Aeshna viridis*, which is dependant on *Stratiotes*, is a sign that *Stratiotes* itself is not native. However, another dragonfly, *A. isosceles*, is restricted in Britain to East Anglia and is there dependant on *Stratiotes* (Leyshon and Moore, in press). The species is less widespread than formerly, and less abundant in its stronghold, Broadland. It is extinct as a native in Cambridgeshire, Huntingdonshire, [what about S.W. Yorkshire?] and has decreased in Lincolnshire and S.E. Yorkshire. It was abundant in the broads in the late 1940s, probably because nutrient levels had increased in the preceding 50 years and taller and more robust species had replaced the charophytes and smaller vascular plants growing in these hitherto calcareous but infertile waters (George, 1992). With further increases in nutrient levels in the 1950s and 1960s it virtually disappeared from the broads themselves. It is still widespread in drainage ditches, although the mesotrophic communities in which it occurs are particularly threatened by eutrophication (Doarks, 1990). By contrast, *S. aloides* may have declined since 1967 at Catfield and Irstead Fens because of progressive nutrient depletion at a site which has become more oligotrophic and acidic (Wheeler and Giller, 1982).

Stratiotes is widespread in central and northern Europe, reaching its northern limit at 68° in Finland; it extends east through European Russia to Siberia. It has been grown as an

ornamental plant for nearly three centuries, and the native range has been obscured by numerous escapes from cultivation. Cook and Urmi-König (1983), who map its distribution, consider that it is most likely to be native in Sweden, Finland, Denmark, the Low Countries, N. Germany, Poland, the Po plain in Italy and the countries along the Danube. The sexes are not evenly distributed: north of a line drawn from Cherbourg to St Petersburg almost all the plants are female, but males predominate in Belgium and both sexes are present by the Danube. Seed set is apparently scarce even when both sexes occur together, although fruiting plants may be overlooked as the seeds ripen in October when most botanists have retreated indoors for the winter. *Stratiotes* is decreasing in Belgium, The Netherlands and Germany.

138/3. *Egeria* Planchon

There are two species of *Egeria*, both native to S. America. One of them, *E. densa*, has become widely naturalised elsewhere. The genus has been monographed by Cook and Urmikönig (1984).

Egeria densa is/was naturalised in a mill stream and canals in S. Lancashire which received warm water discharge from cotton mills. Here it grows/grew with other alien aquatics, including *Lagarosiphon major* and *Vallisneria spiralis*. At one locality the plants were described as "growing in hot oily water". It is also established in the unheated Calder and Hebble Navigation, where it has persisted for over ten years, and it has been recorded in the nearby R. Calder. Plants have also been reported from a pit in Wallasey and a quarry pool S. of Llanelwedd Rocks, but it is not known whether these were casual occurrences.

Egeria densa overwinters as leafy shoots, which can survive short periods under ice but are killed by prolonged cold. Plants flower freely at temperatures between 15° and 25° C, and in the warm canal water at one Lancashire site the population flowered continuously from May to December (Savidge, 1963). The flowers are borne above the surface of the water. The Lancashire population is/was male, and the same is likely to be true of all the British plants. The species lacks specialised means of vegetative dispersal. Short stem fragments root readily from "bud nodes". Long distance dispersal depends on human agency.

Egeria densa was first identified in the Ashton Canal, Droylesden, in 1953 (Kent, 1955); it had been known there for some years but misidentified as *Elodea canadensis*. It was still present in the Lancashire canal system in 1976. The species was discovered in the Calder and Hebble Navigation and in the nearby R. Calder in 1978, and was still present in small quantity in the canal in 1992. The records from Captains Pit, Wallasey, and the quarry pool at Llanelwedd Rocks were made in 1976 and 1988 respectively. All British populations were probably introduced by aquarists emptying their tanks into outside waters.

This species is a native of S. America (Brazil, Uruguay, Argentina and perhaps Chile), where it is usually found in still water 1-2 m deep. Both sexes occur within the native range but male plants are commoner than females and seed is very rarely set. This "is perhaps the most universally available aquarium plant" (Cooke and Urmi-König, 1984) and is cultivated in tanks and ponds both for horticultural reasons and as an experimental subject. Male plants are recorded in natural habitats in Europe, E. Africa, Japan, Australia, New Zealand and N. and C. America. Many populations are transient, but the species is truly naturalised in warm temperate and cool sub-tropical regions. Unlike some other aquatics it has not become a serious pest in many areas, but in the south-eastern states of the USA it can be a troublesome weed. The native and naturalised populations are mapped by Cook and Urmi-König (1984).

138/4. *Elodea* Michaux

The genus *Elodea* is native to temperate N. America and temperate and sub-tropical S. America; in C. and tropical America it is replaced by the related genus *Apalanthe*. In its native range *Elodea* is difficult taxonomically: plants are so variable in vegetative characters that flowers are necessary for a confident identification. H. St John recognised 17 species of *Elodea* in a series of papers published between 1962 and 1965, but his work proved to be unsatisfactory and in a recent revision Cook and Urmi-König (1985) have reduced the number of species to five. Hybrids between *E. canadensis* and *E. nuttallii* have been created artificially and are believed to occur in the wild.

Three species of *Elodea* have become established in Europe, and all of them have been recorded from Britain. "Outside America *E. canadensis* and *E. nuttallii* are remarkably constant, and it is rare to find plants that cannot be assigned to one or the other species" (Cook and Urmi-König, 1985). The species of *Elodea* are dioecious and almost all the plants currently established in Europe are female, so there is a negligible possibility of *in situ* hybridisation. Plants fragment readily and the fragments produce adventitious roots. The fragments are presumably distributed by birds, boats or anglers. The rapidity with which two species have spread in Britain is remarkable in view of the fact that they rely on the dispersal of unspecialised vegetative fragments.

Much of the information cited below is taken from Cook and Urmi-König's (1985) monograph, and from the studies of the history, taxonomy and ecology of *Elodea* in Britain published by Simpson (1984, 1986, 1988, 1990).

A shallow rooted plant, found in still or slowly flowing, mesotrophic or eutrophic, often calcareous water in lakes, reservoirs, ponds, rivers, streams, canals and ditches. It extends from shallow water to depths of at least 3 m, and can form dominant stands in the most deeply colonised zones of lakes (Spence, 1987). It is favoured by high levels of silt deposition, and often replaces *Fontinalis antipyretica* or *Nitella flexilis* in those parts of lakes where most silt is deposited (Spence, 1982). It is one of the few species which can persist in anaerobic substrates, and it became abundant in Rescobie Loch when many of the macrophytes which were formerly recorded there were eliminated by eutrophication (Spence, 1964). It is a primarily lowland species, but occurs up to 440 m at Loch Loch.

Plants of *E. canadensis* die down in the winter, regrowing from underground stems in spring. The female flowers are borne on long hypanthia and float on the water surface. The male flowers are initially attached to long fragile pedicels which usually break so that the flower floats freely. Pollen is released onto the water surface and thus reaches the female stigmas. In the native range of the species fruits are rarely found, probably because the sexes rarely grow together. In Europe all populations currently known are female, although male plants were discovered in a pond [check] on the Braid Hills near Edinburgh in 1879 (Douglas, 1880) and persisted until 1903. Reproduction is entirely by vegetative means. Plants produce rather unspecialised turions in early autumn but reproduction and dispersal is probably also achieved by the spread of undifferentiated fragments.

E. canadensis provides one of the classic examples of the explosive spread of an alien plant. It was recorded in a pond near Waringstown, Co. Down, in 1836 and in a lake (Hen Poo) at Duns Castle, Berwickshire, in 1842. Although there is an insubstantiated record from the English canal system in 1841, and it has been suggested that it was perhaps present even earlier, the first definite English records were made in 1847 at a reservoir connected to the Grand Union Canal at Foxton, Leics., and at Leigh Park in Hampshire. Thereafter it spread rapidly. From Foxton it spread into the canal system, reaching several midland counties (including Derbyshire, Northamptonshire, Staffordshire and Warwickshire) by 1850. Plants from Foxton were taken into cultivation in Cambridge Botanic Garden in 1847 and placed in a nearby stream in 1848, from whence they spread into the R. Cam and R. Great Ouse and thus colonised Fenland (Marshall, 1852, 1857). In Berwickshire plants were found in the R. Whiteadder in 1848, and by 1850 "had occupied almost every part of the river where the water ran sluggishly almost to choking" (Johnston, 1853). By 1880 *E. canadensis* was widespread in lowland England, S. Scotland and Ireland and expanding into hitherto uncolonised areas. In many newly colonised sites it initially grew in abundance: drains and sluices were blocked and navigation impeded in some rivers. During the 1880s observers noted that it had declined in abundance in areas where it was once dominant, although it usually persisted in smaller quantity. By 1909 it was certainly less abundant than formerly in areas which had been colonised initially, but still expanding into new localities (Walker, 1912). In recent years it has been replaced in many sites by *E. nuttallii*, although at other localities the two species grow together. For a detailed account of the spread of *E. canadensis* in Britain and Ireland, see Simpson (1984). The origin of the British material is uncertain, but it was probably introduced with America timber (Cook and Urmi-König, 1985).

E. canadensis is a native of temperate N. America. British material was grown in botanical

gardens on the European mainland, and from these foci the species spread in the nineteenth century to become widespread in all regions S. of the Arctic. The species is also naturalised and pestilential in Australia and New Zealand.

British material was initially described as a new species, *Anacharis alsinastrum*, by Babington (1848) and only later equated with the American *E. canadensis*. It was also given a number of pseudoscientific names, including *Growforevva aquatilis* and *Babingtonia pestifera*, during the period of its initial expansion.

E. nuttallii favours still or slowly-flowing eutrophic water. Like *E. canadensis*, it is found in a wide range of water bodies including lakes, reservoirs, sand and gravel pits, ponds, rivers, streams, canals and ditches. It is often found in species-poor macrophyte communities in managed rivers, canals with heavy boat traffic and newly colonised gravel pits, where characteristic associates include *Myriophyllum spicatum*, *Potamogeton pectinatus*, *P. pusillus* and filamentous algae. In ponds and shallow streams it can be abundant, sometimes growing in such dense masses that birds such as wagtails can walk from one side of the water to the other. It is resistant to oil pollution (Birk, 1977). Although most frequently found in shallow water, it can occur to depths of 3 m or more in Windermere (Simpson, 1990). It has only been recorded in lowland habitats.

Plants of *E. nuttallii* overwinter as prostrate shoots at the bottom of the water. New shoots grow upwards in spring, elongating rapidly. If they reach the water surface they branch to form a dense canopy just below the surface. The female flowers, like those of *E. canadensis*, are borne on long hypanthia and float on the water surface. The male flower, however, is released by abscission of the pedicel when still in bud. The bud contains a gas bubble and floats to the surface, where it opens to release the pollen. Only female flowers are known in Britain. Turions are not known in this species, and plants spread by vegetative fragments.

E. nuttallii was first recorded in Britain from a ditch at Beard Mill, Stanton Harcourt, in 1966. It was again found near Oxford in 1969, and from 1970 onwards in an increasing number of sites in England. It apparently spread rapidly, but its appearance caused some taxonomic confusion and the details are therefore less well documented than those of the spread of *E. canadensis*. It was first found in Scotland near Allangrange House, Munlochy, in 1978 and in Ireland at Lough Neagh in 1984 (Simpson, 1985). At many sites it has replaced *E. canadensis*, but at others the two species grow together. *E. nuttallii* is certainly now commoner than *E. canadensis* in S.E. England, and is continuing to spread in Scotland and Wales. Its current distribution is probably under-recorded on the map. British material probably originated from plants grown in aquaria or garden ponds and then discarded into the wild.

E. nuttallii is native to temperate N. America. It has a similar range to that of *E. canadensis*, although with a more southerly bias. It was first recorded in Europe in Belgium in 1939, and was also known in The Netherlands (1941) and Germany (1961) before it was discovered in Britain. Although most European plants are female, a male colony is known from Germany. In Japan, where the species was first found in the early 1960s and has since spread rapidly, all plants are male.

The belief that *E. nuttallii* is a phenotype of *E. canadensis* which develops in eutrophic water is still held by some observers (eg Haslam, ???), although it is belied not only by Simpson's (1988) experimental work but by the fact that when both species are found growing together they are easily distinguished. Detached fragments of *E. nuttallii* root more rapidly than those of *E. canadensis*. Simple growth studies suggest that *E. nuttallii* has a competitive advantage over *E. canadensis* as its stems elongate much more rapidly in the period after planting, and are therefore likely to form a canopy more rapidly (Simpson, 1990). A more detailed study of the competitive relationship of the two species would be worthwhile.

Elodea callitrichoides (Rich.) Caspary (*E. ernsticae* H. St. John) South American Waterweed

This species has been recorded from still and slowly flowing water in draining ditches, canals, ponds, ornamental lakes and boating pools in parks and the quieter stretches of lowland streams and rivers. It was present in great abundance in some ditches, canals and rivers when it was first discovered, sometimes to the exclusion of most other aquatics.

The flowering behaviour of *E. callitrichoides* is similar to that of *E. canadensis*, but male flowers remain attached to the parent during anthesis. Only females are recorded in Britain. The species lacks specialised turions, and dispersal is presumably by the spread of vegetative fragments.

Elodea callitrichoides was first collected in Britain in the R. Colne near Harefield in 1948, and in the Longford River at Stanwell in 1950 (Grigg, 1951; Simpson, 1984). Although it originally grew in great profusion at Stanwell, it was very scarce there by 1964 and has not been seen since (Kent, 1975). It has been recorded since 1950 at a number of scattered localities but most populations have proved to be transient. The longest established colony is in the Chichester Canal, where it was first found in 1959 and still present in 1988. British populations are believed to be derived from material discarded by aquarists.

Elodea callitrichoides is a native of temperate S. America, where it appears to be uncommon. Unlike *E. canadensis* and *E. nuttallii*, it is not widely naturalised elsewhere. Female plants were first recorded on the European mainland near Strasbourg, France, in 1958, and have since been seen at several sites near the R. Rhine in Germany. The only persistent populations are in thermally polluted water. As in Britain, these populations are believed to derive from plants grown by aquarists: the species is known to have been available in Germany since 1928.

138/5. *Hydrilla* Rich.

Hydrilla is a monotypic genus. The taxonomy distribution and ecology of the sole species, *H. verticillata*, have been reviewed by Cook and Lüönd (1982a).

This species is only known from one locality in Britain and from one in Ireland. It was discovered at Esthwaite Water by W.H. Pearsall in August 1914. It grew in slightly peat-stained water some 2-3 m deep, with *Callitriche hermaphroditica*, *Najas flexilis* and *Potamogeton berchtoldii* over inorganic, blue-grey clayey mud (Pearsall, ???). In 1935 it was discovered by Pearsall's son, also W.H. Pearsall, in Lough Rusheenduff. Here it can grow in water as shallow as 5 cm but it is usually found washed up from deeper water, often mixed with *Najas flexilis*.

Hydrilla was never seen to flower at Esthwaite, although Pearsall (1921) looked carefully for flowers for six years. The Irish plants have only once been found flowering in the wild, in shallow water during a spell of warm weather, but female flowers are produced abundantly when plants from L. Rusheenduff are cultivated under glass (Scannell, 1976; Scannell and Webb, 1976). Reproduction is by turions which develop in the leaf axils, or terminally on stems and branches, and become detached in late summer or autumn. Bulbil-like buds are also formed beneath the substrate at the tip of the stolons.

Hydrilla seems unlikely to have been introduced to Britain or Ireland by human agency. It has been suggested that both populations might arise from turions carried on the feathers or feet of wildfowl (Pearsall, 1921; Webb and Scannell, 1983). The fact that the Irish plants are apparently all female, and could therefore represent a single clone, is consistent with this hypothesis. Although originally present at Esthwaite in some abundance (Druce, 1916), and still present in unchanged quantity twenty years later (Pearsall, 1936), it was last seen in 1941. It has not been found subsequently despite frequent searching (Lund, 1979) and is believed to have become extinct as a result of eutrophication (ref?). It still survives in Lough Rusheenduff, although not in the abundance described by the younger Pearsall (Webb & Scannell, 1983).

Hydrilla is native to the Old World, but it is rapidly expanding its range in warmer regions and the original distribution is uncertain (Cook & Lüönd, 1982a). In mainland Europe it is confined as an apparent native to the north-east, where it extends from N.E. Germany through Poland and the Baltic States to White Russia. Here it grows in alkaline, moderately calcareous, mesotrophic or slightly meso-eutrophic waters with associates such as *Ceratophyllum demersum*, *Myriophyllum verticillatum*, *Potamogeton natans* and *Stratiotes aloides* (Pietsche, 1981). It is also reported as an alien from warm springs in Austria. It is widespread in Asia from Iran and Afghanistan southwards and eastwards to Manchuria, Japan and New Guinea. It is probably native in Australasia and Africa, but in both continents it is actively spreading. In N. America it was first recorded in Florida in 1960 and is now known from several south-eastern states; it has also been recorded recently in California, C. America and Jamaica. As an introduction it tolerates a wide range of water conditions from acidic and oligotrophic to eutrophic or brackish, "thrives on many kinds of pollution and nutrient enrichment, and it tolerates a great deal of disturbance" (Cook & Lüönd, 1982a). It has become a pest of shallow waters in the tropics and subtropics, as it grows rapidly and can block fish ponds, irrigation ditches and canals.

H. verticillata is both phenotypically and genetically variable (Verkleij *et al.*, 1983). Material from Britain and Ireland has been included with plants from N.W. Poland in var. *pomeranica*

(Reichenb.) Druce, and is said to differ from plants growing further east in Europe, but Cooke & Lüönd (1982a) do not recognise any intraspecific taxa. For detailed accounts of the Irish plant, see Scannell and Webb (1976) and Czapik (1978).

138/6. *Lagarosiphon* Harvey

There are nine species of *Lagarosiphon*, all natives of Africa. One species, *L. major*, has become naturalised in Europe. A monograph of the genus is available (Symoens & Triest, 1983).

L. major is found in standing water in chalk, clay and gravel pits, disused quarries and in lakes and ponds. In some small ponds it can be present in dense masses. It is also established in canals. It is confined to lowland sites.

The female flowers of *Lagarosiphon*, like those of *Elodea*, are borne singly in the axils of the leaves. The hypanthia are long and the flowers float on the surface of the water. The male inflorescence produces numerous flowers which are released as buds and float to the surface of the water, where they open. Each flower has a sail composed of three staminodes, and the flowers are blown by the wind across the water surface. Pollination occurs after a male flower is captured by a female. Few observers have noted the sex of British populations, but the available evidence suggests that all are female. Plants persist and spread within a water body by vegetative propagation, as small fragments can root and become established. At some sites short lateral branches become detached and washed up in quantity around the edge of the water. There is, however, no evidence that plant fragments or lateral shoots can be carried from site to site by natural agents of dispersal.

L. major was first recorded in Britain from a chalk pit near Arlesey in 1944, where it has persisted for over 40 years, (Kent, 1955b; Belcher and Swale, 1990). It has subsequently been found in numerous localities, and at many sites it has become well established. It is clearly able to persist through the coldest winters. *L. major* is widely sold as a plant for aquaria and garden ponds (often as '*Elodea crispata*' or even 'Canadian pondweed'), and British populations almost certainly result from the deliberate or accidental release of such material.

L. major is a native of southern Africa, where it is 'often an obnoxious water pest' (Obermeyer, 1964). It has become naturalised locally in W. Europe and much more extensively in New Zealand, where it was first recorded in 1950 and is now a troublesome weed (Mason, 1960).

138/7. *Vallisneria* L.

A small genus of 2-4 closely related species. As with many dioecious plants, the taxonomy of *Vallisneria* is complicated by the fact that taxa have often been described on the basis of only one sex. The genus has been reviewed by Lowden (1982) who recognises two species, each with 2 varieties. One of these taxa, *V. spiralis* var. *spiralis*, is native to Europe and occurs in Britain as a naturalised alien.

V. spiralis is recorded from several canals and a brick-pit. It is well naturalised in the R. Lea Navigation Canal, where it was first found in 1961 (Harris & Harding, 1973). Here it grows in water of negligible flow over a substrate of mud and gravel. In shallow water at the edge of the canal it forms dense clumps and can be the dominant macrophyte, but it is absent from water deeper than 1 m in the central channel and the vicinity of locks. This canal does not receive heated effluent. In the Reddish Canal (now drained), *V. spiralis* formerly grew in water heated by mill effluent to 29° C, but it was absent from the hottest stretches where temperatures could reach 38° C (Savidge, 1963).

The solitary female flowers are borne at the end of long pedicels, and float on the surface of the water. The male inflorescence bears hundreds of flowers which are released as buds and float to the surface, where they open. Pollination occurs after the male flowers are trapped by the female. After pollination the pedicel spirals and the flower is drawn back under the water. British populations flower freely; Sledge (1942) noted that in a canal near Halifax plants flowered twice a year in May and September. [Do both sexes occur?] Plants are stoloniferous and reproduce vegetatively. In the R. Lea Navigation Canal dispersal may be aided by dredging, which releases large rafts of plants which drift downstream (Harris & Harding, 1973).

V. spiralis was first recorded in Britain in 1868, when it was collected in stagnant water at Knapp's Brickyard, Northwick (Amphlett & Ree, 1909). This population was apparently only transient, but in 1906 *V. spiralis* was discovered in the Reddish Canal, where it persisted for at least forty years. It also became established in other thermally polluted canals in industrial N. England, but the only records since 1970 have been from the R. Lea Navigation Canal. The species is also recorded from the Berkeley Canal and the R. Avon in Gloucestershire but there is no evidence that it persisted at either site. The British populations presumably result from plants discarded from cultivation; early this century it was "frequently grown in aquariums and bowls by the botanically inquisitive" (Amphlett & Ree, 1909) and it is still a popular aquarium plant.

Vallisneria spiralis var. *spiralis* occurs as a native in S. Europe, north to northern France; it is reported as an alien from scattered localities further north. It is also native in S.W. Asia, and occurs as an introduction in the West Indies. It is replaced by var. *denseserrulata* Makins in Africa, Asia and Australia. A similar species, *V. americana* Michaux, is frequent in eastern N. America; a detailed account of its ecology is provided by Korschgen and Green (1988).

The pollination mechanism of *Vallisneria* was cited by Paley [ref.] as evidence for the existence of God.

139. APONOGETONACEAE

This family contains a single genus, *Aponogeton*.

139/1. *Aponogeton* L.f.

This genus contains 43 species, all of which are aquatic plants. The genus is native to the tropical and subtropical regions of Africa and Asia, with its centre of diversity in Madagascar. The species are found in a range of habitats from shallow, seasonal pools and brackish lakes to fast-flowing torrents. They are perennials which survive unfavourable seasons as rhizomes or starchy tubers: the roasted tubers are sometimes eaten by man. The plants have submerged and/or floating, and occasionally emergent, leaves. Their inflorescences which are held above the water level on peduncles which are inflated and floating or rigid and erect. The plants are monoecious or dioecious, and have flowers which appear to be adapted to pollination by insects. Some species are thought to be apomictic: these may have perfect flowers or may lack stamens, depending on the species. The inflorescence sinks after anthesis and the fruits develop under water. *A. undulatus* is viviparous. The basic source of information on the genus is a recent monograph by van Bruggen (1985).

Several species are popular aquarium plants which are normally grown from imported tubers. *A. distachyos* is widely grown outdoors in temperate climates and has become established in our area.

This species persists as a relic of cultivation in water up to two metres deep in lowland lakes and ponds.

A. distachyos is a tuberous perennial, with floating leaves and an inflorescence of sweet-smelling flowers. There are few observations on its reproductive biology in Britain, but seedlings have been found at a site near Bristol. *A. distachyos* spreads within a pond, but although some of its sites are remote from houses they may all originate from planted or discarded stock.

It is difficult to specify the point at which a population of this species ceases to become planted and counts as naturalised, and correspondingly difficult to identify the first record of naturalised plants. *A. distachyos* was recorded from a fountain at Avery Hill, Kent, in 1906 (Grinling *et al.*, 1909-CHK REF), where it was presumably planted. It was collected at Keston, Kent, in 1909, where it still persists (Burton, 1983). There were also early records from Tremough, Cornwall, in 1910, and the Bristol area, where White (1912) recorded it from two localities. The first Scottish record appears to be from a lochan at Hilton, where it was first seen in 1953 (McCallum Webster, 1978) and still present in 1975.

A. distachyos is native to the Cape Province of S. Africa, where it grows (sometimes in abundance) in shallow pools and slow-flowing streams. It has been naturalised at a site in France for over 150 years, and is also established as an alien in S. America, Australia and New Zealand.

In S. Africa the inflorescences are stewed with mutton and eaten; they are canned commercially and sold as 'waterblommetjies'. We have eaten the canned product and find it of more interest as a curiosity than a delicacy. For a recipe, see van Bruggen (1985).

142. POTAMOGETONACEAE

This exclusively aquatic family contains two genera. *Potamogeton* is one of the largest genera of aquatic plants whereas *Groenlandia* is monotypic. The closely related genus *Ruppia* is often included in the Potamogetonaceae, but Stace (1991), following Cronquist (1981), treats it as a separate family, Ruppiceae.

142/1. *Potamogeton* L.

There are 80-90 species of *Potamogeton*. The genus has a virtually cosmopolitan distribution, with its centre of diversity in eastern N. America and more species in temperate regions than in the tropics. In Europe there are 22 species, of which 21 occur in the British Isles. This is the largest aquatic genus in our area, and it is ecologically important as some species can occur in abundance in a wide range of water bodies.

An overview of the taxonomy of the genus is provided by Wiegleb (1988), but there is no recent world monograph, and there are many taxonomic problems which need to be tackled before one can be prepared. However, the European species are relatively well understood, in part due to the work of J.E. Dandy and G. Taylor, who devoted many years to the study of the genus. Their work is summarised by Dandy's account of the European species (Tutin *et al.*, 1980). Although the *Potamogeton* species have the reputation of being difficult to identify, they are not critical like those in genera such as *Callitriche* and *Ranunculus*. The superbly illustrated monograph of the British and Irish taxa by Fryer & Bennett (1915) is now outdated, and a new account has been prepared (Preston, 1995).

The British and Irish plants can be divided into two distinct subgenera. Subgenus *Potamogeton* contains the majority of the species. The first nine species in the following account (*P. natans*-*P. perfoliatus*) are included in Section *Potamogeton*. They are rhizomatous plants with broad leaves which may be submerged or floating. The next nine species (*P. epiphydrus*-*P. acutifolius*) are in Section *Graminifolii*. *P. epiphydrus* is a rhizomatous plant with narrow submerged and broad floating leaves, but the other members of this section lack rhizomes and have only submerged, linear leaves. They are shallow-rooted plants which are restricted to still or very slowly flowing water. The rhizomatous *P. crispus* is the only member of Section *Batrachoseris*. There are two plants in Subgenus *Coleogeton*, *P. filiformis* and *P. pectinatus*. They are rhizomatous plants with submerged, linear leaves.

All *Potamogeton* species have bisexual flowers which are individually inconspicuous, but are aggregated into spikes. The members of Subgenus *Potamogeton* have emergent inflorescences which are borne on rigid peduncles. The flowers are protogynous and they are traditionally regarded as wind pollinated. Although this is often true, particularly for the larger species with more robust peduncles, they may also be pollinated under-water or by pollen floating on the surface of the water. If plants are forced to flower under water, perhaps after a sudden rise in water levels, an air bubble forms when the anthers of the submerged flowers dehisce, and the pollen collects on its surface. As the bubble expands the pollen is carried to stigmas on the same flower. Pollen shed from aerial inflorescences may collect on the water surface and be deposited on stigmas as inflorescences are drawn below the water by strong currents, or released again to resurface.

The peduncles of the species in Subgenus *Potamogeton* are flexible and the inflorescences float on the surface of the water. Pollen is transferred on the surface of the water. These species may also flower under water, and pollen can then be transferred to the stigmas on air bubbles.

There are few detailed studies of the reproductive biology of *Potamogeton* species. Some are known to be self-compatible, but there is evidence that others may be self-incompatible. Many species set fruit freely, and others sparingly. The seeds are hard-coated and will not germinate unless this coat is ruptured. *Potamogeton* seeds are often eaten by birds, and those which are not totally digested are shed in the droppings and germinate more freely than intact seeds. It is, however, very difficult to find seedlings in the wild. It seems likely that new populations may be established by seed, but that plants in existing colonies usually reproduce vegetatively.

The members of *Potamogeton* Section *Potamogeton* may spread by rhizomatous growth, or by establishment from fragments of stem. Some also reproduce by buds which develop on stolons in the axils of the leaves. Plants persist through the winter as leafy stems, buds formed on the rhizomes or swollen rhizomes. The linear-leaved species in Section *Graminifolii* have specialised turions which develop in the leaf axils. The mature plants decay in the autumn and the species overwinter as turions. These plants are therefore functionally (but not genetically) annual. In Subgenus *Coleogeton* plants overwinter as tubers which develop on the rhizomes, and sometimes as leafy shoots.

The genus *Potamogeton* is notable for the occurrence of sterile hybrids, many of which are known to be able to persist vegetatively for many years. The eight most frequent hybrids in our area are treated here. A further 14 hybrids are recorded in Britain and Ireland, and many of these can be found in the absence of one and sometimes of both parents. For details of these hybrids, see Dandy (1975) and Preston (in press).

The Quaternary history of *Potamogeton* is well documented, as the fruits are frequently found in deposits laid down in lakes and other aquatic habitats. Many species were apparently frequent in the last glacial and the early stages of this interglacial. As most hybrids do not produce fruits their history is not documented, but some of those now found in the absence of one or both parents may be relics dating from a period when the parents grew together.

As the taxonomy of *Potamogeton* was not clarified until the 1930s, records made before 1940 have only been accepted if supported by herbarium material. Most of the older records on the maps come from a card index of 20,000 herbarium specimens determined by J.E. Dandy & G. Taylor, or by Dandy alone, and now held by the Natural History Museum. For the period after 1940 we have accepted localised records from reliable observers, but we have not included records from 10-kilometre squares or tetrads if we do not know the locality or the recorder. The excluded records include those collected by 'square-bashing' for the *Atlas of the British flora* and those plotted on maps in 'tetrad' floras. A few relatively common and easily identified species (*P. crispus*, *P. natans*, *P. pectinatus*, *P. perfoliatus*, *P. polygonifolius*) may therefore be under-recorded in some areas where botanists have not made localised records. The comments on the ecology and distribution of the taxa are based solely on records accepted for the maps.

P. natans is often present in abundance in the still waters of sheltered lakes, ponds or flooded quarries, or in slowly-flowing canals, streams and ditches. It can also grow in the quiet backwaters of more swiftly flowing rivers, and sometimes persists in the more rapidly flowing reaches. Its floating leaves may cover the entire surface of the water, or the species may grow with other floating-leaved species (e.g. *Nymphaea alba*) or in open stands of emergents such as *Carex rostrata*, *Equisetum fluviatile* or *Schoenoplectus lacustris*. It tolerates a very wide range of water chemistry, growing in acidic and oligotrophic lakes and ponds, and in calcareous waters which may be nutrient-poor, mesotrophic or eutrophic. It is found over a correspondingly wide range of substrates, including peat, sand and soft mud. It is most frequently found in water of moderate depth (1-2 metres), but it can occur as dwarf plants in very shallow water, or on moist ground where lakes or ponds have dried out. It is also found in deeper water, down to depths of 5.4 metres in particularly clear water in a rain-fed quarry at Castlederg, and it was reported from depths of 6 metres by West (1910). It occurs from sea-level to 760 metres (below Stob Ban).

This species overwinters as plants with rather moribund stems, or as rhizomes. These plants initially produce submerged phyllodes in early spring, then floating leaves develop at the surface of the water. In strongly flowing streams and rivers the phyllodes may persist throughout the season. The inflorescence is borne on a robust peduncle and is wind-pollinated. In still or slowly flowing water plants usually flower and fruit freely. However, recent isozyme studies of a population in ditches at Wareham which fruits freely have failed to detect any genetic variation, suggesting that it does not reproduce sexually (Hollingsworth *et al.*, in press). Plants spread by growth of the rhizome, and perhaps by stem fragments (Sauvagau, 1893-94). They usually lack specialised means of vegetative reproduction, but fascicles of phyllodes are occasionally produced in the leaf axils and act as propagules (Fryer, 1886). The species is an effective colonist of isolated water bodies (Grime *et al.*, 1988), presumably reaching them as seeds transported by birds.

Fossil evidence shows that *P. natans* is a long-established native which persisted through the last glacial period and has been widespread since the late glacial. It is still a frequent species in suitable habitats throughout Britain and Ireland. As the most frequent species of *Potamogeton* in lowland ponds and ditches, *P. natans* has doubtless decreased in many areas as many of these water bodies have been lost. Local studies of a Norfolk grazing marsh which was converted to arable showed that *P. natans* persisted in the drainage ditches, but in reduced quantity (Driscoll, 1985).

P. natans is widespread in the boreal and temperate regions of the northern hemisphere. In Europe it extends south from Iceland and northern Scandinavia, but is scarce in southern Europe where it tends to be replaced by *P. nodosus*.

Potamogeton × *sparganiifolius* Laest. ex Fries (*P. gramineus* L. × *P. natans* L.)

Ribbon-leaved Pondweed

P. × *sparganiifolius* is found in non-calcareous, oligotrophic or mesotrophic water, in some sites which are calcareous but nutrient-poor, and in at least one eutrophic ditch where *P. pectinatus* is abundant. It can be abundant in shallow and rather rapidly flowing water of rivers and streams, where it may be the dominant macrophyte. It also grows, although not so abundantly, in deeper and slower rivers. Other habitats include sheltered lakes and fenland drains. The Anglesey population grows subterrestrially in moss carpets and in shallow fen pools, as do some plants in Tiree. There is a single record from the Basingstoke Canal. In still waters it is usually found in the vicinity of its parents, but in running waters it may occur in the absence of one or both putative parents. It is confined to the lowlands.

This is a variable hybrid. Plants in running water can have long, ribbon-like submerged leaves resembling those of *Sparganium emersum*, with which it sometimes grows. In still water the submerged leaves are short, narrow and phyllode-like, and floating leaves predominate. Some populations flower very sparingly (Heslop Harrison, 1949); others flower more frequently but the hybrid is sterile and fruits do not develop. It is a perennial which spreads by rhizomatous growth, and detached fragments can perhaps become established as new plants. Like both of the putative parents, *P.* × *sparganiifolius* lacks specialised means of vegetative dispersal. It can be very persistent in some sites, still surviving, for instance, in the Bealanabrack River at Maam where it was first collected in 1853.

P. × *sparganiifolius* was first collected in our area at Maam by T. Kirk, and identified by Babington (1856). At this period the existence of *Potamogeton* hybrids had not been recognised, and *P.* × *sparganiifolius* was regarded as a species. Fryer & Bennett (1915) suggested that it was probably a hybrid, and it is now accepted as the hybrid between *P. gramineus* and *P. natans*. For many years it was regarded as a very rare plant, and even Pearsall (1931), writing over 70 years after its discovery, only knew it from Maam. However, Dandy & Taylor (1939) reported some additional localities, and subsequent fieldwork has revealed further sites. The plant has been found in several new localities in recent years, and others doubtless remain to be discovered.

This is a frequent hybrid in Scandinavia, and is also recorded from The Netherlands, European Russia and Siberia (Dandy, 1975). As in Britain and Ireland, its distribution lies within the range of its rarer parent, *P. gramineus*.

CHK Fryer, BEC Rep. 1895 p.497 (1897)

P. polygonifolius is a calcifuge, which grows as an aquatic in oligotrophic and mesotrophic water and in moist subterrestrial habitats. As an aquatic it is typically found in water less than one metre deep at the edge of lakes, and in the backwaters of rivers, moorland streams and ditches, flooded peat cuttings and roadside ditches. Unlike other European *Potamogeton* species *P. polygonifolius* frequently grows subterrestrially in flushes, *Sphagnum* lawns and 'brown moss' communities dominated by *Scorpidium scorpioides*. Its many associates include *Callitriche hamulata*, the aquatic form of *Juncus bulbosus*, *P. natans* and *Myriophyllum alterniflorum* in deeper waters, and *Carex nigra*, *C. rostrata*, *Eleogiton fluitans*, *Menyanthes trifoliata*, *Potentilla palustris*, *Ranunculus flammula* and *Utricularia intermedia sensu lato* in shallow water or on damp ground. *P. polygonifolius* is most frequent over peat but also grows on mineral substrates. Although normally strictly calcifuge, it has been found in highly calcareous flushes and fenland pools in N. England and W. Ireland. It occurs from sea level to 915 metres (Meall nan Tarmachan), being equally frequent in lowland and upland habitats.

In deep or rapidly flowing water *P. polygonifolius* may be found as vegetative plants with submersed leaves. In other habitats it usually possesses floating or aerial leaves, and flowers and fruits freely. Plants spread by rhizomatous growth, but lack specialised vegetative propagules.

Fossil evidence suggests that this species has been present in Britain and Ireland since at least the middle of the last glacial period (Godwin, 1975). In the acidic peatlands of northern Britain and western Ireland this is the most frequent *Potamogeton* species, which in many areas can be found in almost any roadside ditch and flooded peat cutting. The map probably under-estimates its frequency in some of these areas. In the south and east, *P. polygonifolius* has decreased as its scattered acidic habitats have been drained and taken into agricultural use. It is extinct in some counties, including Middlesex and Cambridgeshire, and it is rare and vulnerable in others, including Kent, Essex, Suffolk and Lincolnshire (CHECK Lincs RDB).

P. polygonifolius is an amphi-atlantic species, known from Europe, N. Africa and N. America. It is most frequent in W. Europe, from C. Norway southwards to Spain, Portugal and the Azores, but it extends eastwards to Finland and Bulgaria. In N. America it is confined to Newfoundland and some nearby islands.

Although this species is closely related to *P. polygonifolius* it is a strict calcicole, and is therefore quite distinct ecologically. It is usually found in shallow, calcium-rich but nutrient-poor water at the sheltered edges of lakes on limestone, and in slow-flowing streams, fenland pools and ditches and pools on calcareous sand dunes. It has also colonised flooded clay and marl pits. It is found over a range of substrates including peat, fine calcareous marl, limestone gravel, sand and clay. It is often associated with charophytes, including *Chara hispida*, *C. pedunculata*, *C. rudis* and *C. vulgaris*. Although it normally grows in different sites to *P. polygonifolius*, the two species can be found together towards the edge of the range of *P. coloratus*, as in swamps on Lismore. *P. coloratus* is confined to the lowlands.

P. coloratus is a rhizomatous perennial which over-winters as leafy shoots. Plants flower freely in shallow water, and are self-compatible. The species usually produces numerous, small fruits. In periods of drought *P. coloratus* may persist as terrestrial plants, or as buds on the rhizome (Fryer, 1887b; Fryer & Bennett, 1915).

Although there is a single fossil record of this species from the last glacial period, it has not been recorded from late glacial deposits. As in previous interglacials, it only appears as fossil fruits once the climate becomes more temperate (Godwin, 1975). In the historic period the British range of *P. coloratus* has contracted as some of its Fenland sites have been drained, or following the conversion of grazing land with a managed ditch system to arable. The species has also been adversely affected by eutrophication. Many of its remaining semi-natural habitats are protected as nature reserves or SSSIs, and are therefore safeguarded from habitat destruction, if not from drying out or eutrophication. *P. coloratus* has also colonised disused clay pits, but these sites are vulnerable to natural successional changes or to use as rubbish tips. The species is still locally frequent in C. Ireland.

P. coloratus is confined to W., C. and S. Europe, N. Africa and S.W. Asia. It reaches its northern limit in Scotland and S. Sweden. It is local or rare in many parts of its range and in The Netherlands it is listed as a most vulnerable species (ref!).

British *P. coloratus* appears to be rather uniform both morphologically and genetically. Hollingsworth *et al.* (in press) found no evidence for isozyme variation within 10 of the 12 populations they studied, 9 of which appeared to share the same genotype. Two genotypes were detected at Wicken Fen, and 7 in ditches in the Gordano Valley.

This species is confined to a few calcareous and moderately but not excessively eutrophic rivers in lowland England. It is found in both shallow and relatively deep water, growing in stretches of moderately rapid flow with species such as *Elodea nuttallii*, *Lemna minor*, *Myriophyllum spicatum*, *Nuphar lutea*, *P. crispus*, *P. pectinatus*, *Sagittaria sagittifolia*, *Schoenoplectus lacustris* and *Sparganium emersum*. In the R. Loddon it is often particularly abundant in well-aerated stretches of the river below weirs and sluices (Archer, 1987). In Dorset it grows in fairly shallow water over a gravelly substrate, and cannot be found where there are soft clay sediments.

P. nodosus is a rhizomatous perennial which appears to vary in abundance from year to year. It flowers freely in summer when growing in shallow water. Plants do not appear to set fruit in the wild but will do so if cultivated in small containers, suggesting that the apparent sterility is caused by environmental factors. Buds develop on short stolons in the leaf axils in late summer and act as vegetative propagules. Established populations overwinter as buds on the rhizome, which develop in response to short days (Spencer & Anderson, 1987). In S. Europe this species grows in a much wider range of habitats than it does in England, and fruits freely.

This species was first discovered in England in the R. Loddon by G.C. Druce in 1893 and named *P. drucei* by Fryer in 1898 (Preston, 1988). It was subsequently discovered in the Bristol Avon, R. Stour (Dorset) and R. Thames. However its correct identity continued to puzzle British botanists until Dandy & Taylor (1939) established that it was the widespread continental species *P. nodosus*. The species has apparently become extinct in the Thames, where it was once locally frequent (Lousley, 1944) but perhaps disappeared as a result of eutrophication and increasing boat traffic in the 1950s. We have been unable to confirm recent reports of its rediscovery. It cannot now be found in the Warwickshire Stour at Alderminster, where it is known from a single 19th century specimen. However, it survives as vigorous stands in the Loddon and the Dorset Stour, and has recently been planted in additional sites in the Loddon and in the nearby Whitewater and Blackwater (refs).

This is the most frequent broad-leaved *Potamogeton* in the Mediterranean region, and extends north in Europe to England, The Netherlands and Estonia. It also occurs in Africa south to Angola and Madagascar, temperate and tropical Asia, and N. & S. America.

Get any reintroduction reports. DG Avon reports.

P. lucens is a calcicole which grows in relatively deep water in lakes, slow-flowing rivers, canals, flooded chalk, gravel or borrow pits and major fenland drains. It is found in the crystal-clear water of unpolluted limestone lakes as well as more eutrophic water in rivers and fenland lodes. Although sometimes found in shallow water at the edge of lakes it has little resistance to desiccation, and plants exposed above the water dry up without producing a modified terrestrial form. It is most frequent in the lowlands, ascending to 380 metres at Malham Tarn.

The leafy shoots of *P. lucens* die in autumn, and the plant persists through the winter as the rhizome, which develops short, thick internodes (Sauvageau, 1893-94). Plants in still or sluggish water may flower freely, with the robust inflorescences supported by a raft of stems floating near the surface of the water (Fryer, 1887a). The flowers are usually wind pollinated but if drawn below the water surface they may also collect pollen floating on the surface, at least under experimental conditions (Guo & Cook, 1989). Mature fruits develop, and may be the way in which the species colonises new habitats. *P. lucens* lacks specialised vegetative propagules, but may spread by rhizomes uprooted during floods and perhaps by detached stem fragments.

In England *P. lucens* has decreased in some areas, including Gloucestershire (Holland, 1986) and Surrey (Lousley, 1976). Nevertheless, it is still locally frequent in strongholds such as the Somerset Levels, East Anglian Fenland, Broadland, and in the R. Tweed and its tributaries. There has been a more marked decline in eastern Scotland, where it once grew in lowland lochs such as Balgavies Loch, Rescobie Loch and Loch Gelly which are now very eutrophic, or, in the case of Kinghorn Loch, have been contaminated by alkaline run-off from industrial waste (Young & Stewart, 1986). There is little evidence for a serious decline in Ireland, where it remains plentiful in calcareous waters. However, it has apparently been lost from its most south-westerly site, Lough Leane, probably because of eutrophication.

P. lucens is widespread in temperate regions of Europe, where it extends north to northern Scandinavia, and western Asia; its distribution further east in Asia is uncertain. It is also known from N. Africa and an outlying site in Uganda. In N. America it is replaced by the related *P. illinoensis*.

Potamogeton × *zizii* Koch ex Roth (*P. gramineus* L. × *P. lucens* L.)

Long-leaved Pondweed

This hybrid grows in a range of water bodies, including lakes, Breckland meres, rivers, streams, fenland lodes and ditches. In lakes it is usually found in water over 0.5 metres deep, with dense stands tending to grow in rather deeper water. In northern and western areas of Britain and Ireland it is found in mesotrophic waters which have some base-enrichment, but are apparently not sufficiently base-rich to support *P. lucens*. In these sites it may grow with *P. gramineus*, or in the absence of both parents. In the south and east it is much less frequent, usually growing in the vicinity of both parents in calcareous but not excessively eutrophic water. In these areas *P. × salicifolius* is the commoner hybrid. It is recorded from sea-level to 340 metres at Crooked Loch, and formerly grew at 380 metres in Malham Tarn.

P. × zizii dies down in the winter, regrowing from the rhizome in the spring. Most populations are of plants which have only submerged leaves, but some populations produce floating leaves in shallow water; whether or not these are genetically distinct is unclear. Although some populations of *P. × zizii* are consistently sterile, others may be at least partially fertile and some plants set well-formed fruit (Fryer, 1892). Their fertility has not been critically studied and we do not know whether the fruits are capable of germination, but there is no reason to suppose that they are inviable. The hybrid lacks specialised means of vegetative dispersal, but spreads by growth of the rhizome and almost certainly by detached plant fragments. Vegetative propagation is almost certainly more frequent than any reproduction by seed that may occur. In times of drought, *P. × zizii* can persist as a terrestrial form with aerial leaves (Fryer, 1887b).

This is a persistent hybrid. It is still present at Cauldshiels Loch, where it was first recognised in our area (Baker, 1879), and it has also been known for over a century at other sites, including Coniston Water and Sessiagh Lough. It can no doubt persist indefinitely in suitable habitats. It is still frequent in parts of Scotland and Ireland, where it may be under-recorded. Like *P. gramineus* it has declined in southern and eastern England and southern Scotland, where the main reasons for its decline have been eutrophication and the loss of species-rich ditches in areas where pasture has been converted to arable.

P. × zizii is widespread in both northern and central Europe.

P. × zizii is a hybrid which almost behaves as an species, having a capacity to produce well-formed fruits and a distribution which in some areas is apparently independent of that of its parents. Fryer (1890, 1892) considered that in the Cambridgeshire fens it was capable of backcrossing with *P. gramineus*, and this possibility deserves further investigation.

CHK Spence, Campbell & Chrystal 1973.

Potamogeton × *salicifolius* Woflg. (*P. lucens* L. × *P. perfoliatus* L.)

Willow-leaved Pondweed

Like both parents, this hybrid grows in relatively deep water which is not subject to marked fluctuations in depth. It is found in moderately or strongly calcareous, meso-eutrophic or eutrophic water. It is recorded from lakes, but most records are from slow-flowing rivers, canals and large fenland drains, perhaps because these are the usual deep-water habitats in the areas where it is most frequent. It may be present as large stands, often growing in the vicinity of both parents. It is confined to the lowlands.

P. × *salicifolius* dies down to the rhizome in winter, regrowing in spring. It has submerged but not floating leaves. It is a sterile hybrid which may flower but never sets well-formed fruit. Although it lacks specialised means of vegetative dispersal, it spreads by growth of the rhizome or by the spread of plant fragments. Detached stem fragments root freely when floating in the water. Like other *Potamogeton* taxa which lack floating leaves, it is intolerant of desiccation and is unable to survive periods of drought as a terrestrial form.

This is a local hybrid which is well established in a number of river systems, including the R. Frome (Dorset), R. Wye, R. Teviot and the lower reaches of the R. Tweed. It may be very persistent in these rivers: it was, for example, first collected in the R. Tweed at Birgham in 1830. It is tolerant of eutrophic water and still survives in many of the water bodies where it has been recorded. However, it has not been seen recently in the Kennett & Avon Canal, where it was first recorded in our area by Baker & Trimen (1867), and it has been lost from the excessively eutrophic Balgavies and Rescobie Lochs. It can be similar to *P. lucens* in appearance, and might therefore be under-recorded.

This is one of the more frequent *Potamogeton* hybrids in both northern and central Europe, and it is also recorded from S.W. Asia.

This very variable species occurs in a wide range of habitats, including lakes, reservoirs, rivers, streams, canals, ditches and flooded sand and gravel pits. It is primarily a plant of shallow water, usually found at depths of less than 1.5 metres although occasionally descending to three metres or more. Although absent from the most acidic and oligotrophic sites it is more tolerant of base-poor and nutrient-poor water than most other broad-leaved pondweeds, often growing in such sites with *Apium inundatum*, the aquatic form of *Juncus bulbosus* and *Myriophyllum alterniflorum*. It extends into meso-eutrophic and moderately base-rich sites, and it also grows in highly calcareous but nutrient-poor waters over chalk and limestone. Spence (1967) classifies it as ubiquitous with regard to its chemical tolerance in Scotland, but in areas where there is a greater range of eutrophic waters it is absent from the more nutrient-rich sites. It is found over a range of fine-grained and coarse-grained substrates, and at altitudes from sea-level to 915 metres (Meall nan Tarmachan).

P. gramineus is a rhizomatous perennial, which dies down in winter to buds on the rhizomes (Spencer & Ksander, 1990). It initially has submerged leaves, later producing floating leaves unless it grows in deep or fairly rapidly flowing water. Plants usually flower and fruit freely. The species lacks specialised means of vegetative dispersal. Terrestrial forms develop in sites where plants are exposed above the water level.

Godwin (1975) concludes that *P. gramineus* has been present in our area since at least the middle of the Pleistocene, and its fruits are well represented in deposits from the last glacial period and through the current interglacial. It is still relatively frequent in the northern and western parts of our area, although it has decreased during the last century in the south and east, where eutrophication and the unsympathetic management of ditches in areas which were once grassland and are now predominantly arable has led to its decline.

This species has a circumpolar distribution, being found in boreal and temperate regions throughout the northern hemisphere. In Europe it is found from Iceland and northern Scandinavia south to C. Europe, with scattered localities further south; it is absent from much of the Mediterranean area.

Potamogeton × *nitens* G. Weber (*P. gramineus* L. × *P. perfoliatus* L.)

Bright-leaved Pondweed

This hybrid is found in more or less mesotrophic water in lakes, reservoirs, rivers, streams, canals, fenland lodes and ditches, and occasionally in flooded sand and gravel pits. In rivers such as the Aderdeenshire Don it can be present in large beds with *Myriophyllum alterniflorum*, *P. alpinus*, *P. crispus* and *P. perfoliatus*. It may also be abundant in standing waters, where it is most luxuriant at depths of 0.5-1.5 metres deep, and sometimes grows around the margins of reservoirs subject to moderate variations in water level. It may grow with one or both putative parents or in the absence of both; in S.W. England its isolated locality in the R. Torridge lies outside the range of *P. gramineus*. *P. × nitens* is recorded from sea-level to 640 metres in Loch Oss.

P. × nitens is a rhizomatous perennial which dies down in autumn. It is phenotypically plastic: it may possess submerged or submerged and floating leaves and vigorous terrestrial forms can be found on exposed mud at the edge of lakes and reservoirs. Plants may flower freely but they are sterile and ripe fruit does not develop. Short stolons sometimes develop in the leaf axils, often just below the inflorescence. They are easily detached and must act as propagules, but the factors which trigger their formation are unclear.

This is the most frequent *Potamogeton* hybrid in our area. Once its appearance is known it can often be identified without difficulty, but it is often overlooked by inexperienced observers and it may be more frequent in Scotland and Ireland than the map suggests. In S.E. England it was always an uncommon plant, and it is now very rare. It has not been seen in drainage ditches in the East Anglian Fenland since 1949, and it is extinct in the Basingstoke Canal. However it was recently discovered in a gravel pit in Cambridgeshire which had been colonised by both parents.

P. × nitens is widespread in both northern and central Europe. It has also been reported from temperate Asia and North America (Dandy, 1975).

P. alpinus is a plant of still or slowly flowing water in lakes, rivers, canals, ditches and flooded clay, gravel, sand and marl pits. It usually grows over a relatively deep silty or peaty substrate, often in sites where silt accumulates such as the point where an inflow stream enters a lake, or the sheltered backwater of a river. The most vigorous stands are found in water approximately one metre deep. *P. alpinus* thus favours deeper water than *P. gramineus* but shallower places than *P. perfoliatus* and *P. praelongus*, although there is considerable overlap in the depth range of these broad-leaved pondweeds and all can be found growing with *P. alpinus*. *P. alpinus* is a plant of oligo-mesotrophic or mesotrophic, often neutral or mildly acidic water. It is found from sea-level to 950 metres (Meall nan Tarmachan).

P. alpinus dies down in the winter to buds produced on the rhizome. The stems are unbranched and in addition to the submerged leaves they usually have a few, small floating leaves if they reach the surface. Populations often flower and fruit abundantly. Plants will regenerate from detached leafy shoots (Brux *et al.*, 1987), and short stolons terminated by buds sometimes develop in the lower leaf axils in the autumn, and provide an additional means of perennation and vegetative propagation. Brux *et al.* (1988) found that there was no regeneration from seed in the German rivers they studied. The distribution of the species in these rivers was rather unstable: stands often disappeared from sites if the perennating buds were washed away, then recolonised in subsequent years. In ponds germinating seeds were found once. In aquaria freshly collected seed germinated, but the seedlings were much smaller than plants grown from buds and remained small for many months.

There is clear evidence that this species is a long established native which was present throughout the last glacial period in both England and Ireland (Godwin, 1975). It is fairly frequent in the northern parts of Britain and Ireland, where there is little evidence for anything other than local decline, but the map suggests a marked contraction of range in S. England. Many of these records are 19th century records from ponds, clay pits, ditches and other small water bodies. In more recent years it has been lost from some rivers, including the R. Stort (Burton, 1983), presumably because of eutrophication.

P. alpinus is a circumboreal species, which is found in arctic and boreal regions throughout the northern hemisphere. In Europe it extends south to the Pyrenees and the mountains of C. Europe.

Potamogeton × *olivaceus* Baagøe ex G. Fischer (*P. alpinus* Balbis × *P. crispus* L.)

Graceful Pondweed

This hybrid is established in a number of mesotrophic lowland rivers in Britain, where it usually grows in swiftly but smoothly flowing water over a gravelly substrate. In the R. Earn beds of this hybrid grow with beds of *P. × zizii*. *P. × olivaceus* also grows in a pool on the flood-plain of the Teifi, where it is found in shallow water with *Callitriche hamulata*, *Elodea canadensis* and *Potamogeton berchtoldii* and *P. natans*.

This rhizomatous perennial which persists through the winter as leafy shoots. Plants flower but are highly sterile, and show no sign of developing fruit. Unlike *P. crispus* and its hybrids *P. × cooperi* and *P. × lintonii*, *P. × olivaceus* does not produce specialised turions. However, stems are easily detached and *P. × olivaceus* probably spreads as fragments of stem or rhizome. As the hybrid is winter-green, it must be particularly likely to be dispersed by winter floods.

P. × olivaceus was first collected in the Leet Water, a tributary of the R. Tweed, by R.D. Thomson in 1831, although the specimen was misidentified for over a century. It was collected from the R. Ythan in 1900 and found in the R. Earn in 1915, when it was first recognised as a British plant (Dandy & Taylor, 1942). It was not discovered in the Teifi until 1972. It is clearly able to persist in rivers for long periods. Neither *P. alpinus* nor *P. crispus* are known from the Teifi. Both parents have a long history in Britain, and are known to have persisted through the last glacial period. This suggests that the Teifi population, and perhaps the others, may be of ancient origin, dating from a period when the parents grew in close proximity.

The only record of this hybrid from outside Britain is from Denmark, where it does not appear to have been found recently (Pedersen, 1976-CHK Danish!). The hybrid is much rarer in Europe than one would expect from its British distribution.

This is the species of broad-leaved pondweed which is most characteristically found in deep water. It is rarely found in water less than 1 metres deep, only grows as dominant stands at depths greater than 1.5 metres (Spence, 1964) and descends to 6.5 metres in Loch Borrallie (Spence *et al.*, 1984). It is found in clear, mesotrophic water in lakes (where it may often be found in deep, sheltered channels between an island and the shore), rivers, canals and major fenland lodes. Its sites vary from those which are slightly enriched by the presence of outcrops of basalt or calcareous sand in the catchment, to highly calcareous but nutrient-poor lakes over limestone. It is usually rooted in fine silts. It is found from sea-level to 790 metres at Lochan an Tairbh-uisge.

P. praelongus is a robust, rhizomatous, winter-green perennial which possesses submerged but not floating leaves. It flowers rather earlier than the other submerged pondweeds, and produces relatively few, large fruits. It does not possess any specialised means of vegetative propagation.

The characteristic fossil fruits of this species are frequent in deposits which date from the last glacial period, and are particularly abundant in the late glacial in both Britain and Ireland. The distribution of fossil records, mapped by Godwin (1975), is remarkably similar to that of the species in historical times. Since 1950 *P. praelongus* has declined markedly in S. England, and the species has disappeared from rivers such as the R. Cam and R. Thames where it had long been recorded. The most likely explanation is that it has been adversely affected by eutrophication, following the increasing use of artificial fertilisers on arable land in recent decades. The species has also declined in The Netherlands, apparently because of pollution and increasing salinity in the waters in which it grows (Weeda, 1976). In northern parts of Scotland and Ireland there is no evidence for a decline. As a species which prefers deep water it is very easily overlooked, and it is almost certainly under-recorded in some areas.

P. praelongus has a circumboreal distribution. In Europe it extends from Iceland and N. Scandinavia southwards to C. Europe, but is absent from S. Europe and the Mediterranean area. For further details of its world range, see Haynes (1985).

The rare hybrid between *P. alpinus* and *P. praelongus*, *P. × griffithii*, is found at a few localities in Ireland, Scotland and Wales in the apparent absence of *P. praelongus* or of both parents; it may be a relic of a period when *P. praelongus* was more widespread (Preston & Stewart, 1992).

CHK Spence, Campbell & Chrystal, 1973.

P. perfoliatus is found in larger water bodies such as lakes, reservoirs, rivers, streams, canals, fenland lodes, large ditches and flooded sand and gravel pits. Scattered plants of *P. perfoliatus* with prostrate shoots may be found in very shallow water in sites where they are not subject to periodic desiccation, but vigorous stands are only found where the water is at least one metre deep. This species is tolerant of a wide range of water chemistry, being frequent in both mesotrophic and eutrophic waters. Characteristic associates include *Myriophyllum spicatum*, *P. crispus*, *P. pectinatus*, and *Sparganium emersum*. In addition to its occurrence in more nutrient-rich sites, *P. perfoliatus* is also occasionally found in oligotrophic lakes. It is recorded from sea-level to 750 metres at Loch Vrotachan.

P. perfoliatus is a perennial which dies down to the rhizome in the winter. It has submerged but not floating leaves, and often flowers and fruits freely. It lacks specialised vegetative propagules.

Like many members of the genus, *P. perfoliatus* can be shown to be a long-established native which was particularly frequent in the late glacial period (Godwin, 1975). Unlike *P. alpinus*, *P. gramineus* and *P. praelongus*, this species is still frequent in suitable habitats in S. England. This general picture conceals some local fluctuations. Philp (1981) comments that it has increased in abundance in the R. Medway at Maidstone in recent years. However, it has declined in Somerset (Roe, 1983), where it has always been surprisingly scarce, Surrey (Lousley, 1975) and in other areas where grazing marshes have been converted to arable land (Driscoll, 1985; Mountford, 1994). Like other members of the genus it is rare in Wales, S.W. England and S.W. Ireland.

P. perfoliatus is widespread in Europe, from Iceland and Scandinavia southwards to the northern edge of the Mediterranean area. It has an extensive world distribution, being found in much of Asia east to Japan and south to S. India, in eastern N. and C. America, N. & C. Africa and Australia. The very closely related *P. richardsonii* is more widespread in N. America. For a map of its world distribution, see Haynes (1985).

Potamogeton × *cooperi* (Fryer) Fryer (*P. crispus* L. × *P. perfoliatus* L.)

Cooper's Pondweed

This widespread but uncommon hybrid occurs in a range of lowland water bodies. Most records are from rivers and canals, but it is also found in lakes, reservoirs, clay pits and fenland ditches. It is a plant of eutrophic water, characteristically associated with plants such as *Elodea canadensis*, *E. nuttallii*, *Lemna minor*, *L. trisulca*, *Myriophyllum spicatum*, *P. crispus*, *P. pectinatus*, *P. perfoliatus* and *P. pusillus*. It may be found in shallow water at the edge of lakes and canals, or in deeper water in rivers.

This hybrid is a rhizomatous perennial which retains its leafy shoots through the winter. It does not often flower freely, and when it does the inflorescences are highly sterile. However, turions develop in the leaf axils and are an effective means of vegetative dispersal.

This hybrid is potentially very persistent: it is still found in the R. Wharfe, where it was first discovered in 1881, and the Union Canal, where records date from 1902 (Wolfe-Murphy *et al.*, 1991). In some sites, such as Carlingwark Loch, both parents are present and the hybrid has apparently arisen *in situ*, but it presumably spread vegetatively in the canal system. It has not been recorded recently in some of the rivers and canals where it once grew, and some of the canals are no longer extant. *P. × cooperi* is superficially similar to *P. perfoliatus* and the map may under-estimate its former, and perhaps its current, distribution.

This hybrid has been recorded from widely scattered parts of Europe: Dandy (1975) cites records from Czechoslovakia, Denmark, Germany and Rumania.

In the Outer Hebrides *P. epihydrus* grows in a few peaty lochans near Loch Ceann a'Bhaigh, where it is found in oligotrophic and base-poor water less than one metre deep. Other species in these lochans include *Eleogiton fluitans*, *Equisetum fluviatile*, the aquatic form of *Juncus bulbosus*, *Littorella uniflora*, *Lobelia dortmanna*, *Nymphaea alba*, *P. natans*, *P. polygonifolius*, *Sparganium angustifolium* and *Utricularia vulgaris sensu lato*. There is also a record from *habitat?* in Loch an Duin. Submerged leaves which appear to belong to this species are washed up in late summer at the edge of a large, oligotrophic loch on Skye, but rooted plants have never been found here and the identification remains unconfirmed. However, *P. epihydrus* is locally plentiful in the mesotrophic water of the Rochdale Canal and the Calder & Hebble Navigation, where it grows with *Elodea nuttallii*, *Lemna minor*, *L. trisulca*, *Luronium natans*, *Potamogeton crispus*, *Sparganium emersum* and *Nitella mucronata* in water 0.4-1.2 metres deep. All the known sites are lowland.

P. epihydrus is a rhizomatous perennial. It has both submerged, linear leaves and broader floating leaves, although floating leaves may not develop on plants in relatively deep water. The species is self compatible and self-pollination takes place once the anthers dehisce if cross-pollination has not taken place (Philbrick, 1983). In the American population studied by Philbrick all the ovules developed into fruits, and plants with floating leaves flower and fruit freely in both the Outer Hebrides and N. England. In addition, short stolons bearing buds or small fascicles of leaves can be found in the leaf axils in September. They are easily detached and act as vegetative propagules.

This species was originally discovered in Britain in 1907, at Salterhebble Bridge near Halifax (Bennett, 1908). It is still well established in canals on both sides of the Pennines, but it has not been seen recently in the R. Calder, where it was collected in 1942. The English populations are believed to originate from an introduction, although it is difficult to imagine the source of the material. The native populations in S. Uist were discovered by W.A. Clark and J.W. Heslop Harrison in 1943 and 1944 (Heslop Harrison, 1949, 1950).

P. epihydrus is widespread in N. America, where it is found in lakes, pools and streams from S. Alaska and Labrador south to N. California and Tennessee; it is restricted to mountains in the southern part of its range. For map of its American distribution, see Fernald (1932). The British records are the only known occurrences in Europe.

There are similarities between this species and *Luronium natans*: both have native sites where the water is oligotrophic and also grow in mesotrophic canals. However, *L. natans* spread from its native sites into the canal system, whereas the canal populations of *P. epihydrus* presumably originated independently.

This is a species of calcareous waters which may be low in other nutrients but are more often eutrophic. It usually grows at depths of 0.5 metres or more. Most of its British localities are in lakes, sluggish rivers and streams, canals, fenland lodes, ditches and flooded clay and gravel pits. It is able to persist in some canals and lodes where there is some boat traffic. In the Outer Hebrides it is restricted to machair lochs, where the water is enriched by bases from calcareous dune sand, and in Shetland it is abundant in a loch influenced by coastal sand. In Ireland *P. friesii* is found in clear calcareous lakes, canals and in the R. Shannon. It is confined to the lowlands.

Like the other species in Section *Graminifolii*, *P. friesii* is an annual species. Its normal mode of reproduction is by robust turions, which may begin to develop in late June but are usually found in July and August. This species appears to flower and fruit rather infrequently.

There are few fossil records of *P. friesii*, although it was probably present in both Britain and Ireland during the late glacial period (Godwin, 1975). It may have been a very local species in Britain until the construction of the canal network, which appears to have allowed it to spread into areas from which it was previously absent. It has subsequently retreated from some of these areas where the canals in which it grew are now dry or have become too heavily used to support it. It fluctuates in response to nutrient levels: it was first recorded in the Thurne valley Broads in the 1930s when their nutrient levels were increasing, but died out once they became very eutrophic (George, 1992); it has also been lost from three lochs in Angus for the same reason. It has only recently been discovered at its outlying sites in Roxburghshire and Donegal, and like other linear-leaved pondweeds it may be somewhat under-recorded.

P. friesii is a circumpolar species, recorded from boreal and temperate latitudes throughout the northern hemisphere but rare, or under-recorded, in E. Asia. In Europe it is absent from the Mediterranean area; it extends north to the Arctic Circle although it is rare at the northern edge of its range.

This hybrid is found in eutrophic water in both natural sites and man-made habitats. It is found in eutrophic lakes in Ireland and Scotland. In the shallow, eutrophic edges of Carlingwark Loch it grows in water 0.1-0.25 metres deep, associated with *Callitriche hermaphroditica*, *Elodea canadensis*, *Myriophyllum spicatum*, *P. friesii* and *P. pusillus* (Stewart & Preston, 1990). There are also records from streams and the backwater pools of rivers. *P. × lintonii* is, however, more frequently recorded from canals. In the Chesterfield Canal it grows in shallow water over fine silt at the edge of the canal, together with *Lemna minor*, *Myriophyllum spicatum* and *P. perfoliatus*. There are also records from a number of other artificial water bodies, including flooded marl pits and a water storage tank. All sites are in the lowlands.

P. × lintonii is a rhizomatous perennial. It is a highly sterile hybrid which sometimes flowers freely in shallow water, but fails to set seed. Turions are produced in the leaf axils, often in abundance, and presumably provide the main means of dispersal.

P. × lintonii was described, new to science, on the basis of material collected by C. Waterfall in the Chesterfield Canal in 1899. Subsequent research showed that specimens had been collected previously from this and other sites, but misidentified (Dandy & Taylor, 1939). The isolated population in Carlingwark Loch is almost certainly the result of *in situ* hybridisation. There are insufficient historical records to allow us to reconstruct its history elsewhere. We do not know whether it spread into the canals from nearby rivers such as the Trent and the Wey, or whether it arose in the canal system. The extent to which the plants in canals result from the spread of a single clone or from different hybridisation events is also unclear. *P. friesii* appears to have declined markedly in recent years as some canals have become disused and dried out and others are now heavily used for recreational purposes. It also appears to be extinct in the Tilling Bourne, where it has not been seen since the stream was thoroughly cleaned out c. 1950. It might, however, be overlooked in some localities as it can be confused with other linear-leaved pondweeds.

Outside our area the only confirmed records of *P. × lintonii* are from Belgium and The Netherlands.

This species grows in unpolluted, lowland, mesotrophic or eutrophic lochs which receive some base-enrichment; it is also found in adjoining streams. In Shetland it grows in water 1-2 metres deep in mesotrophic lochs, some of which receive drainage from limestone rocks. In the Hebrides the sites are machair lochs at the junction of acidic rock and calcareous dune sand. **Other sites ?** The habitat of *P. rutilus* at its remote British sites has not been studied in detail, partly because it is difficult to find in the deep water in which it often grows, and plants are normally detected after they have become detached and been blown to the side of a loch. In a dry summer when water levels were exceptionally low it was recorded in water only 0.5 metres deep in Loch Ballyhaugh, growing in a substrate of fine silt with *Littorella uniflora*, *Najas flexilis* and *Potamogeton gramineus* and abundant *Chara aspera*.

Although flowering material of this species has been collected in Britain, fruiting plants have never been found. Plants over-winter as turions, which develop in the autumn and also provide a means of dispersal within a lake.

This species was completely misunderstood by British botanists until Dandy & Taylor (1938) revised the existing records and showed that the only correctly determined specimens were from Shetland. *P. rutilus* was discovered in the Outer Hebrides by Clark (1943). All the sites known to Perring & Walters (1962) were in these two archipelagos, but the species has subsequently been found in an increasing number of sites as a result of the more systematic recording of Scottish lochs in recent years. The only site where it is thought to be extinct is Loch Flemington, where it was discovered in 1975 but appears to have been eliminated by pollution from silage effluent and other sources.

P. rutilus is endemic to northern Europe, where it is found from the Arctic Circle south to N. France; Germany and Poland. It is a local plant throughout its range, and it may be the rarest of the European pondweeds at a world scale.

P. pusillus grows in standing or slowly flowing water in a wide range of habitats, including sheltered lakes and reservoirs, ponds, rivers, streams, canals, fenland lodes, ditches, and in flooded clay, sand and gravel pits. It usually grows in fairly shallow water over fine, silty substrates. It is found in mesotrophic and mildly acidic water with *P. obtusifolius*, but it is more frequent in eutrophic water. It is also tolerant of slightly brackish water at the seaward side of machair lochs and in coastal lagoons and ditches. Characteristic associates include *Elodea nuttallii*, *Myriophyllum spicatum*, *P. pectinatus*, *Zannichellia palustris* and, in southern England, *Potamogeton trichoides*. It is virtually confined to the lowlands: the highest recorded altitude is 320 metres at Stoney Middleton.

P. pusillus often flowers and fruits freely in shallow water. As with other *Potamogeton* species there is little direct evidence of reproduction by seed. However, *P. pusillus* is a very frequent colonist of disused gravel pits to which it is presumably introduced by bird-borne seeds. The normal mode of reproduction of established populations is by slender turions, which are produced in abundance from July onwards.

The smaller linear-leaved pondweeds were all aggregated as '*P. pusillus*' by Linnaeus. The differences between *P. berchtoldii* and *P. pusillus sensu lato* were set out by Hagström (1916), but the two species continued to be confused in our area until Dandy & Taylor (1938, 1940a,b) revised the available herbarium material. This taxonomic confusion makes it difficult to draw any conclusions about trends in the distribution of *P. pusillus*, but it may have increased in recent years. It is the most frequent species of *Potamogeton* in disused gravel pits, and in a detailed local study Driscoll (1985) demonstrated a dramatic increase in its frequency in ditches following the conversion of the surrounding land from pasture to arable.

P. pusillus is widespread in Eurasia, Africa and N. & C. America. In Europe it is found from the Mediterranean region to Scandinavia. Compared to *P. berchtoldii*, it tends to be commoner in southern Europe and rarer and more coastal in the north.

P. obtusifolius is normally found in standing waters such as ponds and lakes or in the backwaters of rivers, canals and ditches where the flow is scarcely perceptible. It is also known as a colonist of flooded sand, gravel, marl and brick pits. It reaches its optimum development in water which is less than 1.5 metres deep, and it is usually found over fine inorganic or peaty substrates. It is difficult to define its ecological preferences as it tends to be frequent in a range of habitats in some areas but absent from others where there appear to be suitable habitats. It is usually found in mesotrophic or meso-eutrophic, acidic or circum-neutral water with species such as *Elodea canadensis*, *Lemna minor*, *L. trisulca*, *Menyanthes trifoliata*, *Myriophyllum alterniflorum*, *Nuphar lutea*, *P. natans* and *P. pusillus*. The canals in which it grows, for instance, tend to be those where the water is not very calcareous: they include the eastern sections of the Basingstoke Canal, the Lancaster Canal and the Exeter Canal. *P. obtusifolius* is absent from the most acidic and oligotrophic water and from both highly calcareous and highly eutrophic sites (cf. Seddon, 1972). It is a predominantly lowland species which ascends to 395 metres north of Bleddfa.

In shallow water *P. obtusifolius* can be abundant, and grows as much-branched plants with masses of leaves in the upper part of the water. It fruits more freely than any other linear-leaved pondweed. However, reproduction is usually effected by turions, which develop from late July onwards.

This is one of the many *Potamogeton* species which can be shown to have persisted in our area since the middle of the last glacial period (Godwin, 1975). In some areas it is one of the commoner members of the genus. It might be more frequent in some areas than the map suggests, and the apparent decline in regions such as Yorkshire could be an artefact resulting from the lack of recent survey work.

P. obtusifolius has a circumpolar distribution, but it is much more frequent in Europe and eastern N. America than in the other parts of its range. It is widespread in Europe, but it is rare in the far north and absent from the Mediterranean area. Reports from Australia, cited by Hultén & Fries (1986), are supported by a single, unlocalised specimen (Aston, 1973).

P. friesii is a superficially similar linear-leaved pondweed which tends to replace *P. obtusifolius* in calcareous sites.

CHECK Spence, Campbell & Chrystal 1973.

No other linear-leaved pondweed grows in as wide a range of still or slowly-flowing waters as *P. berchtoldii*. It is frequent in a variety of base-rich or base-poor, mesotrophic and eutrophic habitats including lakes, reservoirs, ponds, rivers, streams, canals, ditches and disused mineral workings. It may grow over a range of substrates from and or calcareous gravel to fine silt, and can also persist in a shade-form in shallow ponds and ditches under trees. It is sometimes found in clear, oligotrophic upland lakes, but it is rare in oligotrophic, peaty water. It is replaced by *P. pusillus* in brackish sites and in some eutrophic localities in S. England. It is found from sea-level to 500 metres (Llyn Anafon).

P. berchtoldii flowers and fruits fairly freely. Philbrick (1983) found that the American population he studied was self-incompatible. Plants with aerial inflorescences and those which flowered under water both set seed, but unlike the self-compatible species the number of seeds which developed was well below the potential maximum. Plants overwinter as turions, which develop from August onwards.

The confused taxonomic history of this species is outlined under *P. pusillus*. It is an inconspicuous plant which is overlooked by some observers and disregarded by others who are not prepared to attempt to identify linear-leaved pondweeds. There may also be a tendency to label all 'pusilloid' pondweeds *P. berchtoldii* in the belief that this is the commonest species, but the map should not include many of these records. The areas in which there is a preponderance of old records on the map tend to be those from which there is a shortage of recent, critically determined records of all *Potamogeton* species. *P. berchtoldii* is still frequent in suitable habitats in many areas of Britain and Ireland, although it may be declining in some counties because of eutrophication.

P. berchtoldii is widespread in the boreal and temperate regions of the northern hemisphere. It is found in most of Europe, although it is rare in the Iberian peninsula and absent from the extreme north and some of the Mediterranean islands. Recent American authors (e.g. Haynes, 1974) treat it as a variety of *P. pusillus*, but there is a case for continuing to treat it at specific rank (Preston, 1995).

P. trichoides is found in shallow, still or slowly-flowing, meso-eutrophic or eutrophic water over soft inorganic substrates. It grows in a range of habitats, including lakes, reservoirs, ponds, rivers, canals, ditches and flooded clay, sand and gravel pits. It is often found as a colonist of newly available habitats, or in disturbed areas such as recently cleared canals and ditches. It can be found as large plants growing by themselves or intermixed with *P. pusillus*, in sparsely vegetated areas, or as scattered stems amongst dense beds of *Elodea nuttallii*. Other frequent associates include *Myriophyllum spicatum* and *Potamogeton pectinatus*. *P. trichoides* is confined to the lowlands.

The turions of *P. trichoides* begin to form from when? onwards. They usually require stratification before they will grow, and a higher proportion of stratified turions germinates in light than in darkness. After a cold pretreatment of 10 weeks they will germinate at relatively low temperatures (10°C), ensuring that growth begins in spring (Van Wijk & Trompenaars, 1985). Plants flower and fruit rather sparingly, and seeds are not thought to be important in maintaining established populations although they may permit survival through unfavourable periods and long-distance dispersal. *P. trichoides* has been rediscovered in sites after a long absence, notably at Malltraeth Marsh where it was collected by H. Davies in c. 1800 and refound in 1990. This probably reflects the fact that it is easily overlooked, although it may also indicate a capacity to persist as a diaspore bank.

Although this species was first recognised in Britain by Babington (1850), it was subsequently confused with the other 'pusilloid' pondweeds. The older records were revised by Dandy & Taylor (1938). *P. trichoides* is often overlooked by inexperienced observers and it is sometimes misidentified. It is therefore impossible to assess trends in its distribution with any accuracy, but there is some evidence that it has increased in recent years in the Somerset Levels, perhaps because of eutrophication. The species is probably more frequent in England than the map suggests.

This species has a more southerly distribution in Europe than most *Potamogeton* species, being found from S. Sweden and C. Russia southwards to the Mediterranean area. It is also found in S.W. Asia, and N. & E. Africa. ?S. Africa? Scarce says so but handbook does not.

This plant grows in still or slowly flowing, calcareous, mesotrophic water, often in sites which contain a rich assemblage of submerged and floating aquatics. It has been recorded from lakes, sluggish rivers and their associated backwaters, ox-bows and ditches, canals, grazing marsh ditches and one or two flooded clay and gravel pits. It is locally abundant in the Shropshire Union Canal, growing in clear, moderately deep water, often in aqueducts or other places where the flow is accelerated, and associated with *Callitriche obtusangula*, *Elodea canadensis*, *Myriophyllum spicatum*, *P. berchtoldii*, *P. friesii*, *P. natans*, *P. obtusifolius* and *Ranunculus circinatus* (Sinker *et al.*, 1985). In Broadland *P. compressus* grows in water up to one metre deep in grazing marsh ditches with a wide range of associates, including *Elodea canadensis*, *Equisetum fluviatile*, *Lemna trisulca*, *Oenenthe fluviatilis*, *Hydrocharis morsus-ranae*, *Sagittaria sagittifolia* and *Stratiotes aloides*. *P. compressus* is confined to the lowlands.

P. compressus flowers and fruits rather sparingly; plants in grazing marsh ditches may fruit more frequently than those in other habitats. The normal mode of reproduction is by turions, which develop in when? This can be established by examination of the lower stems of plants, which can be seen to arise from a characteristically robust turion.

The current scarcity of this species in Britain is the result of a long period of decline. The species was discovered by Ray (1660) in the River Cam, but it has not been seen in the Cambridge area since 1860 and was last collected in the county in 1912. In the Thames valley it was last seen in Surrey in 1898, Buckinghamshire in 1940, Berkshire in 1944 and Oxfordshire in 1947. Investigate 1970 Oxfords. Cropredy record. In Angus it was formerly known from four lochs: it disappeared from them from the middle of the 19th century onwards and was last collected from Balmadies Loch in 1943. The reasons for the disappearance in Cambridgeshire were not documented, but eutrophication was almost certainly responsible for the other extinctions. The species must have expanded its distribution in the 18th or 19th centuries when it spread into the canal system, but it has subsequently retracted as canals have become disused and dried out or been affected by eutrophication and increasing pleasure boat traffic. In Broadland it has decreased in recent years in mesotrophic grazing marsh ditches, even in areas where management has been designed to maintain their botanical interest (Doarks, 1990). It has, however, recently been discovered in a new Scottish locality, the Loch of Aboyne.

P. compressus is widespread in the boreal and temperate zones of Eurasia. In Europe it is only absent from the extreme north and from the Mediterranean region. It is replaced in N. America by the closely related *P. zosteriformis*.

P. acutifolius and *P. compressus* are two closely related species. They are the most threatened British pondweeds, and will require positive conservation measures if they are not to be reduced to extreme rarity or extinction.

P. acutifolius has a narrower habitat range than most aquatics in our area, as it is virtually restricted to shallow, species-rich drainage ditches in lowland grazing marshes. It is found in calcareous, mesotrophic or meso-eutrophic water, where typical associates include *Elodea canadensis*, *Hottonia palustris*, *Hydrocharis morsus-ranae*, *Lemna minor*, *L. trisulca*, *Myriophyllum verticillatum*, *Potamogeton natans*, *Ranunculus circinatus*, *Sagittaria sagittifolia* and *Spiridola polyrhiza*. It is also recorded from a pond in Middlesex and there are single records from the Hereford & Gloucester and Oxford Canals. There is, however, no evidence that the species ever became established in the canal system, nor is it known from other newly available habitats such as gravel pits.

P. acutifolius flowers and fruits more freely than some other linear-leaved pondweeds, including the closely related *P. compressus*. Turions are apparently produced in smaller quantity than in some other species, but they can usually be found from August onwards. The life history and reproduction of the species requires detailed study.

The decline of this species is apparent from the map. It has not been seen in Yorkshire and Lincolnshire since the late 17th century. It was last seen in Essex in 1700, Hertfordshire in 1846, Warwickshire in c. 1859, Gloucestershire in 1870, Hampshire in 1898 and Northamptonshire in 1910. In many of these counties the only evidence for its occurrence is a single herbarium specimen. It may be extinct in Surrey, where it was last seen in 1965, and if it still survives at its sole site in Middlesex it does so very precariously. Although it still survives in the Wareham area, its distribution there has contracted since the last century and it now occurs in small quantity in one small area; it has also been lost from some of its sites in Norfolk. The reasons for the decline appear to be habitat destruction, the conversion of grazing marshes to arable, and eutrophication. The headquarters of this species are now in Sussex, where it occurs in abundance at Amberley Wild Brooks and has also been recorded recently in other localities. In Norfolk it has been successfully introduced to the Strumpshaw R.S.P.B. reserve.

P. acutifolius has a restricted world distribution, being confined to temperate regions of Europe. It is found from S. Sweden southwards to France, Italy and the Balkans, but it is absent from the Mediterranean area.

This is a frequent species in mesotrophic or eutrophic, standing or flowing waters. It is sometimes found in water only a few centimetres deep, and usually grows at depths shallower than one metre, but it can be found in water 6 metres deep (West, 1910). The habitats in which it occurs include lakes, reservoirs, ponds, rivers, streams, canals, fenland lodes, ditches and disused sand and gravel pits. It is found over a wide range of substrates from stony gravel or sand in clear rivers with moderate flow, to deep mud in lakes and ponds. It is capable of surviving in very eutrophic water, and can even be found in small quantity under a blanket of *Lemna gibba* and *L. minor*. Driscoll (1985) found that, like *Potamogeton pusillus* and *Zannichellia palustris*, it increased in frequency in ditches in an area where grazing land was converted to arable. It may also grow in slightly brackish conditions. It is a primarily lowland species which reaches 350 metres in Drumore Loch.

P. crispus is a rhizomatous perennial which persists through the winter as short, leafy shoots. The longer stems which grow in summer produce turions in late spring and summer in response to a combination of high temperatures and long days (Chambers *et al.*, 1985). These germinate in autumn, and therefore ensure vegetative spread but (unlike the turions of the linear-leaved species) are not a means of over-wintering. In shallow water plants may flower and fruit freely.

P. crispus has very characteristic fruits, which have been found in deposits laid down throughout the last glacial period (Godwin, 1975). It is frequent in suitable habitats in Britain and Ireland. The absence of recent records from Yorkshire is not an indication of decline, but reflects an absence of recent localised records of aquatics from the county.

P. crispus is a native of Eurasia, Africa and Australia. In Europe it occurs from southern Scandinavia southwards. It is naturalised in N. America, where it was first introduced in the 1840s. It had been recorded in most of the coterminous United States by 1950, and it has become a serious weed in some areas (Stuckey, 1979). It is still spreading in Canada (Catling & Dobson, 1985). It is also recorded as an introduction in New Zealand.

P. filiformis is characteristically found in shallow water (less than one metre deep) where the vegetation cover is reduced by a fluctuating water level or by erosion. It usually grows in water which is base-rich, eutrophic, brackish or possesses a combination of these attributes. It is found over a range of substrates including calcareous gravel and marl in limestone lakes, sand on the seaward side of machair lochs and eutrophic mud at the edge of lakes and reservoirs. Other habitats include streams and ditches, flooded quarries and, rarely, cliff-top rock pools in western Scotland. The open, brackish or base-rich habitats in which *P. filiformis* grows often support a rich charophyte flora, and *Chara aspera*, *C. hispida*, *C. vulgaris* and *Tolypella glomerata* can be found growing with it. Another frequent associate is the closely related *P. pectinatus*, but this species reaches its optimum development in deeper water. Although *P. filiformis* is often found in eutrophic water, its biomass in the most eutrophic sites can be reduced by algal growth in the summer months (Jupp & Spence, 1977). *P. filiformis* is primarily a lowland species, which reaches 350 metres at Drumore Loch. There is a single herbarium specimen from 760 metres, above Coire Dhubhchclair, but the occurrence at such a high altitude requires confirmation.

P. filiformis is a perennial, and its long pioneer rhizomes can be seen invading open ground in shallow water. Growth begins in March and plants may begin to flower in May (Heslop Harrison, 1949). Plants are self-compatible and mature fruits can be found from June onwards. Plants overwinter as small tubers which develop on the rhizome.

This was a widespread and apparently frequent species in the full and late glacial periods in both Britain and Ireland (Godwin, 1975). Since then its distribution has contracted to the north and west. In Britain it has not been recorded from Anglesey since 1826, but it is frequent in suitable habitats in Scotland. In Ireland it is still present in quantity at its most south-westerly site, Lough Gill. It is probably somewhat under-recorded in both Scotland and Ireland.

This species has a circumboreal distribution, which in Europe extends south to scattered localities in Spain, the Alps, Italy and the Balkans.

Potamogeton × *suecicus* K. Richter (*P. filiformis* Pers. × *P. pectinatus* L) Swedish Pondweed

P. × suecicus is a sterile hybrid which is recorded from shallow, standing and flowing waters. The largest and most vigorous stands are found in mesotrophic rivers, where the hybrid may form dense masses in shallow water over sandy, gravelly or stony substrates. Where the flow of water is moderately strong, plants are often rooted under large boulders or the supports of bridges. *P. × suecicus* also grows in shallow water at the edges of lakes or in their outflow streams, growing over sand in some coastal sites and over stony or silty substrates away from the sea. It is also locally abundant in the shallow stream and backwater pools of An Fhaodhail, Tíree, and has also been found in a pool amongst sand dunes in Donegal. It is restricted to the lowlands.

Populations of this hybrid may occur in the absence of both parents (as in the R. Lossie), or even south of the southern limit of *P. filiformis* (R. Wharfe, R. Ure). The hybrid is a sterile perennial which perennates as the rhizome, which may be very thick in robust, riverine plants. Vegetative reproduction and dispersal may occur by the production of tubers on the rhizome, or when large masses of material are washed downstream in floods (Dandy & Taylor, 1946). Plants may flower freely but fruits never develop, and old, shrivelled inflorescences and flowers at anthesis may be found on the same plant late in the season. The pollen of *P. × suecicus* initially develops normally, but later the grains split and their contents appear to disintegrate (Bance, 1946). At some localities the population may represent a single clone, but in others it includes more than one genotype (Hollingsworth *et al.*, in prep.).

P. × suecicus was first recognised in Britain by Dandy & Taylor (1940), although some of the specimens they cited had been collected in the 19th century, but misidentified (Dandy & Taylor, 1940). The populations in the Yorkshire rivers were detected by Dandy & Taylor (1946); plants in the R. Tweed and R. Till referred to this taxon by Dandy (1975) and Dandy & Taylor (1946) are now thought to be another taxon (Hollingsworth *et al.*, in prep.). The hybrid is very persistent: it still occurs at An Fhaodhail, where it was collected in 1897, and in the R. Wharfe, where it was gathered in 1868. The Yorkshire plants are believed to be relicts of a time earlier in this interglacial when *P. filiformis* was more widespread. *P. × suecicus* is easily overlooked as a form of the immensely variable *P. pectinatus*, and only tends to be recognised by experienced observers. In recent years it has been added to the Irish flora (Preston & Stewart, 1994) and found in a number of new Scottish localities. It is almost certainly under-recorded.

Check Spence & Chrystal, 1970a.

P. pectinatus is one of the most frequent and characteristic species of eutrophic water. It is found in a wide range of standing and flowing waters, including lakes, rivers, streams, canals, ditches, ponds and flooded sand and gravel pits. It grows at a range of depths, but is most abundant at moderate depths of 0.5-1.5 metres, where it may frequently form dense and dominant stands. It tolerates disturbance in navigable and highly managed waters (Murphy & Eaton, 1983), and is a frequent colonist of gravel pits and other newly available habitats. It is also tolerant of brackish conditions in coastal lagoons and ditches. It is sometimes found in highly calcareous but nutrient-poor lakes, but rarely occurs in these sites in abundance. Characteristic associates include *Elodea nuttallii*, *Myriophyllum spicatum*, *P. crispus*, *P. pusillus* and *Zannichellia palustris*. *P. pectinatus* is confined to the lowlands.

P. pectinatus is a rhizomatous perennial. Plants are self-compatible and those which reach the surface of the water fruit freely, although less than half the carpels develop into fruits; plants pollinated under water show reduced fruit set (Guo & Cook, 1989). Tubers develop on the rhizomes and most populations overwinter as tubers, but some are winter-green. In addition to propagation by tubers, plants may also regenerate from broken and even apparently moribund stems. Both tubers and fruits are an important source of food for wildfowl. For detailed account of the reproductive biology of this species, see Van Wijk (1988, 1989).

This species has a long history in our area, and it appears to have persisted through the last glacial period (Godwin, 1975). It is frequent in suitable habitats in Britain and Ireland, and in areas where water bodies are eutrophic and highly managed it is the commonest member of the genus. In northern and western regions it becomes increasingly confined to brackish, coastal sites.

P. pectinatus has a very extensive world distribution: it is found in all continents except Antarctica and it is sometimes a troublesome aquatic weed. It is present throughout most of Europe, although it is absent from the most northerly regions. It is a variable plant, and although much of the variation is environmentally induced some of it is genetically based (Van Wijk *et al.*, 1988).

142/2.

Groenlandia Gay

This monotypic genus is closely related to *Potamogeton*. The sole species was formerly treated as *Potamogeton densus* L., and is still found under this name in some contemporary floras.

G. densa grows in shallow, clear, base-rich water in rivers, streams, canals, ditches and ponds. It is particularly characteristic species of streams flowing from calcareous springs, where it is often found with *Apium nodiflorum*, *Berula erecta*, *Callitriche obtusangula*, *Zannichellia palustris* and, in larger streams, *Ranunculus penicillatus* subsp. *calcareus*. It is rarely found in lakes and reservoirs, but the isolated site in Co. Antrim is a lake which receives base-enrichment from nearby basalt rocks. Here it is abundant in the shallows, and is present in smaller quantity to a depth of 1.4 metres. It is rarely found as a colonist of newly available habitats, but it is sometimes introduced to ponds outside its native range by gardeners. It is a predominantly lowland species which reaches 380 metres in the outflow stream from Malham Tarn.

G. densa is a rhizomatous perennial, although the rhizome is less distinct from the stem in this species than in the rhizomatous *Potamogeton* species. It continues to grow throughout the winter. The flowers are usually self-pollinated, either above the water or below the surface; if a plant flowers under water the pollen is carried from the anthers to the stigmas on the surface of a bubble (Guo & Cook, 1990). There is a possibility that out-crossing may occur if flowers are fertilised by pollen floating on the water surface. Seed set is normally very high. The species has no specialised means of vegetative reproduction, but it almost certainly regenerates from plant fragments, which may be easily detached. The extent to which it reproduces by seed is unknown.

Rather surprisingly, the fossil fruits of this species are often found in full glacial deposits (Godwin, 1975). In the historical period it has declined in Britain and, to an even greater extent, in Ireland. It is now extinct as a native species in Scotland, where it was most frequently recorded in habitats near the centre of Edinburgh which have now disappeared (Preston, 1986). Elsewhere it has suffered from habitat destruction and eutrophication. In Cambridgeshire older records indicate that it was once widespread in the county but it has now disappeared from parishes on boulder clay and it is now confined to a few sites on the chalk and in the fens.

G. densa is found in Europe north to Britain and Denmark. It is also recorded from adjacent parts of Asia and N. Africa.

143. RUPPIACEAE

The Ruppiaceae is closely allied to the Potamogetonaceae, and many authors consider that it is best regarded as a subfamily of that family. It includes a single genus, *Ruppia*.

143/1. *Ruppia* L.

This widespread genus of aquatic plants is widespread in temperate and subtropical waters. In many areas it is confined to brackish waters near the sea, but it also occurs at saline sites inland and sometimes in fresh water. The species are difficult to identify as the plants (like many aquatics) have a reduced morphology and are phenotypically variable. The wide range of *R. cirrhosa* and *R. maritima* creates additional problems. It is difficult to assess whether or not the differences between plants in different continents have a genetic basis, especially if only fragmentary herbarium material is available for study.

Although the classification of *Ruppia* on a world scale is not yet resolved, the taxonomy and ecology of the genus in N.W. Europe have received detailed study in recent years (Reese, 1962, 1963; Verhoeven, 1979, 1980a,b; Verhoeven & Van Vierssen, 1978; Van Vierssen *et al.*, 1981, 1984). There is general agreement that there are two species, *R. cirrhosa* and *R. maritima*, which are cytologically, morphologically and ecologically distinct. There are some problems in equating these taxa to those present in S.W. Europe, and critical comparisons with material from other continents have not yet been made.

Before the two species of *Ruppia* were distinguished, all *Ruppia* material was called *R. maritima*. When the species were separated the name *R. maritima* was first applied to the one now called *R. cirrhosa*, and only later to the species that currently bears the name. Historical records therefore require careful interpretation.

This species is virtually confined to coastal, brackish waters. It is typically found in lakes, including artificial boating lakes, natural lagoons and sheltered tidal lochs, pools on salt marshes, raised beaches and shingle beaches, small rock pools which receive salt spray, the tidal stretches of streams and rivers, ditches, creeks and shallow runnels on mud flats and on the mud flats themselves. It also colonises coastal clay and gravel pits. It has also been recorded in pools associated with inland salt marshes in Cheshire (Lee, 1977) and, exceptionally, from a canal some 56 kilometres from the sea near Talybont (Barrett, 1885-J. Bot. 23:112-copy). It is usually found in water less than 0.5 metres deep, and it can grow on mud which is exposed at low tide. In lakes and ditches it may grow with other salt-tolerant aquatics such as *Myriophyllum spicatum*, *P. filiformis*, *Potamogeton pectinatus* and *Zannichellia palustris*, but in the smaller pools and more saline habitats it is often the only vascular plant present.

R. maritima may behave as an annual or as a perennial. In The Netherlands populations are often annual and reproduce by seed, but plants may overwinter as quiescent vegetative stems. In the milder climate of the Welsh coast plants may grow and even flower through the winter. This species normally flowers and fruits more freely than *R. cirrhosa*. The flowers are borne on short peduncles and are usually submerged. Plants are self-pollinated by the transfer of pollen within an inflorescence on the surface of air bubbles which develop when the anthers dehisce and which remain attached to the inflorescence for several hours. The seeds lack an impermeable seed coat. Germination is stimulated by cold temperature pretreatments and in The Netherlands plants regenerate from seed in the spring. The growing plant is killed by desiccation but the seeds survive. For further details of the life cycle of this species, see Verhoeven (1979) and Van Vierssen *et al.* (1984).

The fossil record of *R. maritima* suggests that it has always been restricted to coastal sites in our area. It may be somewhat under-recorded, both because it often has to be searched for deliberately in habitats which are not otherwise very rewarding to the aquatic botanist, and partly because vegetative material of *Ruppia* may not be identifiable to species level. There is little positive evidence of a decline on the stretches of coast where there are no recent records, and further fieldwork is required to establish whether the plants has disappeared from these areas.

In Europe *R. maritima* is found in coastal habitats and at scattered sites inland from Iceland and northern Scandinavia southwards. It is widespread in Asia, N. Africa, N. America and Australia, occurring in coastal sites and at saline or other alkaline sites inland. The world distribution, which is discussed by Verhoeven (1979), is uncertain because of the rather chaotic state of *Ruppia* taxonomy.

In N.W. Europe plants of *R. maritima* are diploid ($2n=20$), and this number has been confirmed for British material by Al-Bermani *et al.* (1993). Both diploids and tetraploids ($2n=40$) occur in S. Europe (Talavera *et al.*, 1993).

This species grows in brackish water in tidal inlets and in coastal lakes and lagoons which are directly connected to the sea, and in other coastal lakes, ponds, pools on salt-marshes and shingle beaches and ditches. It may colonise artificial lakes and ponds and flooded gravel pits. It usually grows over sand or soft mud and, unlike *R. maritima*, it is often found at depths of 0.5 metres or more. In its less brackish sites associates include *Potamogeton pectinatus* and *Ruppia maritima*. However, *R. cirrhosa* tolerates more saline conditions than *R. maritima*, or any other macrophyte in our area except those in the marine genus *Zostera*. In The Fleet it grows in mixed communities with *Zostera angustifolia* and *Z. noltii* and in brackish lakes elsewhere it may also grow with seaweeds such as *Fucus ceranoides* and *F. vesiculosus*.

R. cirrhosa is a perennial which persists through the winter as quiescent rhizomes or stolons (Verhoeven, 1979). The species flowers less freely than *R. maritima*. The peduncle elongates rapidly until the flowers reach the surface of the water. As it elongates, the anthers are released. They float to the surface, where they burst to release the pollen, which then floats. Cross-pollination is more likely than self-pollination, and the proportion of carpels which are successfully fertilised is smaller in *R. cirrhosa* than in *R. maritima*. Van Vierssen *et al.* (1984) attempted to germinate the seeds under a variety of experimental conditions but failed to get more than a small proportion to germinate, in marked contrast to the results they obtained for seeds of *R. maritima*. The conditions required for the successful establishment of plants from seed in the wild are unknown.

The map suggests that this species has declined in some parts of its range. One locality in Sussex was destroyed by gravel dredging (Hall, 1980) but there is little other direct evidence of decline. The species is easily overlooked, and a detailed survey of former localities is needed to establish whether it has decreased. It was rediscovered in Yorkshire in 1981 (Crackles, 1983) and found for the first time in Westmorland in 1991, records which suggest that it might be overlooked elsewhere.

R. cirrhosa is found along all but the arctic coasts of Europe. It is also known from W. Asia, Africa and N. & S. America. Although it is usually found in saline habitats it grows in fresh water in montane lakes in the Andes.

Two cytotypes of *R. cirrhosa* are found in N.W. Europe, a tetraploid ($2n=40$) and a hexaploid ($2n=60$). There is no information about the chromosome numbers of plants in our area.

144. NAJADACEAE

This family contains a single genus, *Najas*.

144/1. *Najas* L.

This is a genus of 40 species, all of which are submerged aquatics. The genus has a cosmopolitan distribution, although most species occur in tropical and subtropical regions. Although there is no recent world monograph, there are detailed treatments of the species in the Old World (Triest, 1988), Africa (Triest, 1987), N. & C. America (Haynes, 1979) and the tropical regions of the New World (Lowden, 1986).

Most species of *Najas* are annuals which reproduce by seed; perennation and vegetative reproduction appear to be unusual (Triest, 1988). The genus contains monoecious and dioecious species. The flowers are submerged and unisexual, with the male flowers consisting of a single stamen. Pollination occurs under water. The species occur in a range of fresh and brackish water habitats, and no less than 11 species are recorded as rice-field weeds in the Old World (Triest, 1988).

Triest (1988) recognises two subgenera. Two of our species, *N. flexilis* and *N. graminea*, are in Subgenus *Caulinia*, which includes species which are usually slender, monoecious plants and lack spines on the stems. The dioecious *N. marina* is the only species in Subgenus *Najas*; it is a robust plant which usually has spiny stems.

N. flexilis usually grows in deep, clear water in mesotrophic lowland lakes. It often occurs in sites which have some base-enrichment from nearby outcrops of basalt or limestone, or in machair lochs adjoining calcareous dune sand. Although it can be found in water less than one metre deep, it is usually found at depths of 1.5 metres or more. It grows over soft, silty substrates, often occurring with *Callitriche hermaphroditica*, *Potamogeton praelongus*, *Nitella flexilis* and occasionally with the tiny *Nitella confervacea*.

N. flexilis is a monoecious annual. The male flowers tend to be at the upper nodes with the female flowers below. Most mature plants appear to set seed, and within a lake the seeds either fall to the bottom or are dispersed when plants are uprooted in autumn gales and blown to the edge of a lake.

Fossil evidence indicates that *N. flexilis* was present in Britain in the middle of the last glacial period, and was much more widespread than it is today in the late glacial and early Flandrian. Its slender habit and deep-water habitat make it a very inconspicuous species. It was discovered in Ireland in 1852 (Oliver, 1852) and in Scotland in 1875 (Sturrock, 1876), but not added to the English flora until 1914 (ref). In recent years more intensive fieldwork, including surveys by divers, have revealed new sites in both Britain and Ireland. It is, however, vulnerable to eutrophication. It has not been seen recently at a number of sites in E. Scotland, including lochs such as White Loch (CHK CDP notes) and Monk Myre, which are now very eutrophic, and it has greatly decreased in abundance in Esthwaite Water, its only English locality (ref). It is threatened by fish farming at one Scottish locality.

N. flexilis has a circumboreal distribution, but it is much more frequent in N. America than in Eurasia. In Europe it has a northerly distribution, extending south to Switzerland. Fossil records, mapped by Hultén & Fries (1986), show that it was once more widespread in Europe, and in many countries it is a rare and declining species. Even in America it is decreasing: in Ohio it was once the most common *Najas* species but it is now becoming rare as many clear lakes have become muddy or turbid (Wentz & Stuckey, 1971).

Najas graminea Del.

This alien species formerly grew in tepid water over soft, black mud in a section of the Reddish Canal which was warmed by effluent from nearby cotton mills and other industrial works. It grew with *Elodea canadensis*, *Myriophyllum* sp., *Potamogeton alpinus*, *P. crispus*, *P. obtusifolius*, *P. pusillus* and the alien charophyte *Chara braunii*.

N. graminea is a monoecious annual which reproduces by seed. In the British population female flowers were more numerous than male flowers; when present the males were usually found alongside the females in the axil of the same leaf. Mature fruits were produced in abundance (Bailey, 1884).

N. graminea was discovered in Britain by J. Lee in 1883. A detailed account of the species was published by Bailey (1884), who believed that it had been introduced to the canal with Egyptian cotton, which was used by one nearby mill. It persisted in the canal until 1947, but disappeared once the mill ceased to discharge hot water into the canal (Savidge, 1963). The canal has now been built over.

N. graminea occurs as a native in the subtropical and tropical regions of Africa, Asia and Australia. It is a weedy species which may colonise irrigation canals. In S. Europe it is naturalised in rice-fields and ditches in France (Camargue), N. Italy, Bulgaria and Rumania; it also occurs as an alien in similar habitats in California.

This species is very variable cytologically, and exists at several different levels of a polyploid series (You *et al.*, 1991).

N. marina formerly grew in the clear, calcareous and nutrient-poor water of the unpolluted Broads (George, 1992). At Hickling Broad, where is some saline influence, it formed a low sward with abundant charophytes in water 1-3 metres deep; Bennett (1883, 1884) listed its associates as *Potamogeton pectinatus*, *Chara aspera*, *C. hispida*, *C. pedunculata* and *Nitellopsis obtusa*. In other sites it colonised bare mud, and could sometimes be found in *Phragmites australis* swamps (Barry & Jermy, 1953). It is now usually found in meso-eutrophic water over deep substrates of silt or peaty mud, growing with species such as *Ceratophyllum demersum*, *Hippuris vulgaris*, *Myriophyllum verticillatum*, *Potamogeton pectinatus* and *Utricularia vulgaris* in water deeper than 0.2 metres.

N. marina is a dioecous annual. In Britain female plants set good seed even in the apparent absence of male plants, suggesting that they may be apomictic (A.C. Jermy, pers. comm.). In cultivation plants may complete their life cycle from seed to seed in 100 days (Viinikka, 1976). The germination requirements have not been studied in Britain, but plants from Sweden, The Netherlands and Israel all have similar germination requirements (Agami & Waisel (1984, 1986, 1988). The seeds usually have a hard coat which needs to be broken before they will germinate, although its thickness varies from seed to seed. The seed coat may be ruptured by passage through the digestive system of fish or waterfowl: most seeds eaten by mallard are digested but the remainder show greatly increased germination compared to intact seeds. Seeds will also germinate after prolonged periods of immersion in cold water. Germination is stimulated by darkness and by anaerobic conditions. Even the most effective pretreatments will not stimulate all seeds to germinate, and *N. marina* has a persistent seed bank. Seeds stored in dry conditions may remain viable for at least 4 years. British populations do not have specialised turions, but may spread by vegetative fragmentation.

Although *N. marina* was present in Britain in the last glacial period, the fossil evidence indicates that it subsequently increased in abundance. At the 'climatic optimum' it was widespread in England and Ireland, and also recorded from S. Wales and the Isle of Man (Godwin, 1975). It is a most distinctive species, which was discovered as a living plant by Bennett (1883) at Hickling Broad. It was discovered in Martham Broad in 1885, and in several more Broads between 1949 and 1952. In the early 1950s its status in Hickling Broad was similar to that described by Bennett (1883), but it declined in the late 1960s in this and other sites as nutrient levels increased (Barry & Jermy, 1953; George, 1992). However, it is frequent in Upton Broad, where phosphorous levels are still low, and it has increased or reappeared in other sites after remedial action was taken to reduce the nutrient levels, probably germinating from dormant seed (George, 1992).

N. marina is a widespread species, found in temperate, subtropical and tropical regions of Europe, Asia, Africa, Australia and N. & C. America, as well as on oceanic islands such as Hawaii and Galapagos. In Europe it is widespread north to England and Finland. It is morphologically and cytologically variable. Triest (1988) recognises 12 subspecies in the Old World. The British plant is subsp. *intermedia*, itself a polymorphic taxon which occurs around the North Sea and the Baltic, and in the Alps, and eastwards in Asia to Thailand. The other European subspecies are subsp. *marina*, which is the more frequent plant in western and southern Europe and occurs at scattered localities throughout Asia, and subsp. *armata* of S. Europe, S.W. Asia, Sri Lanka and Australia.

145. ZANNICHELLIACEAE

This family contains four small and closely related genera of aquatics with submerged, linear leaves. One of these genera, *Zannichellia*, is found in our area and another, *Althenia*, occurs in southern Europe. The remaining genera are found in S. Africa (*Pseudalthenia*) and Australasia (*Lepilaenia*). Five genera of sea-grasses are sometimes included in this family, but are grouped by Cronquist (1981) in the exclusively marine family Cymodoceaceae.

145/1. *Zannichellia* L.

The taxonomy of the genus *Zannichellia* is in a state of confusion: Pearsall's (1933) comment that it is 'by no means easy to reconcile the divergent taxonomic views of authors in this genus' is still true sixty years after he made it. At one extreme are those authors who recognise a single species which is both morphologically and cytologically variable, *Z. palustris*. This was J.E. Dandy's opinion, and it was followed by *Flora Europaea* (Tutin *et al.*, 1980). Most botanists in Britain and Ireland have adopted this view in recent decades, including Stace (1991) and Kent (1992), although Clapham *et al.* (1952) suggested that our material might be divisible into two subspecies. Continental botanists usually recognise more taxa. Van Vierssen (1982a,b) distinguished four species which differ in morphology, ecology and chromosome number. Three of these occur in western Europe, *Z. palustris* (which is divided into subsp. *palustris* and subsp. *repens*), *Z. pedunculata* and *Z. major*; a fourth, *Z. peltata*, is found in southern Europe. The European distribution of these species is mapped by Talavera *et al.* (1986), who recognise two additional species, *Z. contorta* and *Z. obtusifolia*. They cite specimens of *Z. palustris* and *Z. pedunculata* from Britain and *Z. palustris* from Ireland. In eastern Europe totally different characters are used to divide the genus into species, so it is difficult to equate the taxa recognised there with those in the west (Uotila *et al.*, 1983).

According to Van Vierssen (1982), *Z. palustris sensu stricto* is a plant of permanent, fresh or brackish waters in northern Europe but further south it becomes confined to fresh water. *Z. pedunculata* grows in coastal habitats, including water bodies that dry out in summer. *Z. major* is confined to deep, brackish water in the Baltic.

We have followed Stace (1991) in recognising a single species, although it is clear that material from our area needs to be reinvestigated in the light of continental work. Most plants from inland habitats in Britain and Ireland are probably referable to the continental *Z. palustris*, whereas some coastal populations correspond to *Z. pedunculata*, and probably include many of the plants recognised as *Z. palustris* var. *pedicellata* or *Z. pedicellata* in older floras.

Z. palustris grows in a wide range of habitats where the water is shallow and calcareous, eutrophic or brackish. It can be found as large patches in clear, calcareous streams which are highly calcareous but not necessarily nutrient-rich, growing in stony substrates, sand or fine silt in the main channel or near the edge. It is widespread in eutrophic lakes, pools, rivers, streams, canals, ditches and in flooded clay, gravel and other mineral workings. It is often found in water less than 0.5 metres deep, but it will also grow through stands of more robust aquatics in slightly deeper water. It is one of the few submerged aquatics which will persist in lakes and ponds which are inhabited by large numbers of waterfowl, where it may be found (often in small quantity) in shallow water over deep, eutrophic mud. It is also frequent in brackish lagoons, pools and ditches. It is a predominantly lowland species, which reaches 380 metres at Llynheilyn.

In some habitats *Z. palustris* is certainly perennial, and in streams emerging at a constant temperature from calcareous springs it flowers throughout the year. Other populations on lakeshores may regrow from seed after periodic desiccation, and there may be localities in which it is usually annual, although detailed observations in our area are lacking. Plants spread by a creeping rhizome, sometimes forming clonal patches. The species is monoecious and the male flowers release pollen into the water in small 'clouds' which sink slowly or are carried away by currents (Guo *et al.*, 1990). The anthers may dehisce before or after the funnel-shaped stigmas are receptive, and both self- and cross-pollination occurs. Fruit set is usually good. There is a wide variation in germination behaviour between populations of *Z. palustris sensu lato*. The seeds of plants attributed to *Z. palustris* by van Vierssen (1982a) are initially dormant and require stratification before they will germinate, whereas those of *Z. pedunculata* do not. Seeds which are desiccated for 3 months retain viability.

Z. palustris has been more or less continuously present in the British Isles since the mid Pleistocene, and persisted through the last glacial period (Godwin, 1975). Unless it is present in abundance it is easily overlooked by inexperienced botanists: it was under-recorded in the *Atlas of the British flora* and may still be more frequent than the map suggests, particularly in Ireland. It is frequent in suitable habitats in England, and is increasing in some Scottish counties, including Angus (Ingram & Noltie, 1981) and Perthshire, as a result of eutrophication.

Z. palustris has an almost cosmopolitan distribution. It is widespread in the northern hemisphere, although absent from the more northerly regions, but somewhat less frequent in the tropics and the southern hemisphere. In Europe it extends from Iceland and the coasts of Scandinavia to the southern fringes of the continent.

147. ARACEAE.

This is a large and predominantly tropical family of 106 genera and nearly 3,000 species. It contains several important food plants, and many houseplants and other ornamentals. A recent book, *The Aroids*, provides an excellent illustrated review of the family (Bown, 1988). Most of the genera are terrestrial, but there are almost 100 aquatic species distributed amongst 20 genera. They include 50 species of *Cryptocoryne* and *Pistia stratiotes*, the water lettuce, which is one of the most troublesome aquatic weeds in the tropics and has been recorded in Britain as a casual (Clement & Foster, 1994). None of the aquatic Araceae are native to our area, but two genera are found as naturalised aliens. A third genus, *Lysichiton*, is also naturalised in moist woodland and on damp ground by streams and rivers.

147/1. *Acorus* L.

The genus *Acorus* is an aberrant member of the Araceae, which differs from all the other members of the family in its vegetative morphology, the absence of raphide crystals and the presence in the leaves of ethereal oil cells. Its systematic position has recently been reviewed by Grayum (1987), who lists 13 more characters of *Acorus* which are unique within the Araceae, including 'the much-ballyhooed co-occurrence of the rust *Uromyces sparganii* on *Sparganium* and *Acorus*'. Grayum concludes that the genus should be moved to its own family, the Acoraceae. The genus contains at least two species, *A. calamus* and *A. gramineus*; some authors recognise additional segregates of both these species. The account below follows the taxonomic treatment of Röst (1978, 1979).

A. calamus is a tall perennial which grows in water less than one metre deep at the edge of standing or slowly flowing, mesotrophic or eutrophic waters. It often forms narrow stands along the fringes of lakes, rivers, streams, canals, ponds and ditches. It can often be found around lakes in the landscaped grounds of stately homes, where it was originally planted but has become thoroughly naturalised. It may spread into neglected ponds and eventually cover large areas of previously open water. It also spreads naturally along canals and rivers, such as the Lancaster Canal (Greenwood, 1974) and the R. Tweed and its tributaries. Dense stands of *A. calamus* exclude almost all competitors; in more open stands it can be mixed with emergents such as *Solanum dulcamara*, *Sparganium erectum* and *Typha latifolia*, with *Lemna minor* floating on the surface of the water (Rodwell, in press). It is confined to the lowlands.

A. calamus is a rhizomatous perennial. The plant naturalised in Europe is a sterile triploid cytotype which flowers (although sometimes rather infrequently) but never produces fertile seed (Röst, 1978). Confirmation that this cytotype is present in Britain is provided by Marchant (1973). This plant spreads by direct growth of the stout rhizome, and by the establishment of new colonies from lengths of rhizome washed out in floods or dislodged by human disturbance. Once established, it may be very persistent (example?).

A. calamus has been used in medicine since ancient times, and later used as a fragrant floor covering. It is believed to have been introduced to Europe in the mid 16th century. Gerarde (1597-CHK) knew it as a recent arrival, but by 1668 Sir Thomas Browne described it as growing 'very plentifully...by the bankes of Norwich river [R. Yare]...so that I hath known Heigham Church in the suburbs of Norwich strewed all over with it. It hath been transplanted and set on the sides of Marish [marshy] ponds in severall places of the county, where it thrives...' (Keynes, 1931-CHK). It decreased in abundance in Broadland as a result of grazing by coypu, but increased after the successful attempt to exterminate these herbivores (George, 1992). In Ireland it was recorded from Moira Demesne in 1744; it had spread into the Lagan Canal by 1866 and thus reached Lough Neagh (Harron, 1986; Hackney, 1992). It continues to be planted by ornamental lakes and ponds.

The sterile triploid var. *calamus* ($2n=36$) is widespread in Europe and western Asia, although it is absent from most of the Mediterranean area. It also occurs in the Himalayan region and in eastern N. America. It was introduced to Europe via Turkey; its native range is unknown. The fertile diploid var. *americanus* ($2n=24$) is widespread in Siberia and N. America; although it can produce seeds it also persists vegetatively in areas where seeds do not mature for climatic reasons. The fertile tetraploid var. *angustatus* ($2n=48$) is more variable than the other cytotypes. It is found in temperate and subtropical S. & E. Asia. For distribution maps of the cytotypes, see Röst (1978) and Packer & Ringius (1984). These taxa might be more appropriately treated as subspecies.

Acorus gramineus Aiton

Slender Sweet-flag

A small clump of *Acorus gramineus* 'Variegatus' grows under trees at the edge of the Basingstoke Canal at Mychett.

Acorus gramineus is a rhizomatous perennial. The species is a fertile diploid, but there is no evidence that the British population reproduces by seed.

This plant was discovered by the Basingstoke Canal by Mrs J.F. Leslie and others in 1986. It is a cultivar which was probably discarded from nearby houses (Mrs J.E. Smith, pers. comm.). It was included in Stace (1991) and Kent (1992) on the basis of this record, but it can scarcely be considered naturalised.

A. gramineus is a variable species which is a native of S. & E. Asia. It is widely cultivated in Europe, but is not listed as a naturalised species by Tutin *et al.* (1980).

147/3. *Calla* L.

This is a monotypic genus which occurs in our area as an introduction.

C. palustris can grow as a floating plant or rooted in wet terrestrial habitats. It is naturalised at the edges of lakes and ponds, in marshes and in wet alder woodland. In lakes it can be present in considerable quantity. It is confined to the lowlands.

This is a perennial which spreads by growth of the long rhizome, and (in floating plants, at least) by fragmentation. The flowers are bisexual or male, and are insect pollinated. The fruits are red berries, which are dispersed by animals. Naturalised plants fruit in Britain (Caulton, 1961), but we do not know if they reproduce by seed.

C. palustris has a long history in Surrey, where it was first recorded by **author? CHK J.Bot. 11, 339-340, 1873 at site?**, where it was planted in 1861 and persisted for at least 30 years. It was subsequently found at Boldermere, where it persisted for over 60 years but is now extinct (Lousley, 1975; Leslie, 1987). It was found at Stanmore Common in Middlesex in 1946, where it is also extinct (Kent, 1975; Burton, 1983), and subsequently from a number of scattered sites elsewhere. It appears to have been recorded with increasing frequency in recent years.

This species has a circumboreal distribution. In Europe it is native from Scandinavia and the Low Countries eastwards, but it has distinctly continental tendencies and it is rare towards the western edge of its range. It is a plant of rather acidic and nutrient-poor shallow waters, swamps and wet alder woods, and grows with species such as *Carex lasiocarpa*, *C. rostrata*, *Equisetum fluviatile*, *Menyanthes palustris* and *Potentilla palustris*. [any more info on plant in Europe?]

CHK Ridley
Sci Gossip 1895, p. 109.
J. Bot. 53:177 (1915).

148. LEMNACEAE

A family of 4 genera of small aquatic plants, 3 of which occur in Britain and Ireland. Five of our six species are free-floating whereas the sixth (*Lemna trisulca*) has submerged vegetative fronds but floating fertile fronds. Vegetative reproduction predominates in the family, with most species flowering only occasionally. The factors which lead to flowering in wild populations are not well understood. In the cool, oceanic climate of the British Isles the duckweeds appear to flower even less readily than they do either in more continental climates at similar latitudes or in the more southerly parts of their range. Martinsson (1984) found that 12 of the 26 *Lemna minor* populations which he studied on Öland (57°N) in the summer of 1982 were flowering. Comparable figures are not available for the British Isles, but it seems most unlikely that they would be as high. Pollination is effected by small invertebrates, which crawl over the surface of the fronds. Dispersal of fronds is by water movement and by animal vectors.

The Lemnaceae of the world have been monographed by E. Landolt and his colleagues (Landolt 1980, 1986; Lüönd 1983; Landolt & Kandeler 1987). Much of the information given below on reproduction, perennation and world distribution is derived from Landolt (1986). There have been few studies of the reproduction and perennation of the British species, and research is needed to relate their behaviour here to that observed in other areas. The literature on the family is covered by bibliographies in Landolt (1980) and Landolt & Kandeler (1987).

148/1. *Spirodela* Schleiden

A small genus of 3 species, until recently included by British botanists in *Lemna*. The main difference between the genera is the fact that *Lemna* species have a single root on each frond (or, rarely, no roots at all) whereas *Spirodela* species have 2 or more roots per frond.

Spirodela polyrhiza (L.) Schleiden (*Lemna polyrhiza* L.)

Greater Duckweed

Spirodela, the largest British duckweed, is most frequent in flat fenland regions which receive drainage from calcareous uplands. It grows in base-rich water in ponds, ditches (especially deeper ditches in grazing marshes), canals and slowly flowing rivers, often in a species-rich assemblage of floating macrophytes which can include *Azolla filiculoides*, *Hydrocharis morsus-ranae*, *Lemna gibba*, *L. minor* and *L. minuta*. It is also recorded from old gravel workings and brick-pits. The presence of several roots on each of its fronds enables *S. polyrhiza* to exploit nutrients in the surface layer of water more effectively than *Lemna* spp. It is confined to the lowlands.

Reproduction is almost entirely vegetative. The species flowers very rarely throughout its range, and in Britain has only been found flowering once, at Wedmore, Somerset, in July 1906 (White 1912). Perennation through the winter is by starch-filled orbicular or reniform turions, which develop in the fronds and sink to the bottom of the water. These are more cold-tolerant than the fronds. Dalglish (1926) reported that they were produced as early as April 17th, and when placed in an aquarium began to grow within a week. A detailed account of the life-history of *Spirodela* in Minnesota, USA, is given by Jacobs (1947).

Spirodela has declined in some areas, as ponds have disappeared and grazing marshes have been converted to arable land. Holland (1986) noted that in Gloucestershire it fails to survive pond clearance; this is presumably because the large fronds can be removed from the water relatively easily and no reservoir of propagules remains. If this is generally true, sensitive management of its habitats will be necessary to ensure its survival.

S. polyrhiza is widespread in Europe, north to 66°N in Scandinavia, but rare in the Mediterranean region. It is recorded elsewhere from all continents except Antarctica, though it is rare in S. America and absent from arid regions. Its world distribution is mapped by Landolt (1986).

148/2 *Lemna* L.

A genus of 13 species with a virtually cosmopolitan distribution.

A plant of still or very slowly flowing eutrophic water in lowland ditches, ponds, canals or the quiet backwaters of streams and rivers. It is usually mixed with *L. minor*, but very eutrophic ditches (such as those alongside arable land) can be completely covered by a dense carpet of pure *L. gibba*, under which no other macrophytes can grow. *L. gibba* can also be abundant in brackish coastal ditches. The competitive advantage of this species over other duckweeds can be attributed to the buoyancy of its swollen fronds, which resemble small pieces of expanded polystyrene; these ride over and shade competitors. The success of *L. gibba* in mixed communities was demonstrated in experimental conditions by Chatworthy & Harper (1962).

Reproduction is primarily by vegetative budding. Flowering is initiated by long days. *L. gibba* flowers more often than most duckweeds, and is probably self-compatible. In warmer climates reproduction by seed is important, and the species even grows in a seasonal pool in Israel where it survives the dry period as dormant seed (Witztum 1977). Seed from this population remained viable after almost 5 years dry storage (Witztum 1986). Flowering in Britain is infrequent, however. Plants persist through the winter as flat fronds with a high starch content, which continue to float on the surface of the water, or as living buds in the pouches of dead, sunken fronds. In the Netherlands the flat winter fronds become gibbous by the end of May over clay soils but sometimes persist until August over sand and peat. In September gibbous plants become less inflated and eventually produce flat progeny (Lange, Pieterse & Wetsteyn 1984).

Lemna gibba is locally frequent in lowland England but rare in Scotland; it reaches its northern limit in the Forth and Clyde and Union Canals. Field botanists probably mistake the flat winter form for *L. minor*, and *L. gibba* might therefore be under-recorded in some areas. Criteria for separating these two species are given by Lange & Westing (1979). There is no evidence that *L. gibba* has declined and its abundance in eutrophic water suggests that it is well-equipped to survive in the modern countryside.

L. gibba, is widespread in Europe, north to southern Scandinavia. Elsewhere it occurs in W. Asia, N., E. and S. Africa and N. and S. America, being most frequent in areas with a Mediterranean climate. Introduced to Japan. For a map of its world distribution, see Landolt (1986).

The most widespread free-floating macrophyte in the British Isles, found in a range of still, mesotrophic to eutrophic, open or shaded waters including ditches, ponds, canals and lakes. In southern England it is often mixed with *Azolla filiculoides*, *Lemna gibba*, *L. minuta* or *Spirodela polyrhiza*; outside the range of these species it is usually found as pure stands. Smaller waters can become covered by a continuous carpet of duckweed, which not only cuts down the light intensity in the water below but reduces the oxygen content, thus retarding aerobic decomposition and leading to an increase in organic matter and hydrogen sulphide. Most submersed macrophytes cannot survive in such conditions, but a few species such as *Ceratophyllum demersum* and *Elodea nuttallii* are sometimes found under *Lemna* swards. In streams and rivers populations of *L. minor* build up where the water flow is impeded, eg in quiet backwaters, in stands of emergents or between moored boats. Small populations can be found in terrestrial habitats such as damp mud in swamps or by lakes, or even on the damp rock faces of cliffs and cuttings. It is usually found in the lowlands, but reaching 500 m on Brown Clee Hill.

Reproduction is primarily by vegetative budding. Flowering is initiated by long days. Landolt (1986) described the species as flowering occasionally on the basis of observations made throughout its range, but in the British Isles flowering is infrequent. Landolt suggests that fruit set is low, perhaps indicating self-incompatibility. Like *L. gibba*, *L. minor* survives the winter as resting fronds which float on the surface of the water or as living buds in the pouches of dead, sunken fronds.

L. minor is frequent in the lowlands of Britain and Ireland. Only in areas where oligotrophic waters predominate does it become more local, being restricted to lakes, streams or ponds near the sea. There is no evidence that its distribution is changing.

This species is widespread in Europe, north to 66°N. Elsewhere it is recorded from W. Asia, Himalaya, N. America and N., E. and S. Africa, being most frequent in areas of cooler climate. It is probably introduced to the oceanic islands of Ascension and St Helena and almost certainly introduced to Australasia, where it is local in Australia but frequent in New Zealand. For a map of its world distribution, see Landolt (1986).

Although apparently innocuous, *L. minor* has rather surprisingly become a children's bogey in those parts of north-west England where there are numerous marl-pits. The green carpet of duckweed, known as Jenny Greenteeth, is said to drag venturesome children down into the depths of the water, closing over them to hide all traces of their presence (Vickery 1983).

A species of still or slowly-flowing water in lowland ponds, lakes, ditches, canals and in the backwaters of rivers. It is perhaps most abundant in clear, mesotrophic water but extends into eutrophic water and is sometimes found in brackish ditches near the sea. It is found over a range of substrates from peat to clay. Although often found beneath a thin layer of *L. minor* and other congeners, or of *Hydrocharis morsus-ranae*, it cannot survive when the surface of the water supports a dense mass of floating *Lemna*. *L. minor* has a competitive advantage over *L. trisulca* in both eutrophic sites and in shaded ponds and ditches. However, *L. trisulca* dominates where nutrient levels are lower, presumably because its thin, submersed fronds are more efficient at nutrient uptake (McIlraith, Robinson & Shay 1989). *L. trisulca* is also found in lakes which are so large that a continuous cover of floating *Lemna* cannot establish because of wind and wave action.

Reproduction of *L. trisulca* is almost entirely by vegetative growth. Plants flower only rarely in the British Isles, and also less frequently than *L. gibba* or *L. minor* elsewhere in the range of the species. The flowering fronds float on the surface of the water; they are shorter than the vegetative fronds, have more air spaces and possess stomata. Perennation through the winter is by resting fronds, which sink to the bottom of the water. They are morphologically similar to normal fronds.

L. trisulca is still frequent in lowland England. There is no evidence that its distribution is changing.

L. trisulca is widespread in Europe north to 68°, but rare in the Mediterranean area. It is a circumboreal species, found throughout the temperate northern hemisphere and in E. Africa, S.E. Asia and Australia.

Like other floating Lemnaceae, *L. minuta* is a plant of still or slowly flowing waters. It occurs in lowland ditches, ponds, canals, streams and rivers; more rarely it has been found in flooded peat diggings and lakes. It is usually associated with *L. gibba* and/or *L. minor*, and sometimes with *Azolla filiculoides*, *Riccia fluitans* and *Spirodela polyrhiza*. On occasion *L. minuta* can be much more abundant than any competitor, forming dense stands completely covering the water surface. Leslie & Walters (1983) found that *L. minor* eventually overgrows *L. gibba*, *L. minor* and *Spirodela* when cultivated in pans containing a mixture of the four species.

Reproduction is by vegetative budding. Green fronds tend to persist throughout the winter, although in very much smaller quantity than in the summer months. Flowering has not been observed in Britain, although a small proportion of the fronds in a population in the South of France flowers and fruit during the winter months (Jovet & Jovet-Ast 1967).

L. minuta is an introduced species, first recorded in Britain in 1977 when it was detected in Cambridge by Professor E. Landolt (Landolt 1979). By 1981 there were records from 17 10-km squares in 10 vice-counties in south-east England, plus an outlying site in N. Wales (Leslie & Walters 1983). In subsequent years it was recorded from many more localities, particularly from 1989 onwards when it attained considerable abundance in some areas including Cambridge (Preston 1991) and Kent (Philp 1992). Its abundance in canals attracted particular attention (Smith 1990, Last 1990, Oliver 1991, Briggs 1992). It is almost certainly under-recorded, because of its recent spread and its similarity to *L. minor*. The origin of the British populations is not certain, but they may have been introduced by aquarists releasing the contents of their aquaria into the wild.

A native of temperate N. and S. America. It was first recorded in Europe in France in 1965 (Jovet & Jovet-Ast 1966), and subsequently found in Germany (1966), Switzerland (1975), Great Britain (1977), Belgium (1983), European U.S.S.R. [presumably Russia - check] (1983), Hungary (1984), Greece (1988) and The Netherlands (1988). It is also known as an introduction in Japan.

148/3 *Wolffia* Horkel ex Schleiden

A genus of 9 species, which (unlike *Lemna* and *Spirodela* spp.) lack roots. *W. arrhiza* is the smallest flowering plant known.

A plant of shallow, base-rich water in lowland ditches and ponds, usually growing with other Lemnaceae including *L. gibba*, *L. minor* and *Spirodela polyrhiza*. It has also been recorded from lakes and gravel-pits. When *Wolffia* is abundant it forms distinctive pea-green patches, but it is much less easily seen when it grows as scattered plants amongst a *Lemna* sward. *Wolffia* is favoured by warm summers and mild winters; Landolt (1986) also considers that it is at a competitive advantage where the nutrient supply is liable to become temporarily depleted, as it can grow quickly and form turions when nutrient concentrations are low. Both fronds and turions are intolerant of low temperatures and of desiccation.

Reproduction in England and Wales is by vegetative budding; flowering plants have never been observed here although plants occasionally flower in other parts of their range. *Wolffia* perennates by resting fronds which sink to the bottom of the water, and by very small, spherical turions with a high starch content.

W. arrhiza was not recognised in Britain until 1866, when it was found in a pond by the R. Thames on Staines Common (Trimen 1866). It is locally frequent on Somerset Levels and in the marshes near Winchelsea and Rye, but it has disappeared from its localities in the London area. It was last seen in Middlesex in 1940, in Surrey in 1957 and in Essex in 1968.

W. arrhiza is widespread in Europe but rare almost everywhere, and known to be declining. It is native to the Old World: Asia east to the Caspian Sea, Africa from the Mediterranean to the Cape, Madagascar. It is probably introduced to Brazil (where it has been known from the Rio de Janeiro since 1872) and has recently been reported as an established alien in California (Armstrong 1989). Its world distribution is mapped by Landolt (1986).

150. ERIOCAULACEAE

A family of 13 genera and 1200 species, many of which are aquatics.

150/1. *Eriocaulon* L.

A genus of c. 300 species, most of them plants of marshes, swamps and seasonally inundated habitats in tropical and warm temperate areas. There are c. 8 species in N. America and a single species occurs as a native in Europe.

E. aquaticum grows as small clumps or extensive mats in shallow water, or terrestrially on damp and periodically flooded ground above the normal water level. It is confined to oligotrophic lakes, and is much more frequent in smaller lakes and pools than in large water bodies. It can sometimes be found in peat cuttings. *Lobelia dortmanna* is almost invariably found with it; other frequent associates include the aquatic form of *Juncus bulbosus*, *Littorella uniflora* and *Ranunculus flammula*, and scattered stems of emergents such as *Carex lasiocarpa*, *C. rostrata* or *Phragmites australis*. *E. aquaticum* never extends far above the water line (often being replaced at higher levels by *Littorella uniflora*) and descends to depths of at least 2 m. It grows over a range of substrates including peat, fine gravel, sand and silt. Although it is usually found in sites where both the substrate and water are acidic, it can occur in slightly alkaline water over acidic substrates (Webb & Scannell, 1983). It is a lowland species, ascending to 300 m in Co. Cork (ref?).

E. aquaticum flowers from August onwards. Plants can flower in water at least 1 m deep, as the stems elongate to carry the flowers above the surface. The flowers are structurally complex and are likely to be insect pollinated or autogamous (Cook, 1988). Little is known about the pollination of plants in Britain or Ireland, nor is it known whether or not they set viable seed. The species probably spreads vegetatively within lakes in which it occurs. Large clumps or single plants of *Eriocaulon* are often found washed up at the edge of the water, and it seems likely that the former, at least, could become established as new colonies.

The distinctive rosettes of *E. aquaticum* are unmistakable, even when they are not in flower. Although it has long been known from Ireland, Coll and Skye, the species was only discovered on the Scottish mainland in 1967 (McClintock, 1968; Ferguson & Ferguson, 1971). Further colonies might possibly await discovery in western Scotland. Scottish populations have been surveyed in detail in recent years (e.g. Farrell, 1983). The species grows in remote localities in both Britain and Ireland and its habitats do not appear to be threatened.

E. aquaticum is an amphi-atlantic species, which is widespread in N. America [add details] but in Europe is confined to Britain and Ireland. It is a member of the small but much-discussed North American element in our flora. Its world distribution is mapped by Hultén (1958).

Within the areas in which it occurs *Eriocaulon* is frequent, but it is absent from much apparently suitable habitat both in Ireland (cf Scully, 1916) and, more particularly, in Scotland. It seems most unlikely that any explanation based solely on current ecological factors could explain this very restricted distribution. *E. aquaticum* must be either a relict species, confined to areas from which it is unable to spread, or a recent colonist. A single grain of *Eriocaulon* pollen from Hoxnian interglacial deposits in Ireland has been tentatively referred to this species (Jessen *et al.*, 1959) and pollen from a postglacial deposit in Connemara has been identified as *E. aquaticum* without qualification. There is therefore no doubt that *E. aquaticum* is a long-established member of the Irish flora (Godwin, 1975; Perring, 1963). Its history in Scotland is less certain. Heslop-Harrison (1953) suggested the possibility that plants might have arrived by long-distance dispersal of seed, and Farmer & Spence (1986) refer to it as 'an historically recent arrival to Scottish freshwaters'. If so it is curious that a species which could arrive by long distance transport has failed to colonise new

localities in Britain, for (pace Farmer & Spence, 1986) there is no evidence that *Eriocaulon* is spreading. A comparative study of the reproductive biology of the American, Irish and Scottish populations would be instructive. The cytology of the species also requires further investigation. Löve & Löve (1958) report that European plants [origin?] with $2n=64$ differ from American plants ($2n=32$) in chromosome number, and fossil and recent pollen from Ireland is larger than recent pollen from America (Perring, 1963). If all American populations differ from those in Europe, the possibility of recent long-distance dispersal would be ruled out.

151. JUNCACEAE.

There are over 300 species in the Juncaceae, most of which belong to the two largest genera *Juncus* and *Luzula*. There are also six small genera. The family is well represented in the temperate and cold regions of both northern and southern hemispheres. Two genera contain aquatic species. One of these, *Juncus*, is found in our area. The other is the monotypic genus *Prionium*, an aloe-like pachycaul shrub which grows in mountain streams in S. Africa. It is the only shrub in the family; all the other species are annual or perennial herbs.

151/1. *Juncus* L.

This is a genus of 255 species, of which 24 are found as natives in the British Isles. Many of these grow in permanently damp or seasonally flooded habitats. One species, *J. bulbosus*, may be found as an aquatic. Some authorities recognise two species within the *J. bulbosus* complex, *J. bulbosus sensu stricto* and *J. kochii*. D.E. Allen and P.M. Benoit regard these as distinct species which are 'readily recognisable over a large area of Europe'. They consider that *J. bulbosus* is the commoner species in lowland England, whereas *J. kochii* is more frequent in the mountainous districts of the north and west. Where the two species grow together, they remain distinct. Both species may be found as a modified, aquatic variant. They rarely hybridise in the wild, although hybrids can be synthesized in cultivation (Allen, 1984; Benoit & Allen, 1968; Benoit, 1954). A. Eddy also regards the two species as distinct, but considers that *J. bulbosus* is a rare arctic-alpine, which is replaced over most of our area by *J. kochii* (Department of Botany, British Museum (Natural History), 1970; Jermy & Crabbe, 1978). Other authors, notably Stace (1991), consider that 'plants known as *J. kochii* have been separated in different ways using various characters that are not correlated' and therefore recognise a single species, *J. bulbosus*. Few species in our flora are the subject of such radically different opinions. We have followed Stace (1991) in recognising a single species, if only because there are insufficient records of the segregates for us to produce adequate accounts of them.

This variable species grows as a terrestrial plant or as an aquatic. It is frequent and locally abundant in terrestrial habitats such as base-poor heaths and bogs, often in areas subject to some disturbance (Grime, Hodgson & Hunt, 1988). As an aquatic it grows in base-poor, clear or peaty waters in lakes, reservoirs, rivers and streams, extending from the shallows to depths of at least 2 metres. It may be found in the most oligotrophic and species-poor lakes, often growing with *Callitriche hamulata*, *Myriophyllum alterniflorum* and *Utricularia vulgaris sensu lato*, or in peaty pools with *Utricularia minor* and *Sphagnum auriculatum*. It may also grow amongst open stands of emergents such as *Equisetum fluviatile* and *Schoenoplectus lacustris*. It is found over a wide range of organic and mineral substrates (Spence, 1964). In some water bodies it can occur in dense masses, sometimes virtually excluding all competitors. It may occasionally be found in highly calcareous but nutrient-poor waters, as in the Burren (Webb & Scannell, 1983). It occurs from sea-level to at least 960 m in Caenlochan Glen.

J. bulbosus is a winter-green perennial. In terrestrial habitats it flowers and fruits freely, and it may, like other *Juncus* species, have a persistent seed bank. Semi-aquatic plants often have proliferous inflorescences (Grime, Hodgson & Hunt, 1988). The aquatic forms are usually vegetative, but sometimes produce buds which fail to develop into flowers. They root freely at the nodes and presumably become established from detached fragments. In a detailed study at Hodson's Tarn, Macan (1977) found that the aquatic plant varied greatly in abundance from year to year.

In Europe *J. bulbosus* extends from Iceland and N.W. Norway to Spain, Italy and the Balkans, although it is most frequent in the west and rare in the Mediterranean area and the south-east. It is also found in N. Africa, Newfoundland and (as an introduction) in New Zealand.

J. bulbosus is a common plant in northern and western Britain and Ireland. In S. England it is still frequent in areas where there is much acidic soil, but has declined in those regions where such sites are few and far between. It has, for example, become very rare in Bedfordshire (Dony, 1976) and Cambridgeshire (Perring *et al.*, 1964), and in Gloucestershire outwith the Forest of Dean (Holland, 1986), but it remains common in Surrey (Lousley, 1976). The aquatic variants have not usually been recorded separately, although they now tend to be distinguished in lake surveys. The aquatic plant has increased in abundance in The Netherlands and Scandinavia in recent years, apparently a result of the acidification of lakes by atmospheric pollutants (Svendång, 1990). The increase in *Juncus bulbosus* and *Sphagnum cuspidatum* in response to the addition of ammonium sulphate, which creates more acidic and more eutrophic conditions, has been demonstrated in greenhouse experiments (Schuurkes *et al.*, 1987).

The terrestrial variant of *J. bulbosus* is a small, neat, densely tufted plant, whereas the most extreme aquatic variant has long, trailing stems and 'tresses of numerous long hair-like leaves' (West, 1905). Intermediate forms grow in habitats in sites where the water is shallow or fluctuating, such as in peat cuttings, ditches or at the edge of lakes and reservoirs. Plants may change from the terrestrial to the aquatic form or *vice versa* in response to changes in water level, and it is therefore inappropriate to give the two variants taxonomic recognition.

152. CYPERACEAE

This large family of 110 genera and 4300 species is dominated by two genera, the predominantly temperate *Carex* (2000 species) and the predominantly tropical *Cyperus* (600 species). Most of the species are perennial herbs, the remainder being annuals, shrubs or lianes. Cook (1990) lists 31 genera with aquatic representatives, some which contain very important emergent species. Most members of the family have small, wind-pollinated flowers. The plants are usually monoecious, although there are some dioecious species.

Mabberley (1987) recognises three subfamilies in the Cyperaceae, all of which are represented in our area. The Cyperoideae includes *Cyperus* itself, *Eleocharis* and *Scirpus* and allied genera; Rhynchosporoideae includes *Cladium*, *Rhynchospora* and *Schoenus* and the Caricoideae includes *Carex* and *Kobresia*. The generic limits in the Cyperoideae are controversial, and the definition of *Scirpus*, in particular, varies from author to author. Koyama (1958) proposed a very broad definition of *Scirpus* which even included *Blysmus* and *Eriophorum*. Dandy (1959) recognised *Blysmus* and *Eriophorum* as distinct, but nevertheless defined *Scirpus* relatively broadly to include 12 species in our area. The classification adopted by *Flora Europaea* (Tutin *et al.*, 1980) and Mabberley (1987) was similar, but Stace (1991) and Kent (1992) include the same 12 species in 7 genera: *Bolboschoenus* (1 species), *Eleogiton* (1), *Isolepis* (2), *Schoenoplectus* (4), *Scirpoides* (1), *Scirpus* (1) and *Trichophorum* (2).

152/3. *Eleocharis* R. Br.

This cosmopolitan genus includes some 150 species. The stems are green and constitute the main photosynthetic organs; the leaves are usually reduced to sheaths. The flowers are bisexual and are clustered in a solitary spikelet at the apex of the stems.

There are 7 species in our area. Two are treated as aquatics in this book. The remaining species are also found in fens, marshes, wet heaths, flushes and other damp habitats. *E. multicaulis* is often found in shallow water at the edge of oligotrophic lakes and pools, but usually in seasonally flooded habitats rather than permanent water.

The *Eleocharis palustris* group of species (which in our area includes *E. palustris* and *E. uniglumis*) is taxonomically complex because of the occurrence of polyploidy and hybridisation. Much of the information in the following accounts of *E. palustris* and its subspecies is taken from Walters (1949) and Strandhede (1966). The nomenclature of the subspecies used here is that of Strandhede (1960), Clapham *et al.* (1962), Tutin *et al.* (1980), Stace (1991) and Kent (1992). *E. palustris* subsp. *palustris* was formerly known as subsp. *microcarpa* Walters. Some authors (e.g. Clapham *et al.*, 1952) have applied the name *E. palustris* subsp. *palustris* to the plant referred to here as subsp. *vulgaris*.

Emergent plants of *E. palustris* are found at the edge of lakes, pools, ditches and slowly flowing rivers and streams, where they may be found in dense stands in water up to 0.5 m deep. On the sandy or gravelly shores of exposed lakes it may be the only emergent; in these sites it is often accompanied by *Littorella uniflora*. It tolerates fluctuations in water level and it is often an abundant species in dune slacks, and in some inland ponds, although although it is sometimes absent from ponds subject to great variations in water level (Grime *et al.*, 1988). *E. palustris* may also grow as a more or less terrestrial plant in fens and moist or seasonally flooded meadows and pastures where taller competitors are eliminated by cutting, grazing or trampling. It is found over a wide range of organic and mineral soils, in both acidic and basic habitats, but it is most frequent in moderately fertile and at least slightly basic habitats, and rarely grows on acidic peat. It also tolerates slightly saline conditions in coastal grazing marshes. It is recorded from sea level to 480 m at Low Tarn (Stokoe, 1983).

E. palustris is a perennial with thick rhizomes. In flooded sites plants often spread rapidly by the growth of the rhizomes, but the rhizomes are less well developed or absent in drier habitats. The flowers are protogynous and wind-pollinated. Seed set is usually good, although the inflorescence is often infected by the ergot *Claviceps nigricans* (CHK name). Freshly sown seed may remain dormant for several months then germinate simultaneously (Walters, 1949). The seeds of *Eleocharis* spp. are eaten, and perhaps dispersed, by birds (Ridley, 1930). Seedlings are rarely seen in the wild, but the species is an effective colonist of new sites which it presumably reaches by bird-borne seed.

Godwin (1975) suggests that *E. palustris* has been continually present in our area since the middle of the Pleistocene. It is still frequent in suitable habitats in Britain and Ireland, and even in the London area it has been lost only from the most heavily built-up areas (Kent, 1975; Burton, 1983). However, detailed recording in Essex suggests that it has decreased in frequency in recent years (Tarpey & Heath, 1990) and this may also be true for other areas of high population and intensive agriculture.

Plants referable to the *Eleocharis palustris* complex are very widespread, being found in boreal and temperate regions throughout the northern hemisphere, and (sometimes as introductions) at scattered sites in the southern hemisphere too. The distribution of *E. palustris sensu stricto* is obscured by taxonomic confusion, but its native distribution is centered on Eurasia, where it is widespread, and it is apparently absent from N. America (Strandhede, 1967).

E. palustris shows great phenotypic variation, especially in height. Two cytologically distinct subspecies are dealt with in the following accounts.

Ridley cites D.C. Marrott, USA Dept Agric Bull 862, 1920 on dispersal.

Eleocharis palustris subsp. *vulgaris*

This is much more frequent in our area than subsp. *palustris*, and the description of the ecology of the species is also applicable to subsp. *vulgaris*.

Subsp. *vulgaris* is self-compatible. Normal plants may produce some aneuploid pollen grains, and some individuals are cytologically abnormal (Lewis & John, 1961).

The two subspecies of *E. palustris* were first recognised by Walters (1949). However, few botanists bother to identify them, and both are under-recorded. Subsp. *vulgaris* is known to be the commoner plant, and it probably occurs throughout the British and Irish range of the species.

In Europe subsp. *vulgaris* has a more restricted distribution than subsp. *palustris*. It is widespread in N., W. & central Europe, but only extends north to S. Scandinavia (Strandhede, 1961), and is rare or absent from much of S. Europe, including the Mediterranean area.

E. palustris subsp. *vulgaris* is variable cytologically and although $2n=38$ is the usual chromosome number, other numbers are not uncommon. Strandhede (1965) has suggested that it evolved from a hybrid between subsp. *palustris* ($2n=16$) and *E. uniglumis* ($2n=46$). A hybrid resulting from the fusion of an unreduced gamete of subsp. *palustris* with a reduced gamete of *E. uniglumis* would have a chromosome number of $2n=39$. Fertile intermediates between subsp. *vulgaris* and *E. uniglumis*, with $2n=c.42$, occur in our area and are particularly frequent in coastal regions of Scotland. They are also known from other parts of N.W. Europe, and similar plants have been synthesised experimentally by Strandhede (1966). The presence of subsp. *vulgaris* and such intermediates means that the distinction between *E. palustris* and *E. uniglumis* is less clear in W. Europe than elsewhere.

Eleocharis palustris subsp. *palustris* Walters

There is apparently no ecological distinction between subsp. *palustris* and subsp. *vulgaris*, and the two taxa may grow together. Subsp. *palustris* is recorded from the edges of rivers, lakes and ponds and from damp meadows, all typical habitats for *E. palustris* in S. England. All records are from lowland sites.

This subspecies is self-incompatible. Normal plants of subsp. *palustris*, like those of subsp. *vulgaris*, may produce some aneuploid pollen grains, and some individuals are cytologically abnormal (Lewis & John, 1961).

Although the subspecies of *E. palustris* are very under-recorded, subsp. *palustris* is known to be much rarer than subsp. *vulgaris*. Most of the records mapped here were collated by S.M. Walters for the map published by Perring & Sell (1968); there have been very few reports of this taxon since then. A survey of its distribution is required to establish whether it is still present at those sites where it is only known from old herbarium specimens, or from records made in the 1950s.

E. palustris subsp. *palustris* is widespread and frequent in Europe, extending from northern Scandinavia to the Mediterranean region. Its very restricted distribution in the British Isles is surprising in view of its wide continental range. The two subspecies are apparently less easy to distinguish in central Europe and S.W. Asia than in our area, perhaps because of the presence of other, hitherto unrecognised taxa.

Subsp. *palustris* differs from subsp. *vulgaris* in morphological characters and in its chromosome number. Fertile hybrids between subsp. *palustris* ($2n=16$) and subsp. *vulgaris* ($2n=38$) have been found with both parents in Port Meadow. They have a chromosome number of $2n=27$, and grow with other plants which may be backcrosses (Lewis & John, 1961). Experimental studies have shown that female flowers of subsp. *palustris* pollinated by subsp. *vulgaris* have almost normal seed set, and the resulting hybrids are fertile (Strandhede, 1966).

E. acicularis usually grows submerged in shallow water or on damp ground exposed by falling water levels. As a submerged plant it is usually found in mesotrophic or eutrophic, mildly acidic to strongly base-rich water less than 0.5 m deep. Typical habitats include sheltered lakes and reservoirs, the still backwaters of rivers, slow-flowing streams, canals, fenland lodes and ditches and flooded sand and gravel pits. At the edges of such water bodies it grows on damp silt, and or sandy shingle in areas which are flooded in winter but exposed in summer, and it can also occur on mud dredged out of ditches. Both aquatic and terrestrial plants may grow in pure stands, but in the water a wide range of other aquatics are recorded as associates. On land it is often mixed with *Chenopodium rubrum*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Persicaria* spp. and *Rorippa palustris*, most of which are frequently found as dwarf individuals in this habitat. *E. acicularis* is a predominantly lowland species, ascending to 365 m at Loch Kinardochoy.

E. acicularis is a perennial with very slender stems and shallowly rooted rhizomes. Submerged plants may become quite tall in the clear calcareous waters of canals and fenland lodes. They spread by growth of the rhizome, or grow through silt deposited over them, but never flower. In some sites the stems may remain green through the winter. Short lengths of rhizome with attached stems are often washed out of the substrate and doubtless become established in new localities. Plants in terrestrial habitats are much shorter than many aquatic forms, but flower and fruit freely. The seeds have been found on mud on the feet of birds, and may be dispersed in this way (Kerner, 1894). Seeds will germinate readily under water with or without a cold treatment, but germination on moist substrates is stimulated by a cold pretreatment (Rothrock & Wagner, 1975). Germination is rapid and all the seeds which germinate have usually done so in 7 days. The species may vary greatly in abundance from year to year, both in aquatic and terrestrial habitats.

This species is often overlooked, especially when growing as an aquatic, and it may be under-recorded. However, the map suggests that it has declined in England. It has been lost from canals which have dried out, and from small ponds which have been filled in, drained or allowed to become overgrown. However, the species has colonised recently flooded sand and gravel pits, where it may sometimes be found in abundance.

E. acicularis is widespread in Europe, although absent from the far north and rare in the Mediterranean area. It also occurs in N. Africa, Asia and N. & S. America.

In the Appalachian Mountains of N. America this species is often exceptionally abundant in shallow, very acidic streams polluted by drainage from coal mines, where it may occur in water with a pH as low as 2.9 (Ehrle, 1960; Rothrock & Wagner, 1975). No other aquatics and few animals are able to survive in such acidic waters. There do not appear to be any records of *E. acicularis* from very acidic sites in Britain or Ireland.

152/4.

Bolboschoenus (Asch.) Palla

This segregate of *Scirpus* includes some 12 species. These are rhizomatous perennials with aerial leaves and relatively large spikelets and fruits. They are often plants of saline habitats in coastal areas or inland deserts. Only *B. maritimus* is found in Europe.

B. maritimus is an emergent which usually grows in dense, almost pure stands on saline ground or in shallow, brackish water. Typical habitats in the coastal zone include the edges of lakes, ponds, borrow pits, tidal rivers, ditches, creeks and pools, upper salt marshes and damp pastures. Its sites range from those which are damp and occasionally flooded to those where there is permanent water up to 0.5 m deep. It tolerates fluctuating water levels and occasional total submergence, but is rarely found in constantly flowing water (Rodwell, 1995). It is usually found over mud (which may be black and very anaerobic) but it may grow at the edges of rock pools and over gravel and shingle. It has a similar tolerance of salinity to that of *Schoenoplectus tabernaemontani* (Ranwell *et al.*, 1964), and the two species are often found by the same water body, with *B. maritimus* growing in a zone nearer the water. In inland sites it has been recorded from pools near saline springs (Lee, 1977) and was recently found in quantity in a lagoon which receives saline drainage from the M23 motorway. However, it also grows inland in a range of fresh water habitats including the edges of lakes, reservoirs, ponds, rivers and grazing marsh ditches, and in flooded clay and gravel pits. It is confined to the lowlands.

B. maritimus is a rhizomatous perennial which dies down during the winter. It reproduces by direct growth of the rhizome and by tubers which are produced on the end of stolons. The flowers are bisexual, protogynous and wind pollinated. They are also visited regularly by syrphid flies which feed on the pollen, but there is no evidence that these are effective pollinators (Leereveld *et al.*, 1981). The roots, tubers and fruits are eaten by wildfowl, especially geese (Cramp *et al.*, 1977). The fruits float, and may be carried upstream as well as downstream in tidal rivers (Ridley, 1930). Kerner (1894) also found the fruits in the mud on birds' feet.

This species is usually abundant in suitable coastal habitats, and is able to colonise newly available habitats. Its distribution in inland sites is rather sporadic. Some colonies are extensive and long-established, notably those in the Somerset Levels (Roe, 1981) and by the River Stour in Dorset, where it was first recorded by Pulteney (1799-look up). At other sites, including recently abandoned clay and gravel pits, it must be a recent arrival and has presumably been dispersed by birds. However, some inland populations have failed to persist. *B. maritimus* is sometimes planted by lakes and ponds.

B. maritimus is widespread in Europe, where it occurs from the Mediterranean region north to central Scandinavia; it has a predominantly coastal distribution in the northern and western part of its range. It extends eastwards to central Asia and is widespread in Africa. It also grows in Australia, New Zealand and (as an occasional introduction) in N. & S. America. Closely related taxa are found in E. Asia and N. & S. America.

This genus of c. 40 species has a cosmopolitan distribution. Most species are aquatic perennials, with tall emergent stems, but the genus also includes some annuals. Aerial leaves are more or less absent but narrow, translucent submerged leaves may be present in some species. The wind-pollinated inflorescence, composed of bisexual flowers, is borne at the apex of the stem, but it appears to be lateral as the lowest bract continues the line of the stem and overtops the inflorescence.

There are four native species in our area, the widespread *S. lacustris* and *S. tabernaemontani*, and the rare species *S. triquetrus* and *S. pungens*. Typical *S. lacustris* differs from *S. tabernaemontani* in its ability to develop submerged leaves, its taller, green rather than glaucous stems, and in a number of floral characters. In some areas (e.g. Donegal) these two species can be identified without difficulty. However, in some other areas plants which apparently combine the characters of both species are not uncommon. Intermediate plants from Cambridgeshire are illustrated by Easy (1990). These intermediates are not given formal taxonomic recognition by Stace (1991) or Kent (1992). Fertile intermediates are also found in The Netherlands, and Bakker (1954) concluded that the boundaries between *S. lacustris* and *S. tabernaemontani* had been obliterated in some localities by introgressive hybridisation. He suggested that *S. tabernaemontani* should be regarded as a subspecies of *S. lacustris*, a treatment followed by Tutin *et al.* (1980). *S. triquetrus* shares the same chromosome number as *S. lacustris* and *S. tabernaemontani* ($2n=42$) and hybridises with both of them. *S. pungens* has a different chromosome number, $2n=78$, and [add details of hybrids from Otzen] (Otzen, 1962).

S. lacustris is found in deeper water than any other emergent in our area. It is most frequent in lakes and slow-flowing rivers, but it is also found in pits, ponds, canals, large ditches and flooded gravel pits. It usually grows at depths of 0.3-1.5 m, and it is often accompanied by aquatics such as *Juncus bulbosus*, *Littorella uniflora*, *Nymphaea alba* or *Potamogeton natans*. In lakes *S. lacustris* may be separated from the shore by clear water, and in rivers it may grow across the full width of the channel, or form isolated 'islands' in the centre and dense bands along the edge. It tolerates a wide range of nutrient states, growing in both eutrophic and base-rich sites and in oligotrophic and base-poor lakes, and it can be found over both fine silts and clays, peat or coarse gravel. *S. lacustris* is grazed in those sites where it is accessible to stock, and it is also eaten by waterfowl, especially geese (Sinker *et al.*, 1985). It is primarily a lowland species, but reaches 400 m at Dock Tarn (Stokoe, 1983).

This is a perennial with a robust rhizome. Submerged leaves develop in clear, standing or flowing water, and in streams and rivers these leaves may predominate. The emergent stems vary in vigour, and may be very slender in clumps which are exposed by falling water levels, as in the Breckland meres (Coombe *et al.*, 1981). Most colonies spread vegetatively, and they may grow by 1-2 m a year in favourable circumstances (Rodwell, 1995). Plants flower and fruit freely, and the seeds are probably dispersed on the mud on birds' feet (Ridley, 1930). Little is known of the circumstances under which the seeds germinate.

S. lacustris has a very long fossil history in our area, where it certainly persisted through the last glacial period (Godwin, 1975). Although there appears to be no evidence for a decline in some areas, in others the species is certainly less abundant than it once was. **Add data on decline in Broadland from George (1992, pp.169-177).** It has also decreased greatly in Shropshire in recent years, perhaps because of the increasing grazing pressure from Canada Geese (Sinker *et al.*, 1985) and it is also regarded as a declining species in Surrey (Lousley, 1975) and S.E. Yorkshire (Crackles, 1990).

S. lacustris is widespread in Europe and N. Africa, extending eastwards to central Asia. In Europe it is found from the Mediterranean to northern Scandinavia, but it is absent from Iceland. It is replaced by *S. acutus* Muhl. in N. America.

This is apparently the true 'bulrush', and it has been suggested that the name was transferred to *Typha* because the latter is prominent in Sir Laurence Alma-Tadema's famous painting 'The Finding of Moses?', first exhibited in 18???. Nowadays 'bulrush' always means *Typha* to the non-botanist, although the name still survives for *Schoenoplectus* in some botanical books. *S. lacustris* was formerly used to stuff saddles, horse collars and mattresses, and to caulk casks, and is still used to make baskets, 'rush' mats and chair seats. The dialect name 'bumble' or 'dumble' has a long-recorded history in Lincolnshire and Yorkshire, and chairs with rush seats were said to have a 'bumble bottom' (Crackles, 1974, 1983).

This species is most frequent in coastal sites, where it grows in shallow, brackish water at the edge of lakes, lagoons, rivers, streams, ditches and borrow pits. It is also found in small depressions in salt marshes, where it may grow through an open mat of *Agrostis stolonifera* (Adam, 1981; Rodwell, 1995). It is more tolerant of saline water than *Phragmites australis*, but (unlike *Spartina anglica*) it cannot grow in sea water and is often absent from the seaward end of salt marshes (Packham & Liddle, 1970; Ranwell *et al.*, 1964). It also grows in pools and ditches at inland salt marshes, and in brackish subsidence flashes associated with colliery or other mineral waste (Lavin & Wilmore, 1994; Lee, 1977). However, at most of its inland sites it grows in fresh water at the edge of lakes and slowly flowing rivers and associated oxbows, and in flooded quarries and sand, gravel, chalk and clay pits. In such localities it is often accompanied by *S. lacustris*. When the water table is low enough for cattle to reach *S. tabernaemontani*, it may be heavily grazed. It is confined to the lowlands.

S. tabernaemontani is a perennial which spreads by growth of the rhizome. It does not produce submerged leaves, and this (coupled with its short stature) is probably one reason why it is unable to grow in deep water or across the entire width of streams and rivers, habitats in which *S. lacustris* is often found. It flowers and fruits freely, but little is known of its reproductive biology.

Although the fossil record of this species is sparser than that of *S. lacustris*, it nevertheless shows that the species was present in our area in the late glacial period (Godwin, 1975). Adam (1981) and Rodwell (1995) have suggested that this species is under-recorded at coastal sites. There is no evidence for any change in its frequency in these habitats. Lousley (1931) regarded it as a very rare plant inland, and was able to cite only nine localities. It is now recorded inland with much greater frequency. The reasons for this apparent change are not entirely clear, but the species may have been overlooked as *S. lacustris* in the past, and it has also spread in recent years because of deliberate planting and natural colonisation of newly available habitats. It has appeared as a natural colonist of a recently flooded gravel pit in Jersey (Le Sueur, 1984) but it appears to be planted in some Cambridgeshire gravel pits (Easy, 1990) and in fresh waters in the London area (Burton, 1983).

S. tabernaemontani is widespread in temperate Eurasia, extending from W. Europe and N. Africa eastwards to Japan; it is also recorded from the Sahara and S. Africa. It is replaced by *S. validus* Vahl in N. America, and by closely related taxa in S. America, Australia and New Zealand (cf Hultén & Fries, 1986).

S. triqueter is an emergent which grows on the muddy edge of tidal rivers. Some stands by the River Thames were completely submerged at high tide, and their inflorescences became entangled in river-borne debris (Lousley, 1931). Associated species by the River Shannon listed by Praeger (1934) included *Alisma plantago-aquatica*, *Apium nodiflorum*, *Groenlandia densa*, *Persicaria maculata* and *S. tabernaemontani*.

This is a rhizomatous perennial. The reproductive biology of the British and Irish plants has not been studied.

S. triqueter is extinct at two of its four British sites. It was first discovered in 1650 by the River Thames near the horse-ferry, at Westminster (Kent, 1975) and it formerly grew along a ?? km stretch of river from Limehouse to Kew. However, it was gradually eliminated as the muddy edges of the river were replaced by artificial embankments, and it was last seen in 1946. A major reconstruction of the river wall in 1946-47 destroyed the last mud bank on which it grew (Burton, 1983; Lousley, 1975). It has also disappeared from the banks of the River Arun, although the reasons are less obvious. It still survives by the River Medway, where it was once feared extinct, and by the River Tamar. It also persists at its sole Irish locality, the River Shannon near Limerick, where it was first recorded by R.D. O'Brien in 1900.

This species is found in central and S. Europe, N. & S. Africa (CHK Africa) and W. Asia. It is naturalised in N. America (Lightcap & Schuyler, 1984).

The hybrid between *S. triqueter* and *S. tabernaemontani* (*S.* × *kuekenthalianus*) is more frequent in our area than that between *S. triqueter* and *S. lacustris* (*S.* × *carinatus*), probably because the salt-tolerant *S. tabernaemontani* is more likely to be found by the estuarine rivers where *S. triqueter* grows. *S.* × *kuekenthalianus* survives by the River Arun in the absence of *S. triqueter*. For further details of these hybrids, see Lousley (1931, 1975) and Perring & Sell (1968). Fertile hybrid swarms involving *S. tabernaemontani* and *S. triqueter* occur in The Netherlands (Bakker, 1968-CHK).

Any info on quantity of plants in current British & Irish sites?

This species was formerly known from the margins of a coastal lake in Jersey, and from a dune slack in Lancashire. In Lancashire it grew in the wettest part of the slack, associated with *Parnassia palustris*, *Pyrola rotundifolia*, *Salix repens* and *Schoenoplectus tabernaemontani*.

S. pungens is a rhizomatous perennial. Little is known of the reproductive biology of the British plants.

This species was first recorded from Jersey by W. Sherard (Ray, 1724). Lester-Garland (1903) described it as abundant at St Ouen's Pond, its only known locality there, and it was still plentiful in the 1940s and 1950s. However, it subsequently decreased in frequency and was last seen in the early 1970s. It appears to have been replaced by *Carex riparia*, which was first seen at this site in 1953 (le Sueur, 1984). *S. pungens* was collected near Formby by W.G. Travis in 1909 but not recognised until it was rediscovered by R.E. Baker in 1928 (Druce, 1929; Travis, 1929). In 1928 a large patch grew in a dune slack. Its origin is uncertain; Druce (1929) concluded that it was unlikely to have been planted as 'one can scarcely credit the most microcephalous sentimentalist endowing this *Scirpus* with sufficient beauty to think he was adding fresh charms to the floral displays of Lancashire'. By 1972 it was noted that the slack was much drier than formerly, and that the *S. pungens* shoots were much shorter, often chlorotic and also subject to rabbit grazing. The species became extinct at this site in c. 1980, but the Lancashire stock survived in cultivation and has been planted in other sites in the area.

S. pungens is found in W. and central Europe, extending north to The Netherlands and Germany and east to Italy. It is widespread in N. America and Australia (native in Oz?), and naturalised in New Zealand, where it is a troublesome weed which 'breaks up footpaths and gutter channels in built-up coastal areas' (Healy & Edgar, 1980).

152/9.

Eleogiton Link

This genus has a cosmopolitan distribution and includes 10 species. Most of the species grow as submerged macrophytes with long, trailing stems and emergent flowers. Each peduncle bears a single spikelet of bisexual flowers. Koyama (1958) considered that the floral characters of the genus suggested that it was allied to *Isolepis*, but the aquatic, predominantly perennial *Eleogiton* has a very different habit from *Isolepis*, which contains many annual, more or less terrestrial species. Only one species of *Eleogiton* is found in Europe.

This is a plant of shallow, acidic water or moist, terrestrial and often seasonally flooded habitats. It may grow in dense masses as an aquatic in ponds, small reservoirs or at the sheltered edge of lakes, and in moorland streams and ditches. Its other habitats include the backwaters of rivers, flushes flowing into lakes, moist, muddy hollows in grassland and wet heath, and the wet floors of disused quarries and sand or gravel pits. It is virtually confined to acidic and oligotrophic habitats, being particularly frequent in peaty areas but also growing over silt and sand. It is often associated with *Apium inundatum*, *Juncus bulbosus* and *Potamogeton polygonifolius*. [any more?] It is recorded from highly calcareous but nutrient-poor fen marl near Lough Fingall in the Burren (Webb & Scannell, 1983), but such records are exceptional even in western Ireland. It is recorded from sea level to 435 m at Llyn Gwngu, and 436 m at Styhead Tarn (Stokoe, 1983).

This is a perennial species which may remain green throughout the winter, at least when growing as an aquatic. It flowers freely, but little is known about its reproductive biology.

Like many calcifuges, *E. fluitans* was probably always rather local in the eastern part of its British range, where moist, acidic habitats are infrequent, but it has declined as acid heaths and moors have been drained and built over or taken into arable cultivation. The many counties in which it has decreased include Somerset (Roe, 1981), Shropshire (Sinker *et al.*, 1985), Essex (Jermyn, 1974) and Suffolk (Simpson, 1982), and it is believed extinct in others, including Durham (Graham, 1988), Northumberland (Swan, 1993) and Berwickshire (Braithwaite & Long, 1990). The map suggests that it has also declined in S.E. Ireland, but there are fewer local studies to substantiate this. It remains a frequent species at low altitudes in peat-covered areas in the north and west, where it may be somewhat under-recorded because of the similarity of vegetative plants to other monocots.

E. fluitans has a disjunct distribution. In mainland Europe it has a markedly oceanic range, extending from the Azores and the western part of the Iberian peninsula through France and the Low Countries to Denmark and S. Sweden; there are a few outlying localities east to Italy and the species is also found in N.W. Africa. It is also known from C. & S. Africa, India, S.E. Asia, Japan and Australia; it is a rare species in Asia. **Are African or Australian plants introduced?**

152/14. *Cladium* P. Browne

This is a genus with two species: the widespread and variable *C. mariscus* and the closely related *C. jamaicense*. The latter is found in southern N. & S. America, and is the main dominant of the Florida Everglades.

Detailed accounts of the autecology of *C. mariscus* have been published by Conway (1936a,b, 1937, 1938a,b) and summarised in a rather brief Biological Flora account (Conway, 1942). This work was based on the population at Wicken Fen, where the results of management experiments also provide an insight into the requirements of the species (Godwin, 1929, 1941; Godwin & Tansley, 1929). For descriptions of the vegetation in which this species grows, see Rodwell (1991, 1995). **Rowell?**

The most vigorous stands of this species grow as emergents in shallow water up to 0.4 m deep. Small stands or extensive, virtually pure swards grow at the edge of lakes and ponds, and in flooded hollows and disused peat cuttings. In peatlands where the soil is moist but only flooded in winter, if at all, the species grows in a more species-rich communities with associates such as **add them**. This vegetation is only maintained by cutting, which prevents the colonisation of shrubs. Cutting in early summer every 3-5 years favours *Cladium*, whereas more frequent cuts reduce its vigour and it cannot withstand annual mowing regimes. If its sites are overgrown the species will persist for many years in fen carr, but eventually dies out. In most parts of its British and Irish range *C. mariscus* is confined to calcareous and oligotrophic or mesotrophic habitats, where it usually grows over peat. In the Breckland it is a particularly characteristic species of the headwater fens, which are more nutrient-poor than the valley fens downstream (Haslam, 1965). It also grows in valleys draining the serpentine plateau in the Lizard peninsula and in extremely oceanic areas (e.g. Outer Hebrides, Coll, Connemara) it is found in acidic and oligotrophic sites. *C. mariscus* is an exclusively lowland species, only reaching 260 m at Sunbiggin Tarn.

C. mariscus is an evergreen perennial with a robust rhizome. The leaf meristems are below ground and the only aerial growing points are those on the flowering stems. The leaves grow for two seasons and then remain green for some months before withering. Their growth rate increases with temperature, being very low in the winter months; in summer it may also be limited by water stress if the water table falls below the surface. The dead leaves remain attached for some time and provide an important pathway for oxygen to diffuse into the rhizome. Plants flower throughout our area but often rather sparingly; the number of flowering stems varies from year to year and is greater in emergent than in terrestrial plants. Relict plants in fen carr often fail to flower. The spikelets contain both bisexual and male flowers and are wind-pollinated. The fruits may float for long periods (Praeger, 1913). Plants are known to fruit in East Anglia but Conway (1942) never saw seedlings, and was unable to get the seeds to germinate. The growing points are sensitive to temperatures below -2°C in winter and below 0°C in summer, but below-ground temperatures rarely fall to these levels at the East Anglian sites.

There is no unequivocal evidence that *C. mariscus* survived in our area during the last glacial period, although fossil remains are often abundant in later deposits (Godwin, 1975). In the eastern part of its range *C. mariscus* has declined in historic times because of the gradual drainage of lakes and fenland sites. It was the plant that gave Sedgemoor its name and it was still abundant there in the late 18th century, but it was feared extinct by 1896, although a few relict patches have since been discovered (Roe, 1981). In Cambridgeshire Babington (1860) described it as 'formerly far more abundant than at the present time throughout the Fens' and it has since been lost from some of the sites he knew. It has disappeared from some areas of Broadland because of eutrophication (George, 1992). It is also threatened by scrub encroachment at some sites, but vegetative plants hanging on in shaded sites will respond to scrub clearance (Fitter & Smith, 1979). *C. mariscus* only colonises newly available habitats in the vicinity of existing stands. Emergent plants in the north and west are easily overlooked, as they are often present as small clumps. The species was under-recorded in W. Scotland and some parts of W. Ireland by Perring & Walters (1962), and may still await discovery in new

squares.

C. mariscus is adapted to warm summers and mild winters. It is widespread in Europe, extending north to S. Sweden and Finland, but it is most frequent in the west and in the Mediterranean region. It also occurs in Africa from the Mediterranean coast to the Cape, S. Asia, Australia and eastern N. America.

This species was once so abundant that it was used as fuel in the Fens, although it was necessary to wear thick gloves when handling it to prevent the serrated leaf edges cutting the skin. It is still harvested for thatching, and is used particularly for the ridge of a roof.

This large genus of some 2000 species has a cosmopolitan distribution. *Carex*-dominated communities occur in wetlands in all climatic zones except the lowland tropics, and include low swards in the tundra, tall 'reedswamps' in temperate wetlands and tussocky vegetation on tropical mountains (Klötzli, 1988). There are 180 species in Europe, and 74 of these grow in the British Isles. Only 12 of these qualify as aquatics by our criteria, but many more are found in habitats such as bogs, fens, moors, wet heaths and flushes.

All *Carex* species are perennials with leafy stems and unisexual, protandrous and wind-pollinated flowers. However, there is considerable morphological diversity in the genus, and if the narrow generic limits now fashionable in the Cyperoidae were applied to the Caricoideae, the genus *Carex* would need to be dismembered (Sell & Murrell, in press). Fortunately, this butchery has not been attempted in our area in recent years. The three subgenera recognised in Britain and Ireland are described by Jermy *et al.* (1982). The only aquatic representative of Subgenus *Vignea* is *C. paniculata*. This has inflorescences composed of spikes which are similar in appearance; most contain both male and female flowers although the male flowers may be missing from some of the lower spikes. The remaining aquatic species belong to Subgenus *Carex*. They all have inflorescences with slender spikes made up of male flowers above more robust female spikes. Both these subgenera can usefully be divided into sections of closely related species. The third subgenus, *Primocarex*, contains a heterogeneous assortment of taxonomically anomalous, more or less terrestrial species.

The chromosomes of the Cyperaceae, like those of *Luzula* but unlike those of other plants, have a diffuse centromere rather than a single centromere at a particular position on each chromosome. As a consequence, the chromosomes are prone to fragmentation. The individual fragments may behave as whole chromosomes, and are inherited in a normal Mendelian manner, so plants with fragmented chromosome(s) are genetically stable. This phenomenon is known as agmatoploidy and, together with aneuploidy, has probably been an important process in the evolution of the species of *Carex* (Davies, 1956; Faulkner, 1972).

The taxonomy of the wetland sedges has recently been reviewed by Kukkonen & Toivonen (1988). Many species are widespread and variable, and are therefore subdivided into subspecies or varieties. The identification of some populations is made difficult by the fact that some species often fail to flower, or to set well-formed fruit, when growing in shade or when subjected to changes in water level. Such plants are often mistaken for hybrids. True hybrids do occur, however. At a world scale they tend to be more frequent in northern or montane areas, as the short growing season, open habitats and frequent occurrence of a mosaic of plant communities enhances the possibility of inter-specific pollinations. Vigorous hybrids which are able to spread vegetatively may also be at an advantage in these communities.

Kent (1992) lists 35 *Carex* hybrids from our area. Eight of these are hybrids between the aquatic species and a further ten have one aquatic and one terrestrial parent. The aquatic species are therefore responsible for a disproportionate number of the recorded hybrids. Seven of the 18 hybrids with an aquatic parent involve a member of the critical *C. nigra* group, discussed below. Most of the remainder are rare, and only *C. × boeninghausiana* (*C. paniculata* × *remota*), *C. × involuta* (*C. rostrata* × *vesicaria*) and the relict hybrid *C. ×*

grahamii (*C. saxatilis* × *vesicaria*) are recorded with any frequency. However, *Carex* hybrids are often overlooked and are probably greatly under-recorded; more hybrid combinations and additional localities for apparently rare hybrids are likely to be discovered in future years.

British botanists formerly thought that the species of *Carex* were difficult to identify, and many were under-recorded in the *Atlas of the British flora* (Perring & Walters, 1962). Jermy & Tutin's excellent identification handbook, *British Sedges*, was published in 1968 and did much to stimulate interest in the group; it was revised by Jermy *et al.* (1982). Most competent botanists would now identify the majority of the species they encounter without much difficulty. The main exceptions are the species related to *C. flava* and those related to *C. nigra*. The former does not include aquatic species but most of the taxa in the *C. nigra* group are aquatics.

The *Carex nigra* group includes the aquatics *C. acuta*, *C. aquatilis* and *C. elata*, the ecologically tolerant *C. nigra* and the montane *C. bigelowii*. These species have been studied experimentally by Faulkner (1972, 1973). All the species are more or less self-incompatible. *C. aquatilis* and *C. bigelowii* are closely related and as much seed is set when these species are cross pollinated as when individuals of the same species are crossed. Similarly, *C. acuta* and *C. nigra* are a pair of closely related species with only a slight breeding barrier between them. However, crosses between *C. aquatilis* or *C. bigelowii* and *C. nigra* are less likely to produce good seed and those between these two species and *C. acuta* are almost sterile. The fifth species, *C. elata*, is a link between the two species pairs, as crosses between it and the other species are less productive than those between the members of a related pair, but more fertile than those between species in different pairs.

Faulkner (1973) also showed that the synthesised hybrids in the *C. nigra* group are partially fertile and will backcross with the parents. More seed is set if the hybrid is used as the pollen parent, as the number of seeds set is limited by the number of fertile ovules and the hybrids have fewer than the parents. Although the pollen of the hybrids is also partially fertile, pollen is usually present in excess and there are sufficient fertile grains to achieve good seed set under experimental conditions. Much of the seed set when species are cross-pollinated or when hybrids are backcrossed is viable, and most of the resulting plants are as vigorous as the parents.

In the wild, the occurrence of hybrids is limited to some extent by the ecological isolation of the species. However, hybrids between the montane *C. bigelowii* and both *C. aquatilis* and *C. nigra* are recorded in upland habitats. In the lowlands there are records of hybrids between *C. elata* and both *C. acuta* and *C. nigra*, and between *C. nigra* and *C. acuta*. Both *C. aquatilis* and *C. nigra* have a wide altitudinal and ecological range and their hybrid has been found in both upland and lowland sites. Hybrids in this group of sedges are not always easy to recognise in the field, and Faulkner (1972) found that some apparent hybrids tended to lose their intermediate morphology in cultivation and proved to be species when examined cytologically.

A sixth species is included in the *C. nigra* aggregate by Jermy *et al.* (1982), Stace (1991) and Kent (1992). This is the rare *C. recta*, which is restricted in our area to marshes in four localities in N. Scotland. Faulkner (1973) has shown that the Scottish populations of this

species are undoubtedly of hybrid origin, and the parentage is almost certainly *C. aquatilis* × *C. paleacea*. *C. paleacea* is a species which has not been recorded in our area. The Scottish *C. recta* sets seed, and at one of its sites there is an extensive hybrid swarm involving *C. aquatilis* and *C. recta*.

The seasonal development of vegetative and flowering shoots of several *Carex* species has been studied, and the relevant papers are cited in the individual species accounts. There is less information on reproduction by seed, perhaps because this is an infrequent event for many of the rhizomatous species. Jermy *et al.* (1982) reported that the seed of most species requires an after-ripening period of 3-12 months, and that this cannot be reduced by low temperature treatment. They also found that abrasion of the testa increases the proportion of seeds that germinate. However, Faulkner (1973) was able to germinate seeds of the *C. nigra* group in the light without any after-ripening period or artificial abrasion of the testa. As Jermy *et al.* (1982) comment, there is much scope for both observational and experimental studies on the germination and establishment of *Carex* species.

This species grows in a wide range of shallow water or seasonally flooded habitats. These include open water at the edge of lakes, ponds, rivers, ditches and canals; open, species-rich stands of emergents such as *Phragmites australis*, *Schoenoplectus lacustris* and *Typha angustifolia*; sedge-dominated fens and swamps with rhizomatous species such as *C. rostrata*; spring-fed marshes; and open fen-carr and swampy woodland dominated by *Alnus glutinosa* or *Salix cinerea*. It is usually found in at least moderately base-rich water, and often in places where there is some water movement. Its sites range from eutrophic to highly calcareous but mesotrophic or even oligotrophic. It is frequent over peat but also grows over other substrates including mud and even boulders (Spence, 1964). It extends from sea-level to 600 m on Glychedd.

C. paniculata is a perennial which forms substantial tussocks which often exceed 1.5 m in height in the growing season, and under exceptional circumstances may reach 3 m (Smith, 1907). It flowers and fruits freely. Seedlings and young plants are sometimes found on the dead and decaying tussocks of the same species (Poore & Walker, 1959).

The tussocks of *C. paniculata* are not easily killed: the population on the Isles of Scilly described by Smith (1907) has survived attempted drainage, toxic chemicals and fire (Lousley, 1971). They may remain alive in dense plantations for several decades. The map does not suggest a significant national decline, but the species has doubtless been lost from many sites because of the artificial embankment of rivers and canals. In the Colne valley many populations have been destroyed during gravel extraction, and 'tussock fens' have ceased to develop in Broadland as the emergent communities of *Schoenoplectus lacustris* and *Typha angustifolia* which were formerly colonised by *C. paniculata* have disappeared (George, 1992). The species will colonise old peat diggings and long-disused sand and gravel pits.

C. paniculata is found in Europe, and in adjacent parts of N. Africa and W. Asia. In Europe it is rare in the Mediterranean region but frequent at middle latitudes, especially in the west, and it extends north to S. Scandinavia. The species is divisible into three subspecies: subsp. *paniculata* is the most widespread but is replaced by subsp. *lusitanica* (Schkuhr) Maire in the western part of the Iberian peninsula and N. Africa, and by subsp. *szovitsii* (V. Krecz.) Ö. Nilsson in Crimea and the Caucasus.

Tussocks of *C. paniculata* are colonised by marsh and fen plants, harbour 'a host of hibernating invertebrates' (George, 1992) and support mosses such as *Plagiothecium latebricola* on the shaded bases. Trees also colonise the tussocks, and the presence of this species may accelerate the succession from open water to wet woodland. Once colonised by trees tussocks may press down the soft lake sediments or disturbed peat on which they grow, so that open water is maintained between them (Lambert & Jennings, 1951). The old tussocks were formerly dried out and used as fireside seats in cottages and hassocks in churches (Ellis, 1965).

This is a species of shallow, nutrient-poor water. It is most frequent in open stands at the edge of lakes and slow-flowing streams and rivers, in swamps, in flushes and wet hollows in fens and as a colonist of old drainage channels and peat diggings. It usually grows as an emergent in water up to 0.3 m deep, but can also occur as a floating raft over water in sheltered bays and pools, or in fens where the water table is below the surface of the substrate, at least in summer. It is frequently mixed with other emergent monocots, particularly *Carex rostrata* but also *Cladium mariscus* or *Phragmites australis*, and often accompanied by *Menyanthes trifoliata* and *Potentilla palustris*. In Scotland stands containing *C. lasiocarpa* tend to grow between those of *Carex rostrata* or *Phragmites australis* (which extend into deeper water) and mixed *C. lasiocarpa*-*Myrica gale* stands and then communities of *Molinia caerulea* and *Myrica gale* on higher ground (Spence, 1964). *C. lasiocarpa* may persist in relatively dry fen on the site of former pools, as a relic of a period when the water level was higher (Proctor, 1974). It is found in both base-poor and base-rich waters, as long as they are oligotrophic or mesotrophic, and over a range of substrates including raw, sandy soils at the edge of lakes and peat. It grows from sea-level to 465 m near Nant-y-maen.

This is a rhizomatous perennial which may form extensive, clonal stands. Studies of an American population (Bedford *et al.*, 1988) showed that shoots were produced continually throughout the growing season. Many of the shoots which emerged in summer and autumn over-wintered as plants with tightly inrolled leaves, which then expanded in the following spring. The species is known to be a very shy flowerer and 99% of ramets tagged in the American population died without flowering. McClintock & Waterway (1993) found that populations in pioneer stands in open water showed greater genetic diversity and clones were smaller than in closed vegetation, suggesting that reproduction by seed is more frequent in open habitats, but they were unable to find any seedlings in their study sites.

The leaves of *C. lasiocarpa* are very thin (the species is aptly known as 'wiregrass sedge' in N. America) and flowering shoots are usually few and far between. The species is therefore easily overlooked, although once learnt its appearance is very distinctive. Systematic surveys of aquatic habitats have revealed that the species is present in many more 10-km squares than were known to Perring & Walters (1962), especially in Scotland. However, the species has certainly declined in eastern England. It is extinct in Suffolk (Simpson, 1982) and Durham (Graham, 1988) and now confined to a single site in Cambridgeshire (Perring *et al.*, 1964). Some sites have been drained and others no longer provide the open, oligotrophic vegetation which this species prefers. In Dorset it is known from three sites, but two are drying out and becoming overgrown by *Molinia caerulea*, and invaded by pine and birch (Pearman, 1994). *C. lasiocarpa* is also extinct in some sites in eastern Ireland, including Lough Neagh (Harron, 1986).

C. lasiocarpa occurs in boreal regions throughout the northern hemisphere. In Europe it extends from N. Scandinavia south to the Pyrenees, central Italy and N. Greece. The populations in E. Asia are referable to subsp. *occultans* (Franch.) Hult. and those in N. America to subsp. *americana* (Fern.) Hult.

Carex acutiformis Ehrh. Lesser Pond-sedge

This tall sedge grows in shallow water at the edges of standing and slowly flowing waters, including lakes, ponds, rivers, streams, canals and ditches, and in swamps. In these habitats it often grows with *C. riparia*. It is rarely found in sites which are subject to great fluctuations in water level, and it is notably intolerant of rivers subject to spate (Haslam, 1975). Like *C. paniculata*, it invaded reedswamps in Broadland, and as the ground surface rose above water level it was itself invaded by trees and shrubs. However, it is relatively shade-tolerant, and large stands persist in the resulting swamp woodland and occur on shaded watersides. In addition to these permanently flooded habitats, *C. acutiformis* also grows in sites where the water falls below the soil surface in the summer months. It is often abundant in fen-meadows, where it frequently grows with *C. disticha* and *Juncus subnodulosus*, and also occurs in tall-herb communities in fens. The herbaceous communities in these habitats may be maintained by seasonal mowing or grazing. *C. acutiformis* is a plant of base-rich, mesotrophic or eutrophic waters. It will grow over a wide range of organic or inorganic substrates, including acidic sands if the water is base-rich (Holmes, 1983), and it is present in some slightly saline coastal marshes. It is absent from sites where both water and substrate are base-poor. It extends from sea-level to 365 m in Weardale (Baker & Tate, 1868-CHK); a record from Widdybank cited by Graham (1988) must have been from a similar altitude.

C. acutiformis is a rhizomatous perennial which dies down during the winter. Plants spread by growth of the rhizome, and may also regenerate from detached rhizome fragments or even by large clumps which float downstream (Grime *et al.*, 1988; Ridley, 1930). New shoots emerge in late autumn or early spring; they may survive the winter and have a maximum life span of at least 2 years (Verhoeven *et al.*, 1988). Plants flower freely in undisturbed, open habitats but may only flower sparingly, if at all, in sites which are mown in summer (Verhoeven *et al.*, 1988) or are shaded (Pearman, 1994). Seed-set is frequently poor (Grime *et al.*, 1988). The fruits float and may be dispersed by water, but reproduction by seed is almost certainly much less significant than vegetative spread. The species rarely colonises newly available habitats.

This is still a frequent species in suitable habitats over much of its British range. However, it has declined in recent years in N. E. Essex (Tarpey & Heath, 1990), and it may have undergone similar decreases in other areas of dense population and intensive agriculture. According to Allen (1984), it is popularly grown as an ornamental plant in water gardens, and it may occasionally escape from cultivation. *C. acutiformis* has a more restricted distribution in Ireland, where it is 'a characteristic plant of the swamps and rivers of the Central Plain' (Praeger, 1901). Further fieldwork is required to see if it is still present in those Irish localities where it has not been recorded since 1950.

C. acutiformis is widespread in Europe, although it is rare in the Mediterranean region and absent from Iceland and N. Scandinavia. It also occurs in N. Africa and eastwards to central Asia, and as an uncommon introduction in N. America. S. Africa according to H & F: see checklist.

Carex riparia Curtis Greater Pond-sedge

This species is often found as pure stands in shallow water at the edge of lakes, ponds, slow-flowing streams and rivers, canals and ditches. It usually grows as a rooted emergent, but it is recorded as a colonist of floating *Glyceria maxima* rafts in Broadland (Lambert, 1946). It sometimes extends into sites where the water level falls below the substrate in the summer months, such as the banks and flood plains of rivers, tall-herb fens and clearings in willow carr. It is a species of base-rich, mesotrophic and eutrophic sites: in Breckland it is characteristic of the nutrient-rich valley fens rather than the less eutrophic headwater fens. In coastal sites it may grow in brackish ditches and marshes, and on flushed sea cliffs. It tolerates a wide range of substrates including peat, clay and silt. Unlike *C. acutiformis*, it is not favoured by grazing (Lambert, 1948). It is confined to the lowlands.

C. riparia is a rhizomatous perennial. It dies down during the winter, but the leaves begin to grow before those of *C. acutiformis* (Grime *et al.*, 1988). Plants flower freely in open habitats. The fruits float and may be dispersed by water. As with other rhizomatous sedges, vegetative spread is a more frequent means of reproduction than establishment from seed. Large clumps at the edge of rivers may become detached and float away to start new colonies downstream (Ridley, 1930).

The fossil record of *C. riparia* is sparse, but fruits have been found in deposits from the middle and end of the last glacial period, as well as in later sediments (Godwin, 1975). The species is now frequent throughout much of its British range, even in the London area (Kent, 1975; Burton, 1983). It has doubtless been able to persist in areas where many aquatics have declined because of its ability to grow in eutrophic habitats and to persist for long periods in unmanaged ditches. As a shade-tolerant species, it even survives when pieces of marsh converted to plantations of poplars or cricket-bat willows (Tarpey & Heath, 1990). However, C.D. Pigott (in Rodwell, 1995) has noted that large stands of this species seem to be declining in the Midlands and East Anglia. It is occasionally planted by lakes and ponds. The distinctly eastern distribution of *C. riparia* in Britain is matched by a corresponding rarity in Ireland.

The world distribution of *C. riparia* is similar to that of *C. acutiformis*. It occurs throughout most of Europe, north to S. Scandinavia, in N. Africa and eastwards to central Asia.

The ecology of this species is similar to that of the closely related *C. acutiformis*. *C. riparia* will, however, extend into deeper water than *C. acutiformis* (Grime *et al.*, 1988) and is less frequent in fen-meadows and other more or less terrestrial habitats. In the rivers described by Holmes (1983) *C. riparia* was recorded in a wide range of eutrophic rivers whereas *C. acutiformis* proved to be particularly characteristic of calcareous waters. These not only have a distinctive water chemistry but also tend to have a relatively stable flow from chalk or limestone aquifers.

Carex pseudocyperus L. Cyperus Sedge

This sedge is a pioneer species of shallow water and wet mud, but is unable to withstand competition from taller, rhizomatous species. It is found in a wide variety of habitats including the edges of lakes, reservoirs, ponds, slow-flowing rivers and nearby ox-bows, canals and ditches. It sometimes grows in open reedswamps and tall-herb fens, and it may invade floating or semi-floating rafts of *Phragmites australis* or *Typha latifolia* over water or unconsolidated mud (Sinker, 1962; Wheeler, 1980a). It will colonise disused sand, gravel, clay and marl pits. It is most frequent in sites which are neither very acidic nor very basic, and are mesotrophic or eutrophic, and it grows over peat and over mineral soils. It tolerates fluctuations in water level and it may be conspicuous when flowering in dried-up farm ponds. Although it is a pioneer species, it is shade-tolerant and will persist in pools and on wet mud between *Carex paniculata* tussocks and in swampy alder woods and willow carr. It is confined to the lowlands.

This is a tussocky perennial with little capacity for vegetative spread. It flowers and fruits freely. Little is known about its reproductive biology, but its ability to colonise open habitats suggests that reproduction by seed is not infrequent.

This is a frequent species in some areas, including the Somerset Levels (Roe, 1981) and the meres and marl pits of Cheshire (Newton, 1971). In much of its British range it is uncommon, but apparently no rarer now than formerly. However, it is declining in certain areas, including at least one area of grazing marsh (Mountford, 1994 - Owen: which one?) and in N.E. Essex (Tarpey & Heath, 1990). It is sold in garden centres and is sometimes planted by ponds and fishing lakes. It was first recorded at its northernmost British locality, Sanquhar House, in 1840 (McCallum Webster, 1978-CHK TPBSE 1:26, 1840), but it might be an ancient introduction at this site. In Ireland it is a scarce and apparently declining species.

C. pseudocyperus is widespread in the cooler parts of temperate Europe; it is virtually absent from the Mediterranean region and extends north to S. Scandinavia. It is also recorded in W. and central Asia, Japan and eastern N. America.

In the north and west this is one of the most frequent emergents. It grows in fens and bogs where the water table usually lies below the soil surface, often over a carpet of *Sphagnum* species or of base-demanding pleurocarpous mosses; in shallow water or as a floating raft, mixed with other rhizomatous species such as *C. lasiocarpa*, *Menyanthes trifoliata* or *Potentilla palustris*; or in water up to 0.6 m deep where it may be found as dense, monospecific stands or with *Equisetum fluviatile* in an open sward. It is found by lakes, reservoirs, pools, rivers, streams, springs and ditches, in swamps, marshes, flushes on hillsides and sea-cliffs, in wet meadows and the wettest dune-slacks and in clearings in wet woodland. It tolerates a wide range of water chemistry, growing in sites which range from base-rich to base-poor. It is most frequent in oligotrophic and mesotrophic waters, and in eutrophic sites it is often restricted to small stands, being replaced as the dominant species by *Glyceria maxima*, *Phragmites australis*, *Typha angustifolia* or *T. latifolia* (Spence, 1964). It is found over a wide variety of organic and inorganic substrates. It is tolerant of a degree of exposure but is absent from the most exposed lake shores. In the south and east it is much less frequent and it is usually an indicator of base-poor conditions, but even here it is sometimes found by nutrient-poor but highly calcareous waters, including those emerging from chalk and limestone springs. It is found from sea-level to at least 840 m on Creag Mhor (McVean & Ratcliffe, 1962), and there are unlocalised records from over 900 m in the Breadalbanes (White, 1898). **McV & R imply presence at 1020 m on Creag Meaghaidh (p. 117-check with DAR?).**

C. rostrata is a perennial with a robust rhizome. New shoots emerge throughout the growing season; the leaves die down in autumn but the young leaves are protected by the dead bases of older leaves and the shoot may survive the winter and regrow in spring. Individual shoots have a maximum life of 2-3 years, but few survive as long as this. The species flowers freely and shoots die after flowering. The fruits float and are presumably dispersed by water. Many fail to survive as little as 2 months dry storage (Spence, 1964). Reproduction by seed is almost certainly less important in established stands than vegetative spread. For further details of the demography of this species, see Bernard (1976), Gorham & Summers (1973)-get this, Hutgren (1988) and Verhoeven *et al.* (1988).

The fossil fruits of *C. rostrata* are recorded more frequently than those of any other *Carex* species, and they demonstrate that the plant was present in our area throughout the last glacial period (Godwin, 1975). It is still an abundant species in suitable habitats in the north and west and, more locally, in areas of acidic soils in the south and east. In these areas it may colonise old peat diggings and disused sand and gravel pits. It has, however, declined in those areas where, in historic times, it has always been an uncommon species. The most marked decline has been in Cambridgeshire, where it was formerly known from a number of widely scattered localities but has not been seen in any of them since 1966 (Perring *et al.*, 1964; Crompton & Whitehouse, 1983). Some sites have been drained and now lack any standing water; at others the species may have been adversely affected by eutrophication.

C. rostrata is widespread in the arctic, boreal and cooler temperate regions of the northern hemisphere. In Europe it extends south from Iceland and northern Scandinavia to N. Spain, Italy and N. Greece, although it is a rare and predominantly montane species in the southern parts of its range.

Carex vesicaria L. Bladder-sedge

This sedge is found in marshes where the water may lie below the soil surface, and as an emergent in water up to 0.4 m deep. It grows at the edge of lakes, reservoirs, turloughs, ponds, slowly flowing rivers and streams and their associated ox-bows, canals, and ditches, in wet meadows and damp hollows in pastures, and in wet sallow carr and alder woodland. It is often found in swamps which have developed in silted-up ponds and ditches, or by the inflow streams entering small lakes and reservoirs. It will also colonise disused sand, gravel and clay pits. Stands in very shallow water often grow with a range of associates including *Galium palustre*, *Juncus effusus*, *Mentha aquatica*, *Potentilla palustris* and *Veronica scutellata*; in deeper water the species may grow with *C. rostrata*, *Menyanthes trifoliata* and *P. palustris* or in virtually pure stands (Spence, 1964). The species tolerates a fluctuating water table. It is often eaten in sites where it is accessible to cattle, and cannot withstand heavy grazing. *C. vesicaria* is a plant of mesotrophic habitats which range from slightly base-rich to highly calcareous. It is found over a range of substrates including mud, clay, silt and peat. It is recorded from sea-level to 455 m (Llyn Gorast).

The life-cycle of this rhizomatous perennial has been studied by Soukupová (1988) in Czechoslovakia. The species retains short leafy shoots throughout the winter. In summer vegetative shoots continue to be produced throughout the growing season, and after flowering the vegetative shoots overtop the shoots which bear ripening fruit. The shoots live for up to 18 months, and always die after flowering. The fruits float, and the seeds are dormant when the fruits are shed but germinate in spring. Soukupová (1988) found seedlings at his study site for five successive years, whereas he only once found seedlings of *C. acuta*, which also grew there. At this site *C. vesicaria* is able to persist when mixed with the taller and more productive *C. acuta* because of its winter-green shoots, production of more numerous tillers which are able to invade gaps between the bulky *C. acuta* shoots and more frequent reproduction by seed.

C. vesicaria is a polymorphic species complex which has a circumboreal distribution. It consists of a number of taxa which are sometimes treated as species, and sometimes as subspecies or varieties (Hultén & Fries, 1986). The typical *C. vesicaria* is found in N. Eurasia and western N. America. In Europe it extends from N. Scandinavia south to the mountains of Spain, Italy and Bulgaria.

The historic records of this species are sometimes confused with those of *C. rostrata*, which complicates any assessment of changes in its distribution. However, there is little doubt that it has declined in lowland areas of England, including Gloucestershire (Holland, 1986), Essex (Tarpey & Heath, 1990), Cambridgeshire (Perring *et al.*, 1964) and S.E. Yorkshire (Crackles, 1990). Some sites have been drained, but the species may also have disappeared because of more subtle changes in nutrient levels or river management which are not fully understood. In Dorset, Pearman (1994) was unable to detect the species at any of the 25 precisely localised sites where it had been recorded in the 1930s by R.D'O. Good. Most of these were by the Rivers Frome and Stour, where *Phragmites australis* had increased in frequency. This may be a response to eutrophication or to improved drainage of riverside land.

This species has similar ecological requirements to those of *C. rostrata*, with which it often

grows. However, *C. vesicaria* is restricted to shallower water and it is often frequent on the landward side of stands of dominant *C. rostrata* (Spence, 1964). *C. vesicaria* is a more lowland species and it has a more restricted trophic range: it does not extend into the very oligotrophic habitats in which *C. rostrata* often grows. The hybrid between these two species, *C. × involuta*, is one of the more frequent *Carex* hybrids. It is highly sterile but it may spread vegetatively to form large stands (Jermy *et al.*, 1982; Wallace, 1975). *C. vesicaria* also appears to be one parent of the enigmatic sterile hybrid *C. × grahamii*. In our area this plant is restricted to montane habitats in Scotland which are well above the current altitudinal limit of *C. vesicaria*; it often grows near the other putative parent, *C. saxatilis*.

Carex limosa L. Bog-sedge

This small sedge is restricted to very wet bogs and fens, and shallow, oligotrophic lakes and pools. It is most frequent in acidic or mildly basic peatlands, where it is found in wet hollows, peat cuttings and at the edge of bog pools. It often grows in carpets of sphagnum, including the floating masses of sphagnum which extend across the open water of bog pools. It is also found in water up to 0.2 m deep at the edge of lakes, where it can be abundant in sheltered bays and sometimes grows in open stands of *Carex rostrata*, *Menyanthes trifoliata* and, less frequently, *Phragmites australis*. Other characteristic associates include *Carex lasiocarpa*, *C. nigra*, *Eriophorum angustifolium*, *Juncus bulbosus*, *Potamogeton polygonifolius*, *Potentilla palustris*, *Utricularia intermedia* and *U. minor*. *C. limosa* can occasionally grow in highly calcareous fens, especially in vegetation which has colonised old peat cuttings (Wheeler, 1980a, b). Here it is particularly associated with 'mud bottom' communities in very wet depressions (Wheeler, 1978). It is most frequent in lowland sites, but it is recorded at altitudes up to 817 m on Meall nan Tarmachan.

C. limosa is a perennial which spreads by growth of the rhizome. Many stands are made up of numerous vegetative shoots but flower only sparingly, and some upland stands seem to persist without flowering. Those flowers which are produced usually set seed, but little is known of the circumstances under which it germinates.

Sparsely flowering stands of *C. limosa* are easily overlooked, and like many sedges this species was under-recorded in the *Atlas of the British Flora* in Scotland, Ireland and Wales. It may still be under-recorded in some western areas. However, it is a declining species in the southern and eastern parts of its range, where it has succumbed to total habitat destruction or to the drainage of bogs resulting in falling water tables, the drying out of pools and the colonisation of woody species. It is extinct in several sites in Northumberland, including all the more easterly localities (Swan, 1993) and in Yorkshire it only survives at Fen Bog (Sykes, 1993). It is restricted to one site in Cheshire (Newton, 1971) and it is a critically endangered species in Shropshire, where only a single plant was known to Sinker *et al.* (1985). It was last seen in W. Norfolk in 1924. It survived in E. Norfolk until c. 1974, but has not been seen since. In Dorset it is still present in several sites but only survives in quantity in one of them (Pearman, 1994). In Ireland *C. limosa* has also been lost from some eastern sites, e.g. in Co. Down (Praeger, 1938).

C. limosa has a circumboreal distribution. In Europe it extends from Iceland and N. Scandinavia southwards to N. Spain, the Alps and N. Greece.

C. limosa is the most frequent associate of the rare *Scheuchzeria palustris* at its only surviving British sites on Rannoch Moor, and it was recorded from at least four of the former English localities for *S. palustris* (Sledge, 1949). Unlike *S. palustris*, *C. limosa* is able to grow in bogs in areas where the climate is very oceanic, and it therefore remains a frequent species in some regions.

Carex recta Boott Estuarine Sedge

This plant grows by estuarine rivers, sometimes extending to sites which are just above the tidal limit. It is found in rough marshy pasture, riverside swamps and on islets. It may grow over large areas, sometimes with *Phalaris arundinacea* and *Phragmites australis*, or with *C. aquatilis* and its hybrid with this species, *C. × grantii*, or as pure stands. It is found over stiff, peaty alluvium or on sandy banks which receive some silt deposition (Jermy *et al.*, 1982).

This is a rhizomatous perennial which spreads vegetatively. The Scottish plants show disturbed chromosome pairing and none of the six plants studied by Faulkner (1972) was a simple euploid. In his experimental studies, Faulkner (1973) found that crosses between different plants of *C. recta* resulted in very low seed set, in contrast to intraspecific crosses of the other species in the *C. nigra* group. When female flowers of *C. recta* were pollinated by other species the resulting seed set was also low. However, more seed was set when pollen of *C. recta* was used to fertilise the flowers of other species in the *C. nigra* group, the cross between *C. recta* and *C. aquatilis* being the most fertile.

This plant was first recorded from Scotland by **who? RWD thought Grant, J. Bot. 50:290, 1885, but never got chance to check.** It is now known from three rivers. The largest populations grow by the River Oyke and the Wick River, and it is by the latter that the species occurs in a hybrid swarm with *C. aquatilis*. There is a smaller population by the Beaulie River. Some stands of the species are threatened by wetland reclamation.

The taxonomy of *Carex recta* requires clarification, and it is impossible to give a satisfactory account of its world distribution. The species was originally described from eastern N. America, where it occurs on the arctic and boreal coasts, but the identity of the American and Scottish populations has not been demonstrated, and is perhaps doubtful. Faulkner (1972, 1973) has demonstrated that the Scottish populations are derived from hybrids between *C. aquatilis* and *C. paleacea*, a plant of brackish marshes and sea-shores which does not grow in Britain but which is fairly frequent around the coasts of Scandinavia. The synthesised hybrid is indistinguishable morphologically from the Scottish *C. recta*. Plants similar in morphology to the Scottish populations are found on the western coasts of Scandinavia, in areas where *C. paleacea* occurs. Other plants referred to *C. recta* in Scandinavia are shorter in stature and are cytologically distinct. They may be hybrids between *C. paleacea* and a smaller species, perhaps *C. nigra*.

Carex aquatilis Wahlenb. Water Sedge

C. aquatilis is most frequently found in lowland sites, including the edge of lakes, reservoirs, rivers and streams, in pools, ditches, swamps, marshes and wet meadows on flood plains, in wet woodland and on the muddy margins of east-coast estuaries and sea-lochs. The lakes by which it grows are mesotrophic or even eutrophic, and in these habitats it may occur in pure stands or with *C. rostrata* and *C. vesicaria*. In sites with a well-developed zonation it may be found below the level of willow carr or stands of *Phalaris arundinacea*, and it can give way to pure stands of *Carex rostrata* or *Phragmites australis* as the water deepens (Spence, 1964). By rivers it is most frequent along slowly flowing lowland reaches where oligotrophic or oligo-mesotrophic water flows over fine, mesotrophic sediments (Holmes, 1983). *C. aquatilis* also occurs in oligotrophic, base-poor sphagnum bogs over peat, sometimes in the lowlands but more frequently at high altitudes where it may grow with *C. bigelowii*, *C. curta*, *C. nigra* and *C. rariflora*. It reaches 975 m in such vegetation at Cairn of Claise and Glen Maol, Caenlochan (McVean & Ratcliffe, 1962).

C. aquatilis is a rhizomatous perennial. Both euploids ($2n=76$) and aneuploids ($2n=77$) occur; the latter are probably derived by chromosome fission (Faulkner, 1972). Plants in open habitats often flower freely but the species may persist in the vegetative state in shade. Under experimental conditions *C. aquatilis* proves to be as fertile as the other species in the *C. nigra* group (Faulkner, 1973). However, Dutch populations set very little fruit in the field: an average of one ripe seed per stem and a maximum of five (Corporaal, 1987). The reasons for this are not clear, nor is it known whether any British or Irish populations set so few seeds.

The distribution of this species is rather patchy, as *C. aquatilis* is found along river valleys in some areas but is rare or absent in the surrounding countryside. There are, for example, strong populations along the Afon Teifi, and the species is abundant in Strathspey. It is difficult to assess any changes in the distribution of the species in Britain for two reasons: lowland populations were formerly confused with *C. acuta* and, perhaps partly for this reason, the species was greatly under-recorded until recently. Many new records have been made since the publication of the *Atlas of the British flora*. The species still appears to be uncommon in Ireland, and has a scattered distribution like that mapped for Britain in the 1962 *Atlas*. This suggests that it may still be under-recorded in Ireland.

C. aquatilis is a circumpolar species which in Europe is frequent at high latitudes and extends south to the British Isles, N. Germany and central Russia. It is one of the few plants in our area with an arctic (rather than arctic-alpine) distribution.

This is a variable species, and even in our area the tall emergent of the lowlands is very different in appearance from the short plants which grow at high altitude. Experimental studies of populations growing on ice-wedge polygons in the Alaskan arctic have shown that genetically distinct ecotypes may occur in the different micro-habitats (ridges, meadows, troughs and ponds) even though the micro-habitats are less than 1 m apart (Shaver *et al.*, 1979). However, Faulkner (1972) was unable to find any cytological distinction between lowland plants, dwarf plants from the Eastern Highlands of Scotland (var. *minor* Boott) and dwarf arctic plants sometimes treated as subsp. *stans* (Drejer) Hultén.

Carex acuta L. Slender Tufted-sedge

This species is found in shallow water or on wet ground in a wide variety of habitats, including the edges of lakes, reservoirs, ponds, rivers, streams, canals and ditches, and in unimproved flood meadows and washland. The shallow, muddy edges of major rivers provide a particularly characteristic habitat, and the species is tolerant of frequent flooding and is not easily uprooted when rivers are in spate (Sinker *et al.*, 1985). *C. acuta* is often found as isolated tufts, which may grow with *Butomus umbellatus*, *Carex acutiformis*, *C. riparia*, *Glyceria maxima*, *Phragmites australis* and *Sparganium erectum*, but more extensive stands are also recorded by lakes, ponds and rivers. It is usually found by calcareous and mesotrophic or eutrophic waters, and sometimes occurs in brackish marshes. It is shade-tolerant and may grow under riverside willows or in wet woodland. It is confined to the lowlands.

C. acuta is a rhizomatous perennial. Faulkner (1972) found that only 19 out of 39 specimens examined were normal euploids, with $2n=84$; the rest had additional chromosome fragments or $2n=83$ or 85 . The life cycle of this species has been studied by Soukupová (1988). The shoots die down during the winter, resprouting in spring; they may live for 2 years, but die after flowering. New shoots begin to develop in autumn but usually emerge above ground in spring. The seeds are dormant when shed and require at least 8 months after-ripening. Germination takes place in spring, and a higher proportion of seeds germinate in the light than in the dark under experimental conditions. The establishment of new plants from seed is rare.

This species was under-recorded in both Britain and Ireland in the *Atlas of the British flora*. It was, for example, not discovered in either the Burren and Connemara until the late 1960s, although both areas are well known to botanists (Webb & Scannell, 1983). Nevertheless, there is evidence that the species is decreasing in some regions. Drainage and the subsequent reclamation of marshy ground has severely reduced the available habitat in the Lough Neagh area (Harron, 1986), and doubtless elsewhere. Populations in Cheshire have been destroyed by canal bank improvements (Newton, 1991). In Dorset all nine of the stands noted by R.D'O. Good in the 1930s have disappeared, and by the River Stour the species only survives as occasional tufts (Pearman, 1994, 1995). However, it is occasionally recorded as a colonist of disused gravel pits and borrow pits.

C. acuta is widespread in the temperate regions of Europe, N. Africa and W. Asia. In Europe it is rare in the Mediterranean region and in northern Scandinavia, and absent from Iceland. It is replaced by the related *C. appendiculata* in E. Asia.

Carex acuta and *C. nigra* can be difficult to distinguish in the field, even in the absence of hybrids, as the differences between the species are quantitative and the most luxuriant individuals of *C. nigra* grow in the wet habitats where *C. acuta* occurs (Faulkner, 1973). [Arthur: is it really as difficult as this?] Intermediate plants are frequent in the wild, and some of these have been confirmed as hybrids by cytological examination. Faulkner (1973) concludes that on balance, the evidence is 'marginally in favour of their retention as independent species, although.....the fertility of the hybrids is certainly high enough to permit either introgression or the formation of hybrid swarms'. In addition to the hybrids with the members of the *C. nigra* group, the variable and partially fertile hybrid between *C. acuta* and

C. acutiformis, *C. × subgracilis*, is known from several localities and is probably under-recorded (Jermy, 1967; Crackles, 1984).

Carex elata L. Tufted-sedge

This is a tussock-forming sedge which grows in shallow, calcareous water up to 0.4 m deep, or in fens where the water table usually lies below the soil surface. Typical habitats include the edges of lakes, ponds, canals, fenland lodes and ditches, swamps, old peat diggings, fen meadows, and wet woodland dominated by willows or alders. *C. elata* often grows with *Cladium mariscus* but it differs from that species in its marked preference for sites with fluctuating water levels. In Broadland the water level is more variable at sites where there are mixed stands of these two species than at those where only *C. mariscus* is present, and at Foulden Common small, deep hollows subject to marked changes in water table are dominated *C. elata* whereas larger hollows with a more stable water regime are dominated by *C. mariscus* (Haslam, 1965; Wheeler, 1980a). *C. elata* can be one of the pioneer colonists of reedbeds dominated by *Phragmites australis*, and its spread into such vegetation at Esthwaite North Fen was documented by Tansley (1939). Its tussocks, like those of *C. paniculata*, may in turn be colonised by woody species, and *C. elata* can persist in the resulting wet woodland. It is also found in fens and fen-meadows which are maintained by periodic mowing, where it is often associated with *Juncus subnodulosus*. In this vegetation the species may lack its normal tussocky form. It is vulnerable to grazing and at Sunbiggin Tarn it is more abundant in ungrazed than in grazed sites (Holdgate, 1955). It is usually found in oligotrophic or mesotrophic sites, but it may grow by eutrophic fenland lodes and ditches, although these sites have probably undergone recent enrichment. It is confined to the lowlands.

C. elata lacks rhizomes and is consequently unable to spread vegetatively. Most plants are euploids with $2n=76$, but aneuploids with chromosome numbers of 75 and 77 are recorded. *C. elata* flowers and fruits freely in the open, although flowering is suppressed in the shade. Little is known about the circumstances in which it reproduces by seed.

This species has been confused in the past with tussocky forms of *C. nigra*. Both West (1905) and Spence (1964) reported the species from Inchnacarroch Bay, Loch Ness, but these records are probably erroneous (R.W. David, *pers. comm.*), and a few mapped records may also be misidentifications. Nevertheless, the available evidence suggests that *C. elata* has decreased in S.E. England. Some sites have been drained, and populations have been reduced or eliminated from others when canals have been dredged and their edges cut away, when ditches and lodes have been widened and deepened, or even when ponds have been dug in areas of base-rich fen. Some of the remaining populations are threatened by similar operations, but many of the *C. elata* sites are species-rich calcareous wetlands which are managed as nature reserves. In some sites all the plants appear to be very old, and an understanding of the reproductive biology of the species is required in order to safeguard these populations. *C. elata* is still locally frequent in some areas of Ireland.

C. elata is widespread in Europe, although it is rare in the Mediterranean region; it extends north to central Scandinavia. It is also recorded from N. Africa and in temperate Asia east to Manchuria. The western and central European plant is subsp. *elata*, which is usually found in base-rich habitats; in eastern Europe it is replaced by the predominantly calcifuge subsp. *omskiana* (Meinsh.) Jalas (Tutin *et al.*, 1980).

The tussocks of *C. elata* are often colonised by fenland plants, as well as woody species. At

Sunbiggin Tarn Black-headed gulls often nest on them, and even outside the gullery the tussocks support nitrophilous species such as *Sambucus nigra*, *Stellaria media* and *Urtica dioica* (Holdgate, 1955).

153. POACEAE (*GRAMINEAE*)

This large and important plant family comprises 737 genera and nearly 8000 species. The family has a cosmopolitan distribution, and is best known for its terrestrial representatives. These include bamboos and grasses with a wide range of morphology, and numerous ecologically and economically important species. An account of the family, with descriptions of all the genera, is provided by Clayton & Renvoize (1986). Cook (1990) lists 61 genera which contain aquatic species, of which 8 are native to our area. Four of these are dealt with in detail in this book. *Agrostis stolonifera* is also listed as an aquatic by Cook. It is frequent in seasonally flooded habitats, and plants which are rooted at the edge of canals and ditches often send out individual shoots which extend over the surface of the water. Three other genera are listed by Cook but do not qualify for inclusion here: *Alopecurus*, *Leersia* and *Spartina*.

153/1. *Catabrosa* P. Beauv.

All the members of this small genus are sometimes included in a single species; other authors consider that they are divisible into as many as four species.

Over much of its British and Irish range this species is usually found at the edge of small streams, springs, ditches and pools. It forms clumps or patches which are rooted in nutrient-rich silt or mud and often extend as floating mats onto shallow, slowly flowing water. It also occurs at the edge of canals and sluggish rivers, at the edge of lakes (particularly at the point where streams enter them) and in flushes and marshy fields. It colonises sites which are trampled by cattle, but it is a very palatable species and in these localities it may be heavily grazed. It is a rather shade-tolerant grass, and is often noticed under bridges, where it can flower in the absence of grazing (Burton, 1983; Kent, 1975). On the northern and western coasts of Britain and Ireland *C. aquatica* is characteristically found where streams fan out and flow over sandy beaches. It is primarily a lowland species, which ascends to 375 m at Malham Tarn. Unusually, it also grows in montane flushes at 710 m on Little Fell, with *Epilobium alsinifolium* and *Saxifraga stellaris* (Roberts & Halliday, 1979).

C. aquatica is a perennial which flowers freely in the absence of grazing. Some observers have suggested that it may be rather sporadic in its appearance, disappearing from sites then reappearing after some years (Tarpey & Heath, 1990).

This is rather a local species throughout much of its British and Irish range. It is tolerant of a degree of nutrient enrichment, and has increased at the Loch of Hillwell in recent years following eutrophication (Scott & Palmer, 1987). However, inland habitats are very vulnerable to destruction by the in-filling of ponds and ditches, or to unsympathetic management such as dredging which destroys the vegetated edge of the shallow streams and ditches which it favours. It has decreased in many areas, including Kent (Philp, 1982), Durham (Graham, 1988), Angus (Ingram & Noltie, 1981), N. Aberdeenshire (Welch, 1993) and N.E. Ireland (Hackney, 1992). Although the species is distinctive, it is easily overlooked when grazed and in some areas it has been under-recorded until recently (Holland, 1986).

C. aquatica sensu lato is widespread in the northern hemisphere, occurring in Europe, N. Africa, W. & C. Asia and N. America. It is most frequent in temperate regions but extends north to Greenland, Iceland and N. Norway. It also occurs in Argentina and Tierra del Fuego.

Populations of *C. aquatica* on the northern and western coasts of Britain and Ireland are often smaller than those elsewhere and have only one flower per spikelet. These plants are treated as subsp. *minor* (Bab.) Perring & Sell by Sell (1967) and as var. *uniflora* Gray by Stace (1991), and their distribution is mapped by Perring & Sell (1968).

This is a fairly small genus of 40 species, all of which grow on wet ground or as aquatics. Two distinct Sections of the genus are represented in our area. *G. maxima* in Section *Hydropoa* Dumort. is a robust plant with long rhizomes, whereas the other species are all members of Section *Glyceria*. These are more slender plants with decumbent stems which often root at the nodes, and sometimes with stolons, but without rhizomes. The three species which are now recognised in our area are superficially similar, and flowering plants are usually needed for a certain identification. They were not distinguished in many floras published before 1940 (Hubbard, 1942), and are still under-recorded in many areas. Consequently there is less information on historical and current trends in their distribution than there is for many more conspicuous species. Two of the species, *G. fluitans* and *G. notata*, are tetraploids; these are ecologically similar and the sterile hybrid between them, *G. × pedicellata*, is fairly frequent. The third species, *G. declinata*, is a diploid and is less frequently found in water than the others.

Mabberley (1987) describes the species as 'luscious pasture grasses for cows'. However, the leaves of *G. maxima* contain cyanogenic compounds which are present at maximum concentration at the start of the growing season. In our area they are usually present at such low levels that they constitute no threat to stock, but in Australia and New Zealand cattle have died after eating this species (Barton *et al.*, 1983; Cooper & Johnson, 1984).

This grass is usually found in dense and often virtually pure stands. It may grow in permanently flooded sites such as pools, ditches, canals and slowly flowing rivers, where it extends into water up to 0.8 m deep. It also grows in seasonally flooded habitats, including marshland in the flood plain of rivers where the water may descend to 0.6 m below the soil surface in summer. It is usually found over substrates which are nutrient-rich and neutral or alkaline; over peat it is only found by flowing waters, which constantly replenish the nutrient supply. It will flourish in ponds which receive treated sewage (Ozimek & Klekot, 1979). Stands sometimes extend as floating masses over the surface of open water, as in the Yare Valley Broads or in ponds or disused canals (Lambert, 1946, 1947a). *G. maxima* is confined to open or very lightly shaded habitats. It persists even when regularly mown, and was formerly regarded as a valuable fodder crop. *G. maxima* favours deeper water than *Phalaris arundinacea* but cannot occur in water as deep as that in which *Phragmites australis* often grows. It is confined to the lowlands; a record from 597 m at Sprinkling Tarn (Stokoe, 1983) is unlikely to be correct.

G. maxima is a perennial with an extensive but shallow network of rhizomes. Rooted stands die down in autumn, regrowing as a dense sward in early spring and continuing to produce new shoots throughout the growing season. Under favourable conditions this enables it to suppress the growth of the later sprouting *Phragmites australis* (Buttery & Lambert, 1965). Floating masses remain winter-green. Plants usually flower well, although the inflorescences may abort in hot summers if plants are droughted (Lambert, 1947b). Only a small proportion (4-18%) of flowers set viable seed. Some seed germinates immediately, but most remains in the seed bank (Roberts, 1986). Seeds will germinate in spring or summer on damp soil or under water. They grow slowly and seedlings only become established on bare mud. The normal method of reproduction is by vegetative spread. In addition to the direct growth of the rhizome, small clumps of the plant or fragments of rhizome which become detached may float away to become established away from the parent clone (Grime, Hodgson & Hunt, 1988).

G. maxima is a member of a complex of subspecies or closely related species which occur in temperate regions throughout the northern hemisphere (Hultén & Fries, 1986). *G. maxima sensu stricto* is widespread in Europe, although it is rare in the Mediterranean region and is native only as far north as S. Scandinavia, although it is naturalised further north. It is also found in W. & C. Asia. It was deliberately introduced to Australia and New Zealand, where it is now thoroughly established.

This species is believed to be native in both Britain and Ireland. In Britain it is common in suitable habitats in S. England, even in the densely populated London area (Burton, 1983). In Broadland it expanded into areas formerly occupied by *Phragmites australis* during a period when *P. australis* was preferentially grazed by coypu, but it retreated as coypu numbers fell (George, 1992). It is sometimes planted as an ornamental species at the edges of lakes and ponds. In N. England and Scotland it has colonised a number of water courses in the last 150 years, often spreading from sites where it was originally introduced. In Aberdeenshire it spread along the R. Don in the mid 19th century, and has subsequently become more widespread (Trail, 1923; Welch, 1993). In the early years of this century it spread along the Forth & Clyde Canal (Lambert, 1947c), and it has subsequently colonised

the Tweed (Swan, 1993). In Ireland it has spread along the canal system from its apparently native sites in the south-east (Lambert, 1947c) and in N.E. Ireland it is being recorded as an introduction with increasing frequency (Hackney, 1992). The history of *G. maxima* in our area parallels that of *Butomus umbellatus*.

These notes are based on Lambert's (1947c) excellent account of the autecology of this species.

This species frequently grows in dense masses on wet ground, on mud at the edge of water bodies or as rooted plants or floating rafts in shallow water. The most vigorous stands are found in wet depressions in pastures, shallow ponds, ditches and slowly flowing streams, and at the edge of sheltered lakes and canals. *G. fluitans* is tolerant of a fluctuating water table, and can grow as decumbent or more or less erect stems with aerial leaves above the water, or as submerged stems with floating leaves. It is found in both acidic and calcareous sites, although Grime, Hodgson & Hunt (1988) noted that in N. England it avoids both the most acidic and the most calcareous soils. It requires substrates which are at least moderately fertile, and vigorous stands may be found in very eutrophic sites such as farm ditches. In oligotrophic lakes in the north and west its presence sometimes indicates places where waterfowl nest or roost. *G. fluitans* is also tolerant of moderate levels of disturbance such as ditch clearance. It is also fairly shade-tolerant. It is recorded from sea-level to 670 m (Loch Phadruig).

G. fluitans is a perennial species. The large anthers are borne on relatively long filaments and hang below the florets. Plants are slightly protandrous, and cross-pollination results in the production of more numerous viable seeds than self-pollination (Borrill, 1958b). The presence of a seedbank at depths in peaty soils has been demonstrated by Chippendale & Milton (1934). In addition to direct vegetative spread by the growth of established patches, detached shoots may be washed away and readily re-root in new localities (Grime, Hodgson & Hunt, 1988).

There is no evidence that *G. fluitans* is decreasing at a national scale. Grime, Hodgson & Hunt (1988) note that it is favoured by disturbance and eutrophication, and suggest that it may be increasing in ponds and ditches in some areas.

This species is found throughout Europe, except in arctic areas, and extends into adjacent regions of W. Asia and N. Africa. It is also recorded as an introduction in N. & S. America, Australia and New Zealand.

G. fluitans is the most variable of the three species in Section *Glyceria*. Populations differ genetically in characters such as their habit, which may be compact or spreading, the length and number of florets in their spikelets and the extent to which plants are self-compatible. When plants from these different races are crossed they are usually genetically incompatible (Borrill, 1958a, 1958b).

Glyceria × *pedicellata* F. Towns. (*G. fluitans* (L.) R. Br. × *G. notata* Chevall.)
Hybrid Sweet-grass

Small colonies or large and persistent stands of this hybrid can be found at the edges of lakes, ponds, rivers, streams and in ditches or wet meadows. It grows in shallow water or on damp, often cattle-poached mud. It can often be found in swiftly flowing streams, and plants with submerged leaves are found in profusion in Baldwin Reservoir (Allen, 1984). It is normally found in nutrient-rich and often in calcareous sites. It may occur in the absence of one or both parents. It is found from sea level to 540 m (Llyn Fyrddon Fach).

This is a stoloniferous perennial. Its pollen is highly sterile and the anthers fail to dehisce. This sterility can be attributed to the failure of many of the chromosomes to pair at meiosis (Borrill, 1956b). However, *G. × pedicellata* reproduces vegetatively by the spread of established plants and by detached ramets which may be carried in moving water to new sites.

This hybrid was described by Townsend (1850, 1853) on the basis of material from Cambridgeshire and Derbyshire. It is, however, easily overlooked and it is still under-recorded. There is insufficient evidence to assess changes in its distribution or abundance in Britain or Ireland.

G. × pedicellata is widespread in N., W. and central Europe (Tutin *et al.*, 1980).

This is a variable hybrid between two tetraploid species. There are differences between individual clones, some of which overlap in their morphology with *G. fluitans* and others with *G. plicata* (Borrill, 1956a). This suggests that the hybrid consists of different genotypes which have separate origins.

This species may be found in shallow water at the edges of ponds and in streams, but it is less frequent in permanently waterlogged habitats than the other members of the genus. Typical habitats include trampled or waterlogged mud by ponds, the muddy banks of streams and ditches, flushes, winter-flooded ruts and depressions on tracks or in pastures, and moist, trampled or cattle-poached grassland. It is even recorded from damp arable fields in Berkshire (Bowen, 1968). It is found over a wide range of acidic or circumneutral substrates, including peat, clay, sand, gravel and river shingle, but it does not grow in the highly calcareous sites in which *G. notata* can be found. Characteristic associates include *Agrostis stolonifera*, *Isolepis setacea*, *Juncus articulatus*, *J. bufonius*, *Lotus uliginosus*, *Ranunculus flammula*, *R. repens* and *Stellaria alsine* (Sinker *et al.*, 1985). In some parts of Scotland it is confined to sites near the coast, and it may grow at the upper edge of salt marshes (Duncan, 1980). It is recorded from sea level to 500 m at Llyn Crugnant.

This diploid perennial is usually self-pollinated (Borrill, 1958b). The anthers are borne on very short filaments and only just emerge from the florets. The stigmas only protrude very slightly, and they are receptive at the time when the pollen is shed. The species is highly self-fertile. Unlike *G. notata* and *G. × pedicellata*, it lacks stolons.

In common with the other species in *Glyceria* Section *Glyceria*, this species is under-recorded in some areas. In Northern Ireland, for example, the species was recorded in only two sites before 1980, but was found in over 20 sites during fieldwork in 1986 (Leach, Wolfe-Murphy & McMullin, 1987). There is insufficient evidence to assess whether its distribution has changed in recent years.

This species is confined as a native to W. & central Europe, where it is found from the Azores and S. Spain northwards to southernmost Scandinavia and eastwards to Russia. It is recorded as an introduction in N. America (California, Nevada).

Although this species is less variable than *G. fluitans*, populations differ genetically. Some have a particularly luxuriant habit, and others have large vegetative and floral parts (Borrill, 1958a).

Like *G. fluitans*, this is a species of shallow, nutrient-rich water. Typical habitats include the gravelly beds of streams, or their slow-flowing margins, shallow runnels and ditches, and the muddy edges of ponds and marl pits. It can also be found in marshes and, less frequently, in seasonally flooded areas. It is more calcicolous than the other *Glyceria* species. It is locally frequent at the edge of streams arising from limestone springs, and is scarce in areas of poor soils. It has a predominantly coastal distribution in some areas, such as Cornwall and the Isle of Man, where calcareous soils are infrequent. It is a predominantly lowland species, which ascends to 380 metres at Malham Tarn. Old records from 460 m in Derbyshire (track source) may be correct but require confirmation.

G. notata is a stoloniferous perennial. It is the only one of our species in Section *Glyceria* in which flowering is often delayed until the second year (Borrill, 1958a). Like *G. declinata*, it is usually self-pollinating and highly self-fertile (Borrill, 1958b). Crosses between populations usually result in good seed-set. However, sterile clones of *G. notata* are sometimes found, and these can be difficult to distinguish from *G. × pedicellata*. When fresh seeds are sown few germinate immediately; most are incorporated into a persistent seed bank and they can remain viable for at least five years (Roberts, 1986). Vegetative reproduction, by detached stolons, is probably frequent.

There is little evidence for any change in the distribution of this species at a national scale.

G. plicata is widespread in Europe from S. Scandinavia southwards. It is also found in N. Africa and extends east to central Asia.

This species appears to be closely related to *G. declinata*, and it may even have arisen from that species by autopolyploidy (Borrill, 1958b). Populations differ genetically in the extent to which they allocate resources to vegetative matter. Some produce a large vegetative biomass in their first year but do not flower until the second year, whereas others are smaller plants which flower in the first year (Borrill, 1958a).

153/38. *Phalaris* L.

This is a genus of 15 species, which includes both annuals and perennials. Most of them are native to the Mediterranean region, or to arid areas in the New World, although many have been deliberately or accidentally introduced to other areas (Anderson, 1961). The single aquatic species in the genus, *P. arundinacea*, is unusual in having a more northerly distribution and a broad geographical range.

This tall grass may form dense and virtually pure stands at the edge of standing and flowing waters, including lakes, reservoirs, rivers, streams, canals, ditches and flooded clay and gravel pits. It is most luxuriant at sites which are subject to large fluctuations in water table, such as the edges of spatey rivers, the margins of reservoirs and the Breckland meres. It is tolerant of a wide range of mineral substrates, from fine mud to coarse riverside shingle, but is rarely found over peat. It may also colonise artificial embankments. It grows at a range of nutrient levels from eutrophic to oligotrophic, although it rarely occurs in the most nutrient-poor sites. Few other species can grow in dense stands of *P. arundinacea* (Rodwell, 1995), and even if the stems are flattened by floodwater they tend to form a deep and tangled mass which prevents other species colonising. Small patches are occasionally found in flushed terrestrial habitats such as cliffs and motorway embankments, or even in sites which appear to be dry. The superficially similar reed *Phragmites australis* differs from this species in its greater tolerance of permanently flooded sites, and its restriction to more nutrient-rich waters. *P. arundinacea* extends from sea-level to 475 m (Llyn y Figyn).

P. arundinacea is a rhizomatous perennial. The shoots emerge in early spring and die back in autumn. Unlike *Phragmites australis*, the dead stems are not persistent. The main method of reproduction of established stands is by growth of the rhizome, but many stands are clearly composed of more than one clone, the clones differing in the pigmentation of their inflorescences. Plants often flower prolifically, and are wind-pollinated. The species is self-incompatible but often sets seed prolifically, although the flowers may become infected by the ergot *Claviceps purpurea* (Grime, Hodgson & Hunt, 1988). The seeds float, and may be dispersed in water. **Add germination details.** Detached vegetative shoots can root at the nodes and may float away to colonise new sites.

This plant is frequent throughout much of Britain and Ireland. There is little evidence for any decline. It remains common along watercourses in the London area (Burton, 1983) and persists by canals in inner Dublin (Wyse Jackson & Sheehy Skeffington, 1984). It colonises newly available habitats such as farm reservoirs and disused gravel pits. Plants with striped leaves (var. *picta* L., or Gardeners' Garters) have been known since the 17th century, and are often cultivated. They are sometimes planted by village ponds or persist as garden throw-outs in terrestrial habitats.

P. arundinacea is found throughout much of Europe, although it is rare in the Mediterranean region and is absent from some of the Mediterranean islands. It is widely distributed in the northern hemisphere, and has been introduced to C. & S. Africa, S. America, Java and Australia. The species is cytologically variable, with diploids, tetraploids, hexaploids and aneuploids all recorded.

153/64. *Phragmites* Adans.

This is a small genus which comprises 3-4 species of perennial reeds, one of which grows in Europe. For brief accounts of the taxonomy of the genus, see Clayton (1967, 1968).

This familiar emergent often forms dense and vigorous stands around the permanently flooded edges of still or slowly-flowing waters, in low-lying areas which are intermittently flooded, or at the upper edge of salt marshes, where it is tolerant of slight tidal scour. It is usually firmly rooted in the substrate, but it may also grow as lightly anchored floating rafts of "hover-reed". Its competitive ability is reduced in drier sites and it tends to be replaced by other emergents at the upper end of swamps or as reedbeds become silted up. It is most frequent over nutrient-rich substrates, becomes confined to flushed areas in regions of poor soils and is absent from the most oligotrophic habitats. Under optimal conditions stands of *P. australis* are dense and may exclude most competitors, but they are thinner and shorter towards the northern end of its range, or where ecological conditions are less favourable. *P. australis* is rarely present in sites where there are large and erratic fluctuations in water level, often being replaced in such habitats by *Phalaris arundinacea*. Its vigour may also be reduced by grazing by stock, wildfowl or, formerly, by coypu, and when grazed it may be replaced by other emergents such as *Glyceria maxima* or *Phalaris arundinacea*. Small colonies grow in a range of terrestrial habitats including moorland, sea cliffs, railway embankments, the central reservation of motorways and the edge of arable fields. This is a primarily lowland species, reaching 510 m on Brown Clee Hill.

P. australis is a perennial with a relatively deep rhizome. All the shoots emerge in spring, and the species is therefore sensitive to summer mowing. The shoots are killed by severe frosts. The dead, hollow stems persist through the winter and are important as oxygen diffuses down them to the rhizome. The flowers are wind-pollinated. Seed set and viability are very variable in Britain and Ireland. Seeds may germinate on damp terrestrial substrates or in very shallow water. Open habitats are colonised by wind-dispersed seed, but reproduction in closed stands is almost entirely by vegetative spread. Shoots detached as a result of disturbance float readily and are capable of regeneration (Grime, Hodgson & Hunt, 1988).

There is no conclusive fossil evidence that this species persisted in our area during the last glacial period, but it is recorded in the late glacial and is abundant in many later deposits (Godwin, 1975). It is a frequent species throughout most of its British and Irish range. However, there has been a progressive loss of *P. australis* swamps in Broadland in the last 50 years, perhaps caused by the weakening of the stems when they grow in nitrogen-rich water and a consequent inability to withstand wind and waves (Boar *et al.*, 1989). This is a widespread phenomenon in Europe, and the reed has been described as "a common species in decline" (Den Hartog *et al.*, 1989; Ostendorp, 1989).

This species occurs throughout Europe north to 70°N, and has a virtually cosmopolitan world distribution. It is phenotypically, genetically and cytologically variable, and there are chromosome races at several ploidy levels from triploid to octoploid, as well frequent aneuploids (Gorenflot, 1976; Gervais *et al.*, 1993). There are no detailed cytological data on plants in our area, although tetraploids ($2n=48$) occur in Co. Dublin (Curran, 1969).

This is an important species both to man and to other animals. For summaries of its ecology see Haslam (1972) and Rodwell (1995). An account of the growth of reed for thatching is provided by Haslam & McDougall (1972). Several birds require large stands of *P. australis*

for breeding (Andrews & Ward, 1991).

154. SPARGANIACEAE

This family contains a single genus, *Sparganium*.

153/1. *Sparganium* L.

There are 14 species in this genus, all of them aquatic, perennial herbs. Most species are found in the northern hemisphere, especially in N. America and E. Asia, although the genus extends to the mountains of S.E. Asia and temperate regions of Australia and New Zealand. The species are cytologically uniform, all having a chromosome number of $2n=30$.

The leafy stems of *Sparganium* species arise from a rather woody corm. Slender stolons or rhizomes with scale-like leaves grow out from the corm. The leaves die down in the winter and the corm itself dies, being replaced by new corms which develop on the upturned tips of some rhizomes. The species are variable in vegetative characters, but have a rather similar reproductive biology. The seeds germinate under water, and produce submerged juvenile leaves. At this stage the species are indistinguishable, but the mature vegetative leaves may remain submerged (as in *S. natans*), or become floating (*S. angustifolium*) or erect (*S. erectum*). The leaves die down in winter. The flowers are borne on emergent shoots. Individual flowers are unisexual, and they are aggregated into compact, globose male or female heads. Plants are bisexual, with the male head above the female head on the same inflorescence. The female heads become receptive before the pollen is shed, with all the flowers in a head maturing simultaneously. Plants are self-compatible and wind-pollinated. The fruits have a hydrophobic surface, and may float for several months. If the fruit is frozen in ice the exocarp ruptures and the endocarp sinks. The seeds may be dispersed by moving water or may perhaps be carried externally by boats and large birds, or by birds which eat the seeds. They have a distinct micropylar plug, which has to be removed before they will germinate.

Like many aquatics, the species of *Sparganium* have a good fossil record. This indicates that all four species currently present in our area were present before the last glacial period and persisted through it (Godwin, 1975).

Sparganium erectum is an easily recognised species. Four subspecies are recognised in Britain and Ireland, differing from each other in the shape of the fruit. These differences are maintained in cultivation. The subspecies are very under-recorded, as they can only be recognised late in the season, when the fruits are mature. The differences between the taxa are not easily grasped, and some are only apparent on dried material. These subspecies do not differ in ecology, and all four can sometimes be found growing together. They are mapped in the following pages, but the accompanying notes deal only with their world distribution and any other individual characteristics of the taxon. Partially sterile plants of *S. erectum* may be hybrids between the subspecies.

S. emersum and *S. angustifolium* are sometimes difficult to separate, and the fertile hybrid between them, *S. × diversifolium* Graebner, is common in northern Europe (Cook & Nicholls, 1986). The hybrid is known from a few sites in Scotland, and has recently been found in

Northumberland. It occurs in disturbed sites or in lakes and streams which were once oligotrophic but are now eutrophic (Cook, 1975), and it may be more frequent in our area than existing records suggest. Dwarf forms of *S. angustifolium* are often recorded as *S. natans*. These errors are presumably made by botanists who are not familiar with the true species, as the small, yellow-green leaves of *S. natans* with small fruiting heads which emerge directly from the leaf axils are distinctive. There are no reliable records of hybrids between *S. natans* and the other species in our area.

Much of the information in the species accounts is taken from the publications of Cook (1961, 1962, 1975, 1985) and Cook & Nicholls (1986, 1987). Maps of the world distribution of the species and subspecies are provided by Cook & Nicholls (1986, 1987).

This relatively short emergent is usually found in narrow bands in permanent water at the edge of lakes, rivers, streams, canals and ditches. Large expanses are infrequent but may occur in swamps or in ponds which are silting up, and the species has been recorded as a floating mass on liquid mud. It grows by still or slowly flowing water but is easily uprooted and is therefore absent from the edge of rapid waters or exposed shores. It is most vigorous in water 10-20 cm deep, but may flower and fruit at depths up to 1 metre. It cannot withstand prolonged emersion. It is often replaced by stands of the leafy reeds *Glyceria maxima*, *Phalaris arundinacea* or *Phragmites australis* on the landward side, and may give way to the smooth-stemmed *Eleocharis palustris* or *Schoenoplectus lacustris* where the water deepens. It is found over a range of fine, and often anaerobic, mineral substrates in both mesotrophic and eutrophic habitats, and is very tolerant of eutrophication. It is palatable to stock and is often absent from lake shores to which cattle have access, but frequent on adjacent, ungrazed stretches. It may also be eliminated by summer cutting. *Alisma plantago-aquatica* is a frequent associate. It is primarily a lowland species, but reaches 425 m at Nant Groes (Salter, 1935).

The leaves of *S. erectum* begin to grow in April; plants flower from July to September and the fruits may not ripen until November. The lowest female heads flower first and are no longer receptive when the pollen is shed by the upper inflorescences. This ensures some cross-pollination, but these lower heads rarely set much seed. Emasculation experiments have shown that there is a much reduced seed set in flowers which are 1 metre from a male inflorescence, but some pollen may travel up to 2 metres. Insects may visit the male flowers, but rarely visit female flowers and are therefore insignificant as pollen vectors (Pinkess, 1980; Cook & Nicholls, 1986). Some plants are partially sterile, and remain so in cultivation. In the wild the mortality of seedlings is high (especially in cloudy water) and, unlike the other *Sparganium* species, *S. erectum* rarely becomes established from seed. Plants spread vegetatively by growth of the rhizome, by dispersal of detached rhizomes and perhaps of uprooted plants. Plants stranded above the water are dwarfed but send out numerous rhizomes. In deep or rapidly flowing water *S. erectum* may occasionally be found with submerged or floating leaves, but such individuals do not flower.

This is a native member of our flora which may have persisted through the last glacial period (Godwin, 1975). It is frequent in much of its British and Irish range, and its tolerance of eutrophication doubtless assists its survival in many lowland habitats. **Boating and canals?** It is able to colonise new habitats: it was present in only two of six Nottinghamshire ponds which were surveyed in 1923, but had reached them all 40 years later (Cook, 1962).

S. erectum is widespread in temperate regions of Europe, N. Africa and Asia, east to Japan, in western N. America from British Columbia to California, and in S.E. Australia, where it may be introduced. It is replaced by a similar species, *S. eurycarpa*, in much of N. America.

Sparganium erectum subsp. *erectum*

This subspecies is common in central and southern Europe, extending north to southernmost Scandinavia. It extends south and east to Turkey and the Caucasus.

In eastern Asia this subspecies is replaced by subsp. *stoloniferum* (F. Hamilton ex Graebner) C.D.K. Cook & M.S. Nicholls. Subsp. *stoloniferum* is the only one of the five subspecies of *S. erectum* which is absent from Europe, but it has the widest distribution of them all, being the plant found in N. America and S.E. Australia.

Sparganium erectum subsp. *microcarpum* (Neuman) Domin

This has the most northerly European distribution of the *S. erectum* subspecies, being particularly common in Scandinavia. It extends south to N. Africa, Turkey and the Caucasus.

· Partially sterile hybrids between this subspecies and subsp. *neglectum* are occasionally found growing with the parents (Cook & Nicholls, 1987). We do not know if they occur in the British Isles.

Sparganium erectum subsp. *neglectum* (Beeby) Schinz & Thell.

Subsp. *neglectum* is widespread in Europe, including the Mediterranean area, and extends north to southern Scandinavia. It is also recorded from W. Asia.

This was the only segregate of *S. erectum* recognised by many British botanists before the publication of Cook's (1961) study of the genus. It was described by Beeby (1885) from Albury Ponds near Guildford.

Sparganium erectum subsp. *oocarpum* (Čelak) Domin

This taxon is recorded from scattered localities in Europe, north to the British Isles. It appears to be most frequent in S.E. Europe, and is also found in N. Africa, Turkey and Iraq.

This subspecies is partially sterile, and Cook (1961, 1975) and others have suggested that it may have originated as a hybrid between subsp. *erectum* and subsp. *neglectum*. However, it is unlikely to be a simple hybrid between these two taxa.

S. emersum is found in still or slowly flowing, mesotrophic or eutrophic water in lakes, ponds, rivers, streams, canals and ditches. It is usually found in water 0.2-1 metre deep. It is found in deeper water than *S. erectum*, and in many sites the partially emergent or floating leaves of *S. emersum* are replaced towards the edge of the water by a band of the emergent *S. erectum*. It is usually found over fine, mineral substrates, and is a particularly characteristic species of rivers over clay (Holmes, 1983). In meandering rivers over coarser substrates it is often found at each curve, in sites where fine silt accumulates (Cook & Nicholls, 1986). It is not easily dislodged by flowing water, and so it may grow in rivers subject to spate. Although it is often frequent, it rarely forms dominant stands in which other species are unable to grow. *Nuphar lutea* is a characteristic associate. *S. emersum* is tolerant of disturbance by dredging or boat traffic, and it persists in heavily managed rivers from which most other aquatics have disappeared. Although it is primarily a lowland species, it ascends to over 500 m in Crook Burn.

This is a deeply rooted perennial which spreads by growth of the slender rhizomes. The leaves are short-lived, dying after 31-39 days, but are rapidly replaced (Wiggers Nielsen *et al.*, 1985). *S. emersum* often persists as vegetative plants, but it flowers and fruits in well-illuminated, relatively shallow, still or sluggish water. It will withstand periods of emersion, but not prolonged drought.

This species may be under-recorded in some areas, as many botanists overlook non-flowering plants or will not attempt to identify them. It has decreased in some areas, and (like *Sagittaria sagittifolia*) it has sometimes disappeared from ponds and ditches in the river plain, but survives in the river channel.

S. emersum is found in temperate and boreal regions throughout the northern hemisphere. The European plant is subsp. *emersum*, which occurs throughout the range of the species. In western N. America populations have some characteristics of *S. angustifolium*, and may represent stabilised hybrids between these two species. Subsp. *acaule* (Beeby ex Macoun) C.D.K. Cook & M.S. Nicholls is confined to eastern N. America, where it is more frequent than subsp. *emersum*.

This is one of the most characteristic species of clear, oligotrophic lakes, and it is also found in pools, rivers, streams and ditches. It is more tolerant of exposure than the other species in the genus, but large stands characteristically occur away from the exposed edges of lakes, growing just offshore in water 0.3-1.5 m deep. It sometimes grows in more mesotrophic waters. The species may grow amongst open stands of *Equisetum fluviatile*, or with submerged plants such as *Juncus bulbosus*, *Myriophyllum alternifolium* and *Utricularia vulgaris sensu lato*. It is recorded from sea level to 990 m on Ben Lawers (Druce, 1932).

This species has narrow floating leaves with an unwettable upper surface. It spreads vegetatively by the slender rhizomes. Many colonies flower only sparingly. The species will grow terrestrially on damp ground exposed above the water level for periods of the summer.

The distribution map of *S. angustifolium* in the *Atlas of the British Flora* greatly underestimated its distribution, and it is probably still under-recorded in northern and western areas where aquatic habitats have not been surveyed systematically. The pencil-thin leaves of some populations are distinctive, and are more likely to be confused with *Glyceria fluitans* than other *Sparganium* species, but plants with broader leaves are more difficult to separate from *S. emersum*. Even if plants are flowering and fruiting, they are often difficult to identify as they often grow several metres offshore and are not easily collected by grapping. Records of *S. angustifolium* outside the main range of the species have only been accepted if they have been verified by experts. The poor historical records make it difficult to assess changes in distribution. There is no reason to suspect that it has decreased in its main strongholds in the north and west, but the map suggests that, like other species of oligotrophic water, it may have decreased towards the eastern edge of its British and Irish ranges.

S. angustifolium is a plant of the boreal regions of Eurasia and N. America, although it is absent from the continental interior of Asia. In Europe it is frequent in the north, and extends south in the mountains to the Iberian peninsula, the Alps and the Balkans.

This small species grows in sheltered bays at the edge of lakes, in slowly flowing streams and drainage ditches, and in fenland pools. It usually grows in shallow water over peaty substrates, most frequently growing at depths of 10-50 cm. It may grow terrestrially in damp moss carpets or as submerged, non-flowering plants in deeper water. It is found in peatlands over chalk and limestone, where it grows in clear, highly calcareous waters. It also grows in more acidic areas, where the water or the substrate is enriched by local outcrops of base-rich rocks, such as limestone or basalt. *S. natans* is a plant of mesotrophic habitats, being absent from eutrophic or turbid waters. **List CDP records and add associates.** It is a mainly lowland species, which reaches 365 m at Loch Kinardochoy.

In shallow water this species has submerged and floating leaves; the floating leaves, unlike those of *S. angustifolium*, are wettable on both sides. Plants in shallow water flower and fruit freely, but those in terrestrial habitats are often less prolific (Cook & Nicholls, 1986). The usual mode of reproduction is probably by seed, and swards of seedlings can sometimes be seen in shallow water. The rhizomes are short and few in number.

There is very clear evidence that the species has decreased in England in historic times. Many populations have been exterminated by habitat destruction, with the drainage of fenland sites and the destruction of small ponds and ditches. The distribution of the species elsewhere is less clear, and there is insufficient evidence to comment on trends in its distribution. Terrestrial forms of *S. angustifolium* are often identified as this species, and *S. natans* is almost certainly over-recorded in descriptions of aquatic vegetation (e.g. Spence, 1964; Rodwell, 1985). The diffuse distribution of *S. natans* compared to *S. angustifolium* makes it difficult to eliminate errors of identification (cf. *S. angustifolium*), and the map doubtless contains some errors, especially in Scotland.

This species is found in boreal and temperate regions of the northern hemisphere; it is absent from much of eastern Asia but is recorded from Japan. In Europe it is absent from the arctic and the Mediterranean regions, but widespread between these zones.

155. TYPHACEAE

This is a small family containing a single genus, *Typha*. It is closely related to the Sparganiaceae, and Müller-Doblies (1970) has even suggested that the two families should be united. Reasons for maintaining the taxa as separate families are given by Cook & Nicholls (1986). The affinity of both families to the rest of the monocots are obscure.

155/1. *Typha* L.

The eight species in this genus are rhizomatous perennials which usually grow on wet ground or as emergents. The genus has a cosmopolitan distribution. The two species found in our area have been well-studied, especially in N. America (where they are known as 'cattails'), and there is a substantial body of literature which deals with them. This is summarised in the ecological accounts by Grace & Harrison (1986) and Grime *et al.* (1988).

Both of our species are tall emergents with conspicuous inflorescences. The male and female flowers are aggregated into separate club-shaped heads, the female head below the male on the same inflorescence. Pollination is by wind. The female flowers become receptive shortly before the pollen is released, but remain receptive for up to 4 weeks so that most of them are self-pollinated. The fertile female flowers are mixed with sterile flowers in the inflorescence. The sterile flowers have club-shaped apices, and both fertile and sterile flowers have long hairs on the pedicels. The heads of the sterile flowers swell in wet weather, protecting the seeds from water. In dry weather the hairs on the pedicels spread and the inflorescence 'bursts'. The fruit drifts away, still attached to the hairy pedicel. If the diaspore lands on dry ground the hairs remain spread, and it is likely to be blown away. If it lands on water it initially rests on the tips of the hairs, and it may be blown across the surface. After a few minutes the hairs on the pedicel fold back, bringing the fruit into contact with the water. When wetted the pericarp springs open, releasing the seed which immediately sinks. For further details of this sophisticated dispersal mechanism, see Krattinger (1975) and Cook (1987).

A hybrid between *Typha angustifolia* and *T. latifolia*, *T. × glauca* Godron, is known from scattered sites in England. Although accounts of it were given by Lousley (1947) and Tutin (1947), it is still unfamiliar to most British botanists and is almost certainly under-recorded. In N. America the taxonomy and genetic variation of these two species and their putative hybrid has been studied in detail. e.g. by Lee (1975), Sharitz *et al.* (1980). and Smith (1967). The hybrid nature of *T. × glauca* has been demonstrated by crossing experiments, and by isozyme studies. *T. × glauca* is partially sterile. It has been suggested that populations are not simple F1 hybrids, and that the hybrid backcrosses with *T. angustifolia*, leading to introgression between the two species. Krattinger (1975) suggests that as the inflorescences are usually self-pollinated, the apparent backcrosses are more likely to be the result of segregation in the F2 generation. Detailed study of the European *T. × glauca* is required to establish whether the situation is comparable to that in N. America.

T. latifolia grows in shallow water or on exposed mud at the edge of lakes, ponds, canals and ditches; it is less frequent by streams and rivers. It is a plant of nutrient-rich sites, which is most frequent on mineral soils but also grows over peat. It is most vigorous in very shallow water, and it often fills shallow ditches and ponds. Vigorous stands exclude most other species. It rarely grows at depths greater than 0.5 m, frequently being replaced by *Phragmites australis* in deeper water, and in saline sites. It is very tolerant of eutrophication. **Note on palatability.** It is recorded from sea-level to 500 metres on Brown Clee Hill.

T. latifolia is a shallow-rooted perennial. The shoots may be produced throughout the growing season. They die in autumn, but the dead stems and infructescences may persist through the winter. Ramets (consisting of a rhizome branch and associated shoots) are fairly short lived, lasting for up to 3 years. Colonies may expand by growth of the rhizome at rates of 4 m per year, and detached portions of rhizome may float and establish new colonies. The pollen of *T. latifolia* is shed in tetrads, but it may be dispersed for at least a kilometre by strong winds (Krattinger, 1975). The flowers at the top of the female inflorescence set more seed, as they receive more pollen from the male inflorescence than those below. The inflorescences may produce over 200,000 seeds (Yeo, 1964). The seeds may germinate when they are shed, but require moisture, light and relatively high temperatures (Sifton, 1959). At low light intensities, fluctuating temperatures will stimulate germination. Germination may take place in anaerobic conditions. If conditions are unsuitable, the seed may remain dormant for long periods. The species effectively colonises ditches, sand and gravel pits, and even static water tanks and flooded building sites, by wind-blown seed.

The tetrads of *T. latifolia* pollen are distinctive fossils, and demonstrate that the species is a long-established native (Godwin, 1975). It appears to be more abundant now than it was last century. This increase has been noted in areas as dissimilar as Cornwall (Margetts & David, 1981), the London area (Burton, 1983) and Northumberland (Swan, 1993). Burton suggests that it increased in response to the relaxation of grazing pressure around ponds on commons, and that these then provided foci from which the species spread. In other areas, such as the Isle of Man, it has apparently spread from stock planted in ponds as an ornamental species (Allen, 1984).

T. latifolia is widespread in temperate regions of the northern hemisphere, although it is rare in eastern Asia. It extends south to S. Africa, Madagascar, central America and the West Indies.

In N. America this has been shown to be a very variable species, with ecotypes which differ in many morphological and physiological characters.

This species is similar in its ecology to *T. latifolia*, and like that species is often found in virtually pure stands. It is usually found in water at least 0.5 m deep, and around some lakes a zone of *T. latifolia* may be replaced by one of *T. angustifolia* as the water deepens. *T. angustifolia* can be an important colonist of open water, sometimes growing in such sites with *Schoenoplectus lacustris*, and it can even extend over the surface of the water as a floating mat (Lambert, 1951; Lambert & Jennings, 1951; Sinker, 1962). In addition to lakes, its habitats include ponds, ditches, flooded clay and gravel pits and, occasionally, the banks of rivers and streams. *T. angustifolia* is less restricted to eutrophic sites than *T. latifolia*, and may grow in mesotrophic waters. It is palatable to stock, although the sites where it grows are often inaccessible to them, and it is also eaten by geese. This species was greatly reduced in numbers at some sites in Broadland when coypu numbers were high, as both the leaves and the rhizomes were eaten (Gosling, 1974). *T. angustifolia* is a lowland species.

T. angustifolia is a rhizomatous perennial. It has fewer but larger rhizomes than *T. latifolia*, and these form a denser mass but spread less rapidly (Grace & Wetzel, 1982). Its ramets live longer than those of that species. Colonies spread by the growth of the rhizome, by detached rhizome fragments or sometimes by large fragments of floating mat which may break off and blow across the surface of a lake. Rather surprisingly, a greater proportion of the biomass of *T. angustifolia* than of *T. latifolia* is devoted to the reproductive structures. The pollen is released singly rather than in tetrads, and therefore blows away more readily. There is more cross- and less self-pollination in this species than in *T. latifolia* (Krattinger, 1975).

It is not easy to generalise about trends in the distribution of this species. In Broadland it spread after 1800 as nutrient levels and sedimentation increased, often acting as a pioneer colonist of open water with *Phragmites australis* following in its wake. It has decreased since 1940, probably because it is intolerant of very eutrophic conditions and of wave-scour from boats (George, 1992). *T. angustifolia* is often planted as an ornamental and has been introduced to new sites both within and outside its native range. It is much less frequent as a colonist of new sites than *T. latifolia*.

This species is widespread in temperate regions of the northern hemisphere. It is replaced in warmer climates by the closely related *T. domingensis* (Pers.) Steudel. In N. America, as in Britain, it does not extend as far north as *T. latifolia*.

Experimental studies have shown that if *T. angustifolia* is transplanted into shallow water it can survive in the absence of *T. latifolia*, but is outcompeted by that species if both are present. *T. latifolia* is at an advantage because of its broader leaves with greater surface area but *T. angustifolia* is able to survive in deeper water because here the narrow leaves and greater food stores in the rhizome enable it to send leafy shoots above the water level (Grace & Wetzel, 1981, 1982).

159. IRIDACEAE

This family contains 92 genera and 1850 species, most of which are geophytes with rhizomes, corms or bulbs. The family has a cosmopolitan distribution, but the species are particularly numerous in the seasonally dry climates of the eastern Mediterranean regions, S. Africa and central and S. America. Many of the species have attractive flowers, and the family is important to horticulturists. It is of less interest to the aquatic botanist: only 2 genera contain aquatics, the S. American *Cypella* and the type genus *Iris*, which occurs in our area.

159/5. *Iris* L.

There are 300 species of *Iris*, most of which grow in north temperate regions. They have large flowers and include some favourite garden plants. The genus is divisible into four subgenera. Subgenus *Iris* contains rhizomatous species, Subgenus *Scorpiris* and *Xiphium* have bulbs [and corms??] and the monotypic Subgenus *Nepalenses* has tuberous roots. The two species native to our area are members of Subgenus *Iris*, the aquatic *I. pseudacorus* and *I. foetidissima*, a plant of dry habitats.

Look at Matthew, B. 1981, *The Iris*; Koehlein, F., 1987 *Iris*, C. Helm.

I. pseudacorus is one of the few aquatics to have complex adaptations to insect pollination. The flower consists of three units, which have to be visited separately by insects. Each of the large outer tepals provides a platform on which the insects alight. A dark yellow patch surrounded by a brown zigzag line acts as a nectar guide. The pollinating insects follow it and crawl into a tube; the lower half of this tube is formed from the stalk of the tepal and the upper half is made of the flattened style and stigma. As the insect enters the tube, any pollen it carries is brushed from its back onto the stigma, and new pollen is collected from a single anther. Only long-tongued insects can obtain nectar from *I. pseudacorus*, which is usually pollinated by bumble bees (Procter & Yeo, 1973).

Hybridisation is well-known in the genus *Iris*. Many of the most popular cultivars are hybrids of ancient origin, and wild species in N. America provided a classic example of introgressive hybridisation (Anderson, 1949). However, no hybrids of *I. pseudacorus* are known, and attempts to synthesise them artificially have been unsuccessful (Dykes, 1913).—

The ecology of *I. pseudacorus* is summarised by Sutherland (1990), and a detailed study of the demography of populations colonising abandoned meadows has been made by Falinska (1986).

This species grows as an emergent in shallow water at the edge of lakes, ponds, streams and rivers, in swamps, fens and the wettest parts of dune slacks, by springs and flushes and in damp pastures, meadows and fen carr. In the south and east it is most frequent in water less than 0.3 m deep at the edge of eutrophic lakes and rivers. It has also been found as a floating mat at the edge of lakes. In some northern and western areas (including the Hebrides) it is less frequent by lakes, but it grows in dense stands by coastal streams, on coastal shingle, upper salt marshes, raised beaches and in lowland pastures (Adam *et al.*, 1977). It is found over a wide range of organic and inorganic, acidic or basic soils, and it may even grow on bare, irrigated rocks. However, it requires sites which are moderately fertile and are moist or flooded for most of the year. It tolerates occasional flooding by brackish water at its coastal sites, and periodic droughts. It is a lowland species, only recorded above 300 m **add details**, **Wilson says Co Sligo**.

I. pseudacorus is a perennial with a thick rhizome. Its shoots may remain green in mild winters, or die back in more severe weather. Plants flower and set seed in open conditions, but flowering is reduced in shade. The seeds float and are dispersed by water. Germination usually occurs in spring and early summer, and the seedling has a remarkably high proportion of root to shoot, an adaptation which anchors it in the water (Whitehead, 1971). Seedlings rarely become established in closed habitats but will do so where conditions are more open. Vegetative spread is by direct growth of the rhizome (clones 20 m in diameter have been recorded in Ireland), or by rhizome fragments which are washed downstream. *I. pseudacorus* contains poisonous glycosides, and it is avoided by almost all herbivorous vertebrates and by many invertebrates, although the brittle leaves are susceptible to trampling.

This species grows in suitable habitats throughout its British and Irish range, and it is particularly frequent in lowland habitats in the north and west. Crawford (19??, **CHK and find out why**) comments that it is one of the few plants that would probably survive a nuclear holocaust! In S.E. England habitat destruction has reduced its frequency, but plants have been deliberately planted by lakes and ponds or have escaped from cultivation, thus obscuring its native range. Both wild-type plants and cultivars are grown in gardens (Leslie, 1992).

I. pseudacorus is widespread in Europe, although absent from northern Scandinavia and Iceland. It also occurs as a native in N. Africa and in Asia east to the Caucasus. In N. America and New Zealand it has spread along water courses, and is now widely naturalised (Cody, 1961; Healy & Edgar, 1980; Raven & Thomas, 1970). There is some cytological variation, but all material from Scotland examined by Dyer *et al.* (1976) was uniform, with $2n=34$.

Send for Cody (1961), Dymes (1920).

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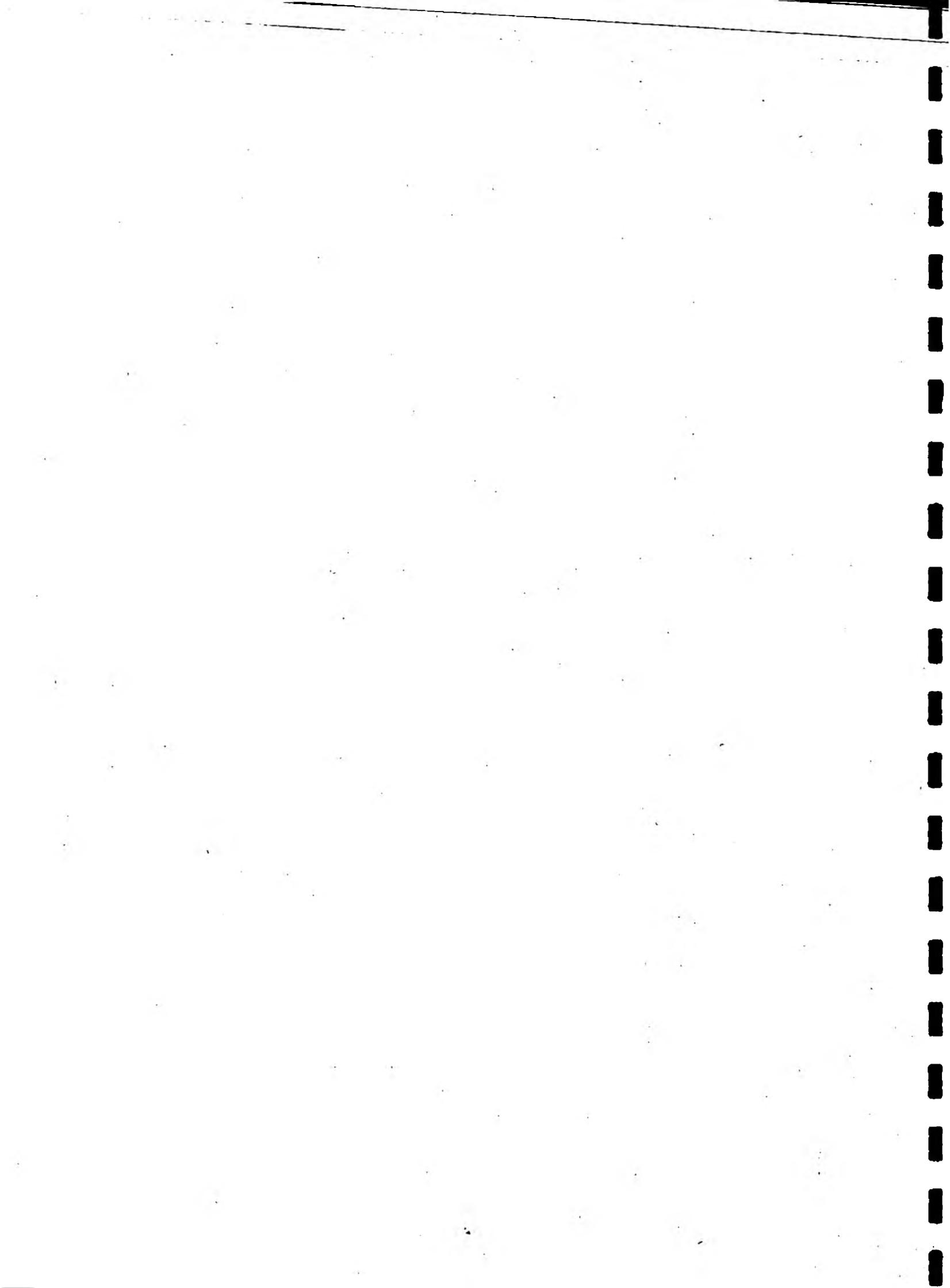
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INDEX TO SPECIES ACCOUNTS

Acorus	219	Calla	222
calamus	220	palustris	223
gramineus	221	Callitrichaceae	108
Alisma	146	Callitriche	108
gramineum	150	brutia	115
lanceolatum	149	hamulata	116
plantago-aquatica	148	hermaphroditica	110
Alismataceae	137	obtusangula	114
Apiaceae	88	platycarpa	113
Apium	97	stagnalis	112
inundatum	99	truncata	111
nodiflorum	98	Caltha	26
Aponogeton	173	palustris	27
distachyos	174	Campanulaceae	132
Aponogetonaceae	173	Canary-grass, Reed	284
Araceae	219	Cape-pondweed	174
Arrowhead	138	Carex	256
Canadian	140	acuta	270
Narrow-leaved	141	acutiformis	261
Arum, Bog	223	aquatilis	269
Awlwort	66	elata	272
Azolla	13	lasiocarpa	260
filiculoides	14	limosa	267
Azollaceae	13	paniculata	259
Baldellia	142	pseudocyperus	263
ranunculoides	143	recta	268
Berula	90	riparia	262
erecta	91	rostrata	264
Bistort, Amphibious	50	vesicaria	265
Bladder-sedge	265	Catabrosa	274
Bladderwort	129	aquatica	275
Greater	128	Ceratophyllaceae	23
Lesser	131	Ceratophyllum	23
Bog-sedge	267	demersum	24
Bogbean	101	submersum	25
Boraginaceae	104	Cinquefoil, Marsh	73
Brassicaceae	57	Cladium	253
Brooklime	121	mariscus	254
Bolboschoenus	244	Club-rush, Common	247
maritimus	245	Floating	252
Bulrush	299	Grey	248
Lesser	300	Sea	245
Bur-reed, Branched	290	Sharp	250
Floating	296	Triangular	249
Least	297	Crassula	69
Unbranched	295	aquatica	70
Butomaceae	135	helmsii	71
Butomus	135	Crassulaceae	69
umbellatus	136		

Crowfoot, Ivy-leaved	35	<i>maxima</i>	277
New Forest	37	<i>notata</i>	279
Round-leaved	36	× <i>pedicellata</i>	280
Three-lobed	38	<i>plicata</i>	282
<i>Cruciferae</i>	57	<i>Gramineae</i>	274
Cyperaceae	239	Groenlandia	206
Damasonium	151	<i>densa</i>	207
<i>alisma</i>	152	Haloragaceae	74
Dock, Scottish	52	Hampshire-purslane	86
Water	53	Hippuridaceae	106
Duck-potato	139	Hippuris	106
Duckweed, Common	229	<i>vulgaris</i>	107
Fat	228	Hornwort, Rigid	24
Greater	226	Soft	25
Ivy-leaved	230	Horsetail, Shore	10
Least	231	Water	9
Rootless	233	Hottonia	67
Egeria	159	<i>palustris</i>	68
<i>densa</i>	160	Hydrilla	166
Elatinaceae	54	<i>verticillata</i>	167
Elatine	54	Hydrocharis	153
<i>hexandra</i>	55	<i>morsus-ranae</i>	154
<i>hydropiper</i>	56	Hydrocharitaceae	153
Eleocharis	239	Hydrocotyle	88
<i>acicularis</i>	243	<i>ranunculoides</i>	89
<i>palustris</i>	240	Iridaceae	301
subsp. <i>palustris</i>	242	Iris	301
subsp. <i>vulgaris</i>	241	<i>pseudacorus</i>	302
Eleogiton	251	Isoetaceae	5
<i>fluitans</i>	252	Isoetes	5
Elodea	161	<i>echinospora</i>	7
<i>callitrichoides</i>	165	<i>lacustris</i>	6
<i>canadensis</i>	162	Juncaceae	237
<i>nuttallii</i>	164	Juncus	237
Equisetaceae	8	<i>bulbosus</i>	238
Equisetum	8	Lagarosiphon	169
<i>arvense</i> × <i>fluviatile</i>	10	<i>major</i>	170
<i>fluviatile</i>	9	Lemna	227
× <i>litorale</i>	10	<i>gibba</i>	228
Eriocaulaceae	234	<i>minor</i>	229
Eriocaulon	234	<i>minuscula</i>	231
<i>aquaticum</i>	235	<i>minuta</i>	231
Fen-sedge, Great	254	<i>polyrhiza</i>	226
Flag, Yellow	302	<i>trisulca</i>	230
Flowering-rush	136	Lemnaceae	224
Forget-me-not, Water	105	Lentibulariaceae	125
Frogbit	154	Littorella	117
Glyceria	276	<i>uniflora</i>	118
<i>declinata</i>	281	Lobelia	132
<i>fluitans</i>	279	<i>dortmanna</i>	133
<i>fluitans</i> × <i>notata</i>	280	Lobelia, Water	133

Ludwigia	85	fistulosa	93
palustris	86	fluviatilis	95
Luronium	144	Onagraceae	85
natans	145	Parrot's-feather	76
Lythraceae	81	Pennywort, Floating	89
Lythrum	81	Persicaria	49
portula	82	amphibia	50
subsp. portula	83	Phalaris	283
subsp. longidentata	84	arundinacea	284
Mare's tail	107	Phragmites	285
Marsh-marigold	27	australis	286
Marshwort, Lesser	99	Pigmyweed	70
Marsileaceae	11	New Zealand	71
Menyanthaceae	100	Pillwort	12
Menyanthes	100	Pilularia	11
trifoliata	101	globulifera	12
Myosotis	104	Pipewort	235
scorpioides	105	Plantaginaceae	117
Myriophyllum	74	Poaceae	274
alterniflorum	79	Polygonaceae	49
aquaticum	76	<i>Polygonum</i>	49
heterophyllum	80	<i>amphibium</i>	50
spicatum	77	Pond-sedge, Greater	262
verrucosum	78	Lesser	261
verticillatum	75	Pondweed, American	192
Naiad, Holly-leaved	216	Blunt-leaved	197
Slender	214	Bog	179
Najadaceae	212	Bright-leaved	186
Najas	213	Broad-leaved	177
flexilis	214	Cooper's	191
graminea	215	Curled	202
marina	216	Fen	180
<i>Nasturtium</i>	61	Fennel	205
<i>microphyllum</i>	61	Flat-stalked	193
<i>microphyllum</i> × <i>officinale</i>	60	Graceful	188
<i>officinale</i>	58	Grass-wrack	200
Nuphar	18	Hairlike	199
advena	22	Horned	218
lutea	19	Lesser	196
lutea × pumila	20	Linton's	194
pumila	21	Loddon	181
× spenneriana	20	Long-leaved	183
Nymphaceae	15	Long-stalked	189
Nymphaea	15	Opposite-leaved	207
alba	16	Perfoliate	190
subsp. occidentalis	17	Red	187
Nymphoides	102	Ribbon-leaved	178
peltata	103	Sharp-leaved	201
Oenanthe	92	Shetland	195
aquatica	96	Shining	182
crocata	94	Slender-leaved	203

Small	198	Ranunculus	28
Swedish	204	aquatilis	41
Various-leaved	185	aquatilis × fluitans	46
Willow-leaved	184	× bachii	46
Potamogeton	175	baudotii	39
acutifolius	201	circinatus	48
alpinus	187	flammula	30
alpinus × crispus	188	subsp. flammula	30
berchtoldii	198	subsp. minimus	31
coloratus	180	subsp. scoticus	32
compressus	200	flammula × reptans	33
× cooperi	191	fluitans	47
crispus	202	fluitans × peltatus	43
crispus × friesii	194	fluitans × trichophyllus	46
crispus × perfoliatus	191	hederaceus	35
epihydus	192	× kelchoensis	43
filiformis	203	× levenensis	33
filiformis × pectinatus	204	× novae-forestae	37
friesii	193	orniophyllus	36
gramineus	185	orniophyllus × tripartitus	37
gramineus × natans	178	peltatus	42
gramineus × perfoliatus	186	peltatus × fluitans	43
gramineus × lucens	183	penicillatus	44
× lintonii	194	subsp. penicillatus	44
lucens	182	subsp. pseudofluitans	45
lucens × perfoliatus	184	reptans	34
natans	177	trichophyllus	40
nodosus	181	tripartitus	38
× nitens	186	Reed, Common	286
obtusifolius	197	Rorippa	57
× olivaceus	188	amphibia	64
pectinatus	205	amphibia × palustris	62
perfoliatus	190	amphibia × sylvestris	63
polygonifolius	179	× anceps	63
praelongus	189	× erythrocaulis	62
pusillus	196	microphylla	61
rutilus	195	microphylla × nasturtium-	
× salicifolius	184	aquaticum	60
× sparganifolius	178	nasturtium-aquaticum	
× suecicus	204	<i>sensu lato</i>	58
trichoides	199	nasturtium-aquaticum	59
× zizii	183	× sterilis	60
Potamogetonaceae	175	Rosaceae	72
Potentilla	72	Rumex	51
palustris	73	aquaticus	52
Primulaceae	67	hydrolapathum	53
Quillwort	6	Ruppia	209
Spring	7	cirrhosa	211
Ranunculaceae	26	maritima	210
		Ruppiaceae	208
		Rush, Bulbous	238

Sagittaria	137	Tasselweed, Beaked	210
latifolia	139	Spiral	211
rigida	140	Tufted-sedge	272
sagittifolia	138	Slender	270
subulata	141	Tussock-sedge, Greater	259
Schoenoplectus	246	Typha	298
lacustris	247	angustifolia	300
pungens	250	latifolia	299
tabernaemontani	248	Typhaceae	298
triqueter	249	<i>Umbelliferae</i>	88
<i>Scirpus maritimus</i>	245	Utricularia	125
Scrophulariaceae	120	australis	129
Sedge, Bottle	264	intermedia	130
Cyperus	263	minor	131
Estuarine	268	vulgaris <i>sensu lato</i>	127
Slender	260	vulgaris	128
Water	269	Vallisneria	171
Shoreweed	118	spiralis	172
Sparganiaceae	288	Veronica	120
Sparganium	288	anagallis-aquatica	122
angustifolium	296	anagallis-aquatica × catenata	123
emersum	295	beccabunga	121
erectum	290	catenata	124
subsp. erectum	291	× lackschewitzii	123
subsp. microcarpum	292	Water Fern	14
subsp. neglectum	293	Water-cress	58,59
subsp. oocarpum	294	Fool's	98
<i>minimum</i>	297	Hybrid	60
natans	297	Narrow-fruited	61
Spatter-dock	22	Water-crowfoot, Brackish	39
Spearwort, Creeping	34	Common	41
Lesser	30	Fan-leaved	48
Loch Leven	33	Kelso	43
Spike-rush, Common	240	Pond	42
Needle	243	River	47
Spirodela	225	Thread-leaved	40
polyrhiza	226	Water-dropwort, Fine-leaved	96
Starfruit	152	Hemlock	94
Stratiotes	156	River	95
aloides	157	Tubular	93
Subularia	65	Water-lily, Fringed	103
aquatica	66	Hybrid	20
Sweet-flag	220	Least	21
Slender	221	White	16
Sweet-grass, Floating	279	Yellow	19
Hybrid	280	Water-milfoil, Alternate	79
Plicate	282	Spiked	77
Reed	277	Whorled	75
Small	281	Water-parsnip, Lesser	91
Tapegrass	172		

Water-plantain	148
Floating	145
Lesser	143
Narrow-leaved	149
Ribbon-leaved	150
Water-purslane	82
Water-soldier	157
Water-speedwell, Pink	124
Blue	122
Water-starwort, Autumnal	110
Blunt-fruited	114
Common	112
Intermediate	116
Pedunculate	115
Short-leaved	111
Various-leaved	113
Water-violet	68
Waterweed, Canadian	162
Curly	170
Esthwaite	167
Large-flowered	160
Nuttall's	164
South American	165
Waterwort, Eight-stamened	56
Six-stamened	55
Whorl-grass	275
Wolffia	232
arrhiza	233
Yellow-cress, Great	64
Hybrid	63
Thames	62
Zannichellia	217
palustris	218
Zannichelliaceae	217