

Taxonomy of *Elodea* Michx in the British Isles

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ABSTRACT

Three species of *Elodea* are now known to occur in the British Isles: *E. canadensis* Michx, *E. nuttallii* (Planch.) H. St John and *E. callitrichoides* (Rich.) Casp. The taxonomic histories of the genus and three species are reviewed. Keys and descriptions of the species are given, together with details of their habitats and distribution.

Elodea Michx is a New World genus, of which several species are known to be adventive in the Old World. A recent investigation (Simpson 1983) has shown three species to be adventive in the British Isles, namely *E. canadensis* Michx, *E. nuttallii* (Planch.) H. St John and *E. callitrichoides* (Rich.) Casp. (following Cook & Urmí-König's (1984) recommendation that plants previously referred to as *E. ernstiae* H. St John should now be assigned to *E. callitrichoides*). Simpson (1984) outlined the introduction and spread of these species in the British Isles. This paper presents a brief taxonomic history of the genus together with the British and Irish species, and summarizes the taxonomic conclusions drawn from the work in the form of a key and brief systematic accounts. A further paper in preparation will give a more detailed account of intraspecific variation in *E. canadensis* and *E. nuttallii*.

The vegetative structure of *Elodea* is comparatively simple, consisting of a series of axillary, branched, terete stems with narrow, sessile and minutely serrate leaves. Three decussate pairs of leaves occur on the lowest part of the stem, above which all the leaves are in whorls. The decussate leaves are also distinctly smaller than the whorled ones. A midrib is present in all leaves but no other venation is apparent. Epidermal hairs are absent from both stems and leaves. A pair of minute, entire, nodal scales (or squamulae intravaginales) are attached between the stem and leaf base on the adaxial side of the leaf. Adventitious roots are produced at the nodes, coinciding with the growth of a new stem. One root is produced with each stem, and root hairs occur only when the root is in sediment. Despite its simplicity, the vegetative morphology of *Elodea* is, in common with other aquatic macrophytes, highly plastic, and this has caused much of the taxonomic confusion. Such variation appears to be brought about by a variety of environmental factors, particularly in relation to light and temperature (Simpson 1983). The main growing season is between mid-April and mid-September. At other times growth is very much reduced or ceases completely. The plant overwinters by means of short, unbranched stems, or by the production of turions (hibernacula). The latter arise in the upper leaf axils during early autumn and may remain in situ, or break free and fall to the substrate, where they germinate the following spring.

The vegetative anatomy of *Elodea* reflects the plant's morphological simplicity. The stem consists of a single epidermal layer, a cortex consisting of parenchymatous and aerenchymatous tissues, and a simple stele with a central protoxylem lacuna. The leaf consists of only two cell layers. Stomata are absent and there is only a thin cuticle. Moreover there are no distinct strengthening tissues in the stem, and only 2–3 rows of sclerenchymatous cells along the leaf margins.

All the British and Irish species are dioecious. The female flowers are sessile and solitary in the leaf axils, and they usually occur within the 3–5 cm of the stem apex. Each consists of a perianth surmounting an elongated thread-like tube connected to the ovary. The latter is unilocular, containing three to ten ovules with either basal or parietal placentation. The ovary and lower part

of the tube are enclosed by a membranous spathe (Fig. 1). The precise nature of the flower structure is disputed and some workers consider it to have a hypanthium (St John 1965; Lawrence 1976), whilst others suggest that it has an ovarian beak (Wylie 1904; Scannell & Webb 1976; Webb 1977; Dandy 1980). Close examination of the flower reveals that the tube is continuous with the ovary, and that there is no separate style within the tube. This suggests that the flower is epigynous, and that the latter interpretation is more likely to be correct.

Initially all parts of the flower are enclosed by the spathe. However the tube elongates rapidly, carrying the perianth bud to the surface and, when above the water, the bud opens, revealing three sepals, petals, stigmas and staminodes. The perianth is minute, being c. 3–7 mm in diameter. The flowers are ephemeral and, once mature, they rarely survive for more than 48 hours. They seem to be produced only when the top of the plant is within c. 0.5 m of the water surface and in still water (Simpson 1983). Consequently the production of flowers is infrequent, and this has undoubtedly added to the difficulties of separating the species.

In *E. canadensis* and *E. callitrichoides*, the general structure of the male flowers is similar to the female, the main differences being that the ovary is absent, and that the staminodes and stigmas are replaced by nine stamens. In *E. nuttallii*, the tube is absent and the spathe is more or less spherical, whilst at anthesis the whole flower breaks free from the plant and floats to the surface. Pollination in all species is achieved by the pollen grains being scattered on the water surface and drifting to the stigmas of the female flowers (St John 1965). Male flowers have only been recorded once in the British Isles, from a population of *E. canadensis* in the Braid Hills near Edinburgh, Midlothian, v.c. 83 (Douglas 1880). These plants were first found in 1879, but were not seen after 1903. I made an intensive search for male plants between 1978–1983, but without success, and it is most likely that no male plants of the three species are present in the British Isles. It is, of course, possible that such plants have been overlooked, but if they are present, then they must be rare.

In the absence of male flowers, reproduction is vegetatively apomictic. This is achieved by stem breakage, the stems being extremely brittle. The detached stems quickly produce adventitious

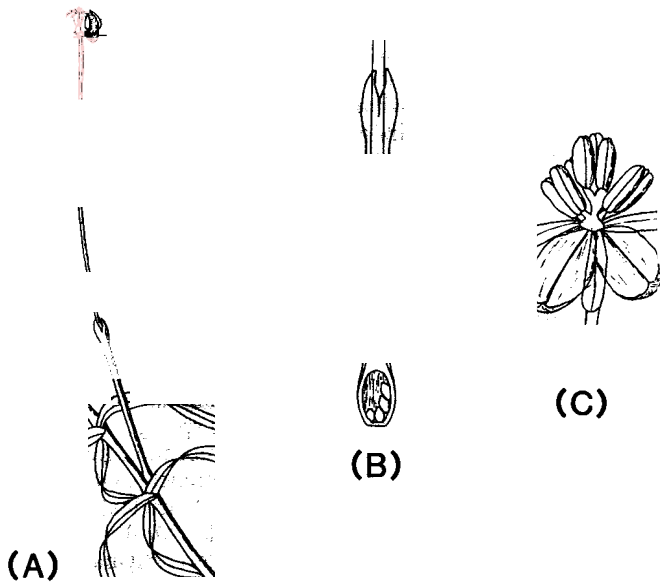


FIGURE 1. *Elodea*, structure of flowers. A, *E. nuttallii* whole female flower. B, *E. nuttallii*, lower portion of flower showing spathe and interior of ovary. C, *E. canadensis*, perianth of male flower from specimens gathered near Edinburgh, v.c. 83 (K). Scale bars = 1 cm.

roots, and soon become established as new plants. The effectiveness of this method as a means of rapidly increasing a population has been amply demonstrated by *E. canadensis* and, to a lesser extent, by *E. nuttallii*.

Determining the precise methods of spread is something of a problem which has never been completely resolved. In canals or rivers it has probably been aided by water movement carrying broken stem pieces. In both cases stem breakage is often increased by boat traffic, and pieces of plant can be carried within the wake caused by the boat. However, it is difficult to identify dispersal methods between isolated habitats, and in these cases agencies such as waterfowl could be involved. Although there is no direct evidence to support this, incidental observations during the present work suggest that plants can survive for several days in a humid atmosphere, and it is also possible that material could cling to, say, birds' feathers by the small teeth along the leaf margin. In some cases deliberate introduction by Man is likely to have occurred.

E. canadensis has the most widespread distribution of the three species. It is native to North America, being particularly common in the northern and eastern United States and southern Canada. It is also adventive in most of continental Europe and Australasia, as well as parts of Africa and Asia. *E. nuttallii* is also native to North America, although it is more or less confined to the northern and eastern United States. It is local but increasing rapidly in western continental Europe (Wolff 1980) and has also been introduced into Japan (Kunii 1982). *E. callitrichoides* is native to South America where it is common in southern Uruguay and northern Argentina. It has been introduced to continental Europe, and is presently known at a few localities in France and West Germany.

TAXONOMIC HISTORY OF THE BRITISH AND IRISH SPECIES

THE GENUS

Elodea was first described by Michaux (1803) in his *Flora Boreali-Americana*, but there were two earlier homonyms mentioned by de Jussieu (1789) and Ventenat (1799). These were orthographic variants of an earlier name, *Elodes* Adanson (1763), given to members of the Hypericaceae. Both de Jussieu and Ventenat attributed the homonyms to Adanson; however neither homonym was validly published, and *Elodea* Michx remains nomenclaturally correct.

Doubt was expressed by Babington & Planchon (1848) and later St John (1962) over the precise authorship of the name. Both produced a range of evidence to suggest that L. C. M. Richard was the original author. St John stated that, for many years, the staff at P believed that *Flora Boreali-Americana* was written by Richard and all names in this Flora should have been accredited to him. Further evidence of this was provided by Hooker (1842), who commented that Richard was the anonymous author of the Flora. Richard (1814) himself made some claim to authorship by stating that "je vais commencer par le description d'une plante qui appartient à un genre encore peu connu et auquel j'ai donné le nom d'*Elodea*". St John also noted the following statement, written by Richard, attached to the holotype of *E. guyannensis* Rich.: "J'ai retrouvé ce dessin et cette description dans une cartier d'observations fait à Cayenne. Je ne l'avais pas sans les yeux lorsque j'ai fait le caractère de la *Flora Boreali-Americana* de Michaux". St John concluded that this evidence was sufficient proof of Richard's authorship. He therefore used the citation "Richard in Michaux" throughout his papers. However there is, in fact, no conclusive evidence of Richard's authorship. The citation is not employed in *Index Kewensis* and, as far as is known, any other work applicable to the genus apart from St John. *Index Nominum Genericorum* does mention *Elodea* Rich., but as a later homonym of *Elodea* Michx, the former referring to Richard's (1814) description of the genus. As *Elodea* Rich. is a later homonym it is invalid. Consequently in the absence of published evidence to the contrary, the name should be credited to Michaux alone and not to Richard in Michaux.

Elodea was described by Michaux as monotypic, the species being *E. canadensis*, and he placed it in the Linnaean Class Triandra, believing the plants to have hermaphrodite flowers. This is interesting, because only pistillate flowers are to be found on the holotype. St John (1962) concluded that Michaux had either examined hermaphrodite flowers, which may occur very occasionally on this otherwise dioecious species or, more likely, he confused staminodes with anthers. Whatever the reason, Michaux's description of *Elodea* as hermaphrodite undoubtedly

caused much of the confusion over the precise use of the name. Richard (1814) assigned a further two hermaphrodite species, both from South America, to *Elodea*, and he described a new genus, *Anacharis*, which contained dioecious material, also from South America. Rafinesque (1818), in a review of Pursh's *Plants of North America*, proposed the rejection of *Elodea* Michx on the grounds that *Elodes*, which was in contemporary use for segregates of *Hypericum*, was similar to *Elodea*. He suggested that the name *Philotria* Raf. should be adopted instead, but this did not gain widespread acceptance. Nuttall (1818) described a monotypic new genus, *Udora*, which was applied to dioecious material from North America. However, the description of this genus was essentially the same as that given by Richard (1814) for *Anacharis*, and it appears that Nuttall was unaware of Richard's work (St John 1962). Nevertheless, by 1848, three generic names were in use for material covered by the present-day concept of *Elodea*. *Elodea* sensu Michaux was hermaphrodite, *Udora* was both hermaphrodite and dioecious and *Anacharis* was dioecious.

Babington & Planchon's (1848) revision brought about a number of changes. The most significant of these was the reduction of *Elodea* to the synonymy of a new hermaphrodite genus *Apalanthe* Planch. By this time it was widely believed that Michaux had erroneously regarded his material as hermaphrodite, and because of this, Babington & Planchon considered *Elodea* to be incorrect for such material. *Udora* was also reduced to the synonymy of *Apalanthe* and *Anacharis*, the latter name being maintained for dioecious material. However Caspary (1857, 1858) restored *Elodea* and his interpretation of the genus included both hermaphrodite and dioecious plants. This concept rapidly gained acceptance in both America and Europe but, in the British Isles, the debate continued, fuelled by attempts to put a correct name to the British and Irish taxon. By the late 1870s, the majority of British and Irish botanical opinion agreed that the floral differences were not important enough to warrant the separation of two or more genera. This is confirmed by *Index Kewensis* which shows that, by 1885, *Elodea* had become generally accepted for both hermaphrodite and dioecious material.

Apart from a few minor nomenclatural changes, little further attention was paid to the genus until Victorin's (1931) revision, in which *Elodea* was again separated on flower structure. In this case he used *Anacharis* for dioecious material and *Philotria* for hermaphrodites. The basis for the change was his examination of a small amount of isotype material in P which did not have mature flowers. From this, Victorin concluded that Michaux's original description was erroneous, and consequently he rejected *Elodea*. Victorin believed it important to recognize the two genera as distinct for two reasons. Firstly, the number and arrangement of the stamens and staminodes differed between them. Secondly, work by Santos (1923, 1924) had shown that in dioecious material corresponding chromosomes differed in size between the sexes, whereas Victorin assumed that they were equal in the hermaphrodite plants.

St John's monograph (1962, 1963, 1964, 1965) again grouped both hermaphrodite and dioecious material into the one genus. However, two subgenera were recognized, *Elodea* for the 14 dioecious species and *Apalanthe* for the three hermaphrodite ones. Subgenus *Elodea* was divided into two sections, *Elodea* and *Natator* H. St John, by the behaviour of the male flowers at maturity. In section *Elodea* they remain attached to the plant, whilst in section *Natator* they break free and float to the surface. St John added a total of ten new species to the seven previously recognized and accepted by him.

THE SPECIES

E. canadensis was first described by Michaux (1803) as a hermaphrodite plant, and this was later taken up by Richard (1814). However Babington & Planchon (1848), having determined its dioecious nature, transferred it to *Anacharis*. It is of interest that their morphological description of the species differed from that of Michaux. In particular, the leaves are described as being linear-lanceolate and acute, whereas Michaux described them as oblong and obtuse. Their observations were made, in fact, on two specimens of staminate plants (*Drummond, K*; *Cleghorn, K*) which had abnormally longer, narrower leaves. Babington & Planchon also produced the first published description of the British and Irish plant, which they named *Anacharis alsinastrum* Bab. They were, however, unsure of the precise relationship between this plant and American material. Therefore they suggested the epithet *alsinastrum* to "prevent it being confounded with the American species and thus extending their range far beyond what may prove to be their natural limits". Their use of the epithet was derived from the plant's apparent similarity to *Elatine alsinastrum* L.

Caspary's (1857, 1858) interpretation of the species included both hermaphrodite and dioecious plants. The hermaphrodite part was based upon Michaux's description of the type specimens and on his personal examination of material from Bethlehem, Pennsylvania (*Schweinitz*, K); these plants are referred to *E. schweinitzii* (Planch.) Casp., a true hermaphrodite species, by St John (1962). The dioecious part was based on Babington & Planchon's descriptions of species assigned to *Anacharis*. Two further species were described: *E. planchonii* Casp. and *E. latifolia* Casp., both of which were later recognized by St John (1965) to be *E. canadensis*. *E. planchonii* was based on the Drummond and Cleghorn specimens mentioned above, and Caspary considered these to be sufficiently distinct to be treated as a separate species. The same applied to *E. latifolia* which had markedly broad, ovate leaves. Indeed, both represented a wide spectrum of variation which misled Caspary. Nevertheless, they were treated as separate species for many years until Victorin (1931) reduced *E. planchonii* to a variety of *Anacharis canadensis* and St John (1965) recognized both to be phenotypic variants of the latter. Moreover *E. canadensis* was considered to be both hermaphrodite and dioecious until St John (1962, 1965) recognized it to be nearly always dioecious. He also recognized *E. planchonii* to be based on staminate plants of this species.

The first specimens of *E. nuttallii* to be described were assigned to *Serpicula verticillata* L.f. (= *Hydrilla verticillata* (L.f.) Royle) by Muhlenberg (1813) as var. *β angustifolia*. However Nuttall (1818) made this variety synonymous with his *Udora canadensis* Nutt. The latter species was described as having oblong-ovate to linear-lanceolate leaves and with staminate flowers sessile and breaking free at anthesis. Nuttall based his description partly on Michaux's type material and partly on specimens collected by himself in Philadelphia (BM). The latter now represent the holotype specimens of *E. nuttallii*. The behaviour of the staminate flowers, which is characteristic of *E. nuttallii*, is also seen in *H. verticillata*, which may account for Muhlenberg describing his plant as a variety of *S. verticillata*. Babington & Planchon (1848) made *U. canadensis* synonymous with *Anacharis nuttallii*, and they suggested that British and Irish *A. alsinastrum* was closely related to this species, if not the same plant. Caspary (1857, 1858) went further and reduced *A. nuttallii* to the synonymy of *E. canadensis*.

Some years later, Small (1903) applied the name *Philotria minor* (Engelm.) Small to plants with linear, acute leaves and flowers less than 3 mm in diameter, occurring in the central part of the United States, whilst Rydberg (1906) described *P. angustifolia* Britton ex Rydb., which was similar to *P. minor*, but with larger leaves and slightly larger flowers, and which occurred in the central-eastern part of the United States. A third new combination was described in Britton & Brown (1913), namely *P. nuttallii* Rydb. ex Britton & Brown. The name was used for plants which were previously assigned to *P. canadensis*, but with more narrowly oblong and somewhat acute leaves. The characteristic feature of all three species was the staminate flowers, which were sessile and broke free at anthesis. St John (1920) amalgamated *P. angustifolia* and *Elodea minor* (Small) Farw. (= *P. minor*) into one species, *E. occidentalis* (Pursh) St John. *E. occidentalis* was described as having linear, flaccid leaves and a globose-apiculate staminate spathe which was c. 2 mm long. St John also recognized *E. nuttallii*, which differed from *E. occidentalis* in having oblong-lanceolate, firm leaves and an ovate-lanceolate staminate spathe 5–6 mm long. However he expressed doubt about the status of *E. nuttallii*, having seen specimens which showed the morphology of *nuttallii* but the floral structure of *occidentalis*. St John (1962, 1965) combined the two as *E. nuttallii*. The epithet, although later than *occidentalis*, had to be retained because Pursh's original use of the name was illegitimate and this invalidated its use by St John. It is of interest that the characters used to delimit *E. nuttallii* in St John (1920) are not used in his later interpretation.

E. callitrichoides has had a simple taxonomic history. It was first described by Richard (1814) as the type species of the genus *Anacharis*. It was transferred to *Elodea* by Caspary (1857, 1858) and remained in this genus as *E. callitrichoides* apart from a brief return to *Anacharis* suggested by Victorin (1931). St John (1963) separated *E. ernstiae* from *E. callitrichoides*, and all European material assigned to the latter was subsequently referred to this new species. However Cook & Urmi-König (1984) suggested that the characters used for separating the two species have no diagnostic value. Therefore *E. ernstiae* should be referred back to *E. callitrichoides*, a view which is accepted by the present author.

Extensive use was made of both living and herbarium material in the study. Herbarium specimens were obtained from ABD, BM, CGE, K, LANC, OXF, P and RNG. A number of private herbaria were also examined, including the Freshwater Biological Association (FBA) and herb R. Stokoe. Although the work was concerned primarily with British and Irish material, specimens from Europe and America were also looked at for comparison.

Particular emphasis was placed on the use, wherever possible, of recently gathered living material. Such material was collected throughout the British Isles, but with a concentration in north-western England, where a wide range of variation was noted. A full list of sites is given in Simpson (1983), and voucher material for these collections is in LANC. Chromosome numbers given in the species descriptions were obtained from counts which I made on British and Irish material from 20 localities. These are also given in Simpson (1983). The counts were made from root-tips, which were pre-treated in paradichlorobenzene for two hours and fixed in 1:3 acetic alcohol overnight at 0°C., followed by hydrolysis in 1N HCl at 60°C for eight minutes. They were then stained in basic fuchsin for two hours and squashes prepared in either aceto-orcein or 45% acetic acid. Ten root-tips per plant and five plants per species were examined at each locality. Voucher material is in LANC.

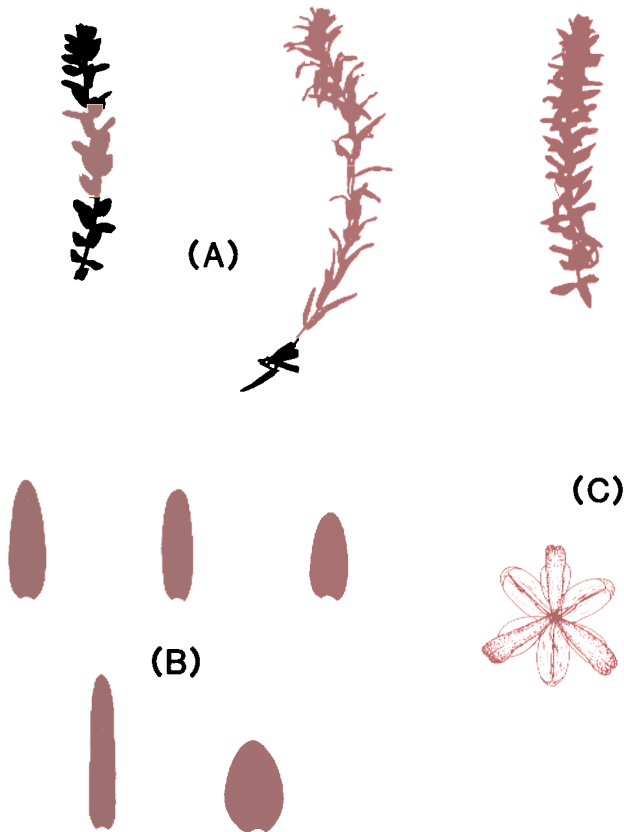


FIGURE 2. *E. canadensis*. A, silhouettes of plants. B, silhouettes of leaves. C, perianth of female flower. Scale bars = 1 cm.

KEY TO SPECIES

1. Leaves linear-oblong, oblong-lanceolate, oblong, oblong-ovate or ovate, rarely linear-lanceolate. Leaf apices broadly acute or obtuse, rarely narrowly acute, (0.7–)0.8–2.3 mm wide c. 0.5 mm below the apex 1. *E. canadensis*
1. Leaves linear or linear-lanceolate. Leaf apices narrowly acute or acuminate, 0.2–0.7(–0.8) mm wide c. 0.5 mm below the apex 2
2. At least some leaves strongly recurved. Leaf lamina often strongly twisted. Leaf margin teeth 60–90(–100) μm long. Adventitious root-tips (in living material) white or grey green. Sepals of female flowers 1.6–2.5 mm long 2. *E. nuttallii*
2. Leaves never strongly recurved. Leaf lamina rarely strongly twisted. Leaf margin teeth (80–)110–140 μm long. Adventitious root-tips (in living material) red. Sepals of female flowers 3.1–4.3 mm long 3. *E. callitrichoides*

SPECIES DESCRIPTIONS

1. *ELODEA CANADENSIS* Michx, *Fl. Bor.-Amer.*, 1: 20 (1803). *Udora canadensis* (Michx) Nutt., pro parte, *Gen. N. Amer. Pl.*, 2: 242 (1818). *Serpicula canadensis* (Michx) Eaton, *Man. bot.*, 5th ed., 390 (1829). *Anacharis canadensis* (Michx) Planch. in *Ann. Mag. Nat. Hist.*, ser. 2, 1: 85 (1848). *Philotria canadensis* (Michx) Britton in *Science*, 11 (2): 5 (1895). TYPE: Environs de Montreal, Michaux (holotype: P). Fig. 2.

Anacharis alsinastrum Bab. in *Ann. Mag. Nat. Hist.*, ser. 2, 1: 83 (1848).

Elodea latifolia Casp. in *Mber. kgl. Pruss. Akad. Wiss.*, 46 (1857).

Elodea planchonii Casp. in *Mber. kgl. Pruss. Akad. Wiss.*, 47 (1857). *Philotria planchonii* (Casp.)

Rydb. in *Bull. Torrey bot. Club*, 35: 462 (1908). *Elodea canadensis* var. *planchonii* (Casp.)

Farw. in *Amer. Midl. Nat.*, 10: 203 (1927). *Anacharis canadensis* var. *planchonii* (Casp.)

Victorin in *Contr. Lab. Bot. Univ. Montréal*, 18: 40 (1931).

Elodea oblongifolia Casp. in *Jb. wiss. Bot.*, 1: 467 (1858).

Philotria iowensis Wylie in *Proc. Iowa Acad. Sci.*, 17: 82 (1910). *Elodea iowensis* (Wylie) Wylie in *Nat. Hist. Bull. Iowa State Univ.*, 6: 48 (1913).

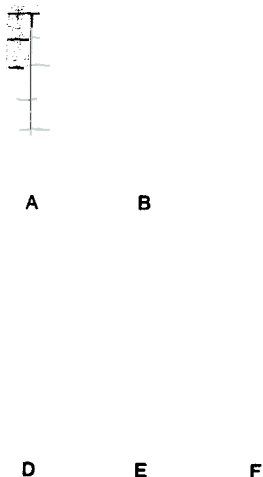


FIGURE 3. Leaf posture types. A, spreading. B, patent. C, erecto-patent. D, arcuate-deflexed. E, slightly deflexed c. 2–4 mm from the leaf base. F, strongly recurved, with leaf bases often touching or overlapping the stem.

Dioecious. Lowermost leaves on stem decussate, ovate, 1.8–9.0 × 0.7–2.0 mm; median and upper leaves in whorls of 3, linear-oblong, oblong, oblong-lanceolate, oblong-ovate, ovate, rarely linear-lanceolate, sometimes weakly twisted, 4.5–17.0 × 1.4–5.6 mm; leaf apices obtuse or broadly acute, rarely narrowly acute, (0.7–)0.8–2.3 mm wide c. 0.5 mm below the apex; leaf posture (Fig. 3) spreading, patent, erecto-patent or arcuate-deflexed, usually firm; leaf-margin teeth 40–70(–80) μ m long. Female flowers with sepals oblong-elliptic, cucullate at apex, 1.9–2.8 × 0.6–1.7 mm, recurved, greenish-white, streaked with purple around apex and midrib; petals elliptic-spathulate, 1.8–2.5 × 0.8–1.5 mm, strongly recurved, translucent, whitish; staminodes linear, c. 1 mm long, white; stigmas strongly recurved or slightly bifid, flattened, 2.3–3.2 mm long, sparsely papillose, the papillae (110–)120–215 μ m long, often purple. Male flowers similar to female but with staminodes, stigmas and ovary absent; stamens 9, anthers bilocular. Flowering period June–September. Adventitious root-tips white or grey-green. $2n = c. 24$.

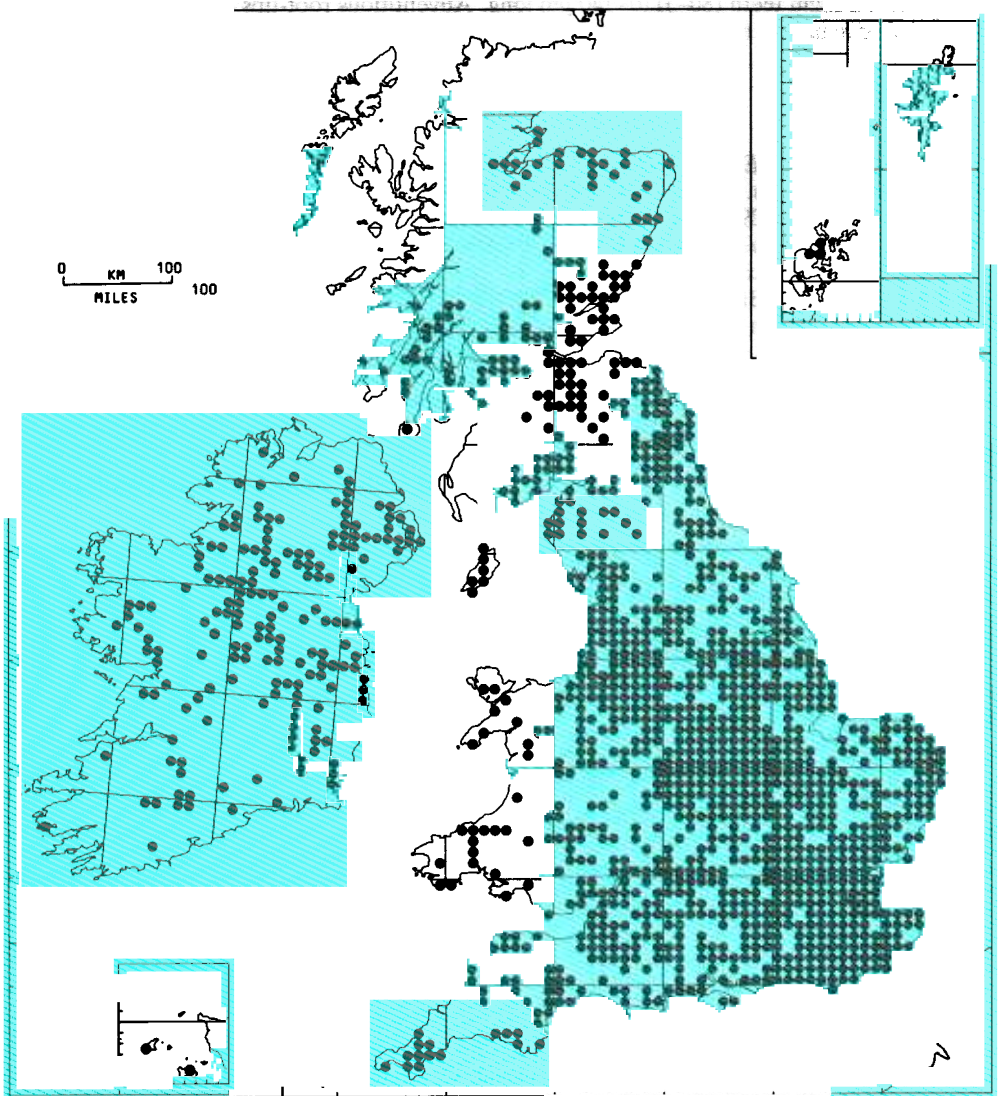


FIGURE A. Distribution of *E. canadensis* in the British Isles.

Habitat and distribution (Fig. 4). *E. canadensis* occurs on fine substrates at c. 0.15–4 m depth, in unshaded, eutrophic to meso-oligotrophic water-bodies, where turbulence through water-flow or wave action is minimal. It is, therefore, most frequently found in lowland ponds, lakes, canals, slow-moving rivers and streams. It is also an early colonizer of new habitats, such as artificial lakes and water-bodies recovering from pollution. *E. canadensis* is widely distributed throughout most of the British Isles, being absent mainly from upland areas in the west and north, where habitats are generally unsuitable.

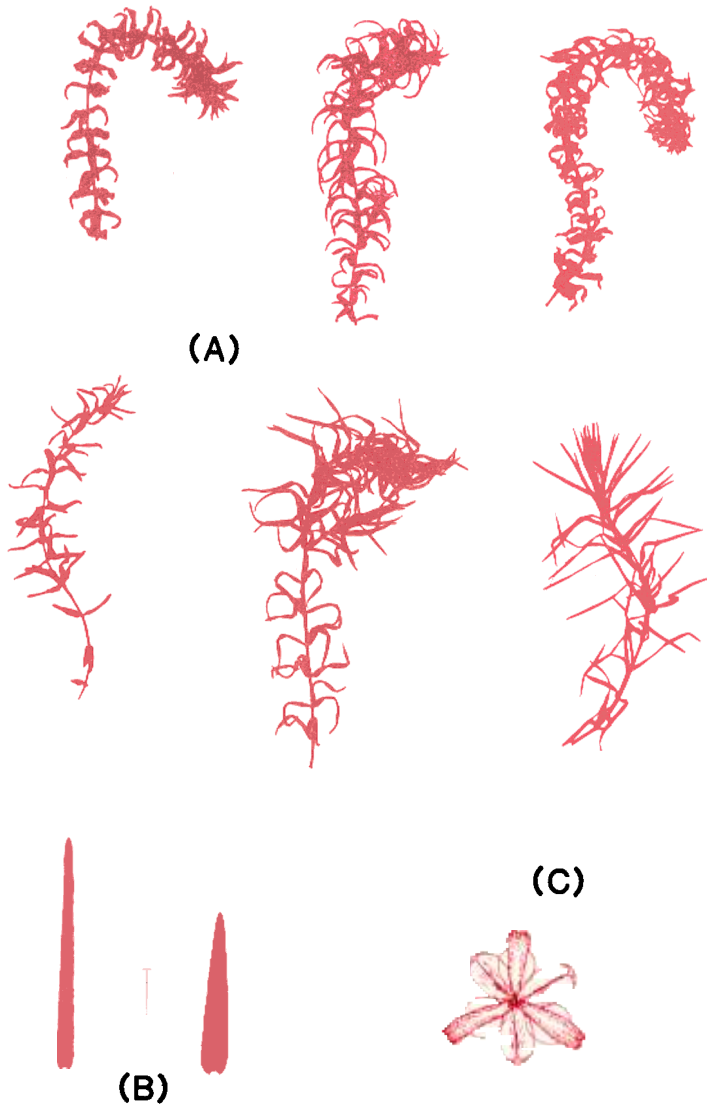


FIGURE 5. *E. nuttallii*. A, silhouettes of plants. B, silhouettes of leaves. C, perianth of female flower. Scale bars = 1 cm.

2. *ELODEA NUTTALLII* (Planch.) H. St John in *Rhodora*, **22**: 27–28 (1920). *Anacharis nuttallii* Planch. in *Ann. Mag. Nat. Hist.*, ser. 2, **1**: 86 (1848). *Philotria nuttallii* (Planch.) Rydb. ex Britton & Brown, *Illustr. Fl. n.-e. U.S.*, 2nd ed., 105 (1913). TYPE: Philadelphia, *Nuttall* (holotype: BM). Fig. 5.

Serpicula verticillata L.f. var. β *angustifolia* Muhl., *Cat. Pl. Amer. Sept.*, 84 (1813). *Elodea canadensis* var. β *angustifolia* (Muhl.) Farw. in *Amer. Midl. Nat.*, **10**: 203 (1927).

Serpicula occidentalis Pursh, *Fl. Amer. Sept.*, 33 (1814), nom. illegit. *Elodea occidentalis* (Pursh) H. St John in *Rhodora*, **22**: 27–29 (1920), nom. illegit.

Udora canadensis (Michx.) Nutt., pro parte, *Gen. N. Amer. Pl.*, **2**: 242 (1818).

Philotria minor Small, *Fl. s.-e. U.S.*, 47 (1903). *Elodea minor* (Small) Farw. in *Rep. Mich. Acad. Sci.*, **17**: 181 (1916).

Philotria angustifolia Britton ex Rydb., *Fl. Colorado*, 15 (1906).

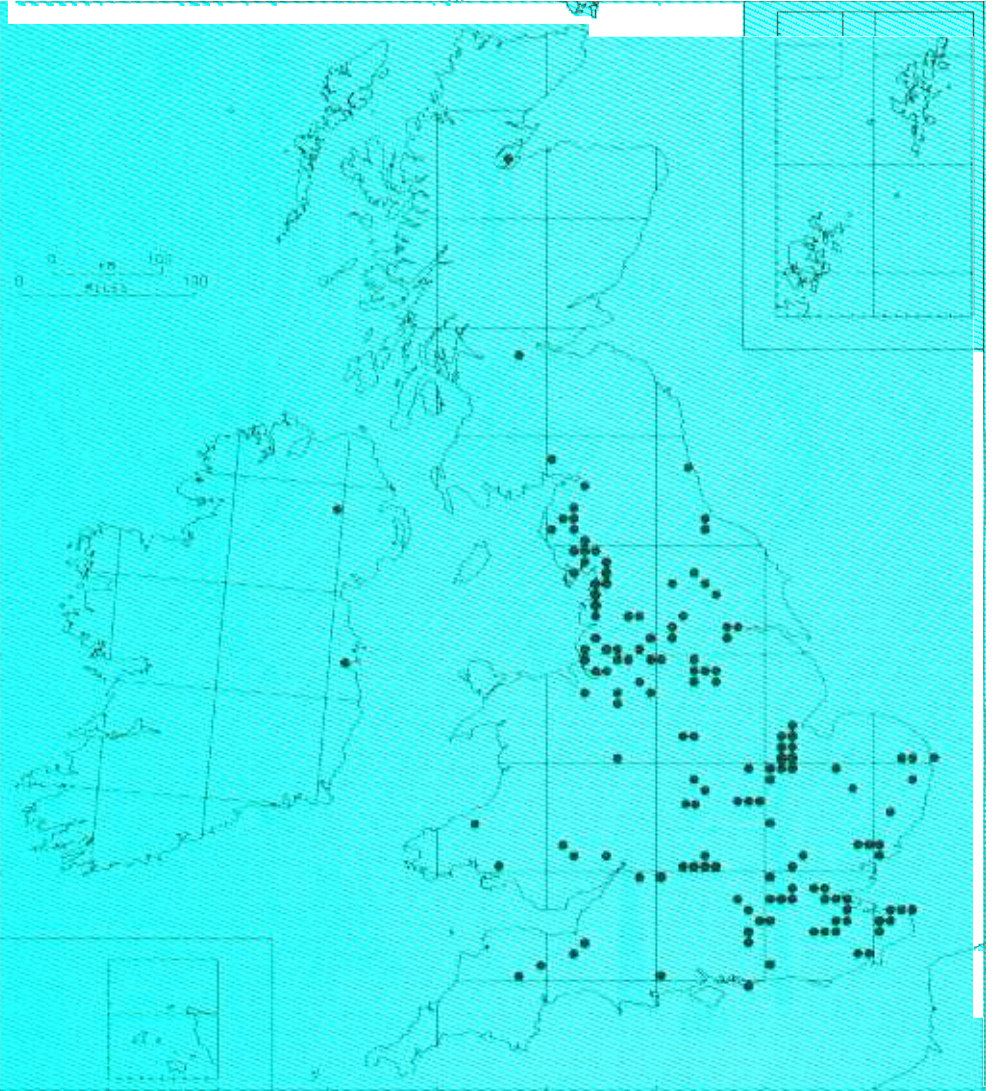


FIGURE 6. Distribution of *E. nuttallii* in the British Isles.

Dioecious. Lowermost leaves on stem decussate, ovate to linear-lanceolate, $2\text{--}8 \times 0.5\text{--}5.0$ mm; median and upper leaves in whorls of 3–4(–5), linear or linear lanceolate, often strongly twisted, $5.5\text{--}35.0 \times 0.8\text{--}3.0$ mm; leaf apices acuminate or narrowly acute, $0.2\text{--}0.7$ (– 0.8) mm wide c. 0.5 mm below the apex; leaf posture (Fig. 3) strongly recurved, spreading, patent, erecto-patent, arcuate-deflexed, or slightly deflexed c. 2–4 mm from the leaf base, firm or flaccid; leaf-margin teeth $60\text{--}90$ (– 100) μm . Female flowers with sepals oblong-elliptic, ovate, cucullate at apex, $1.6\text{--}2.5 \times 0.9\text{--}1.8$ mm, recurved, greenish-white streaked with purple around apex and midrib; petals suborbicular-spathulate, $1.9\text{--}2.6 \times 0.9\text{--}1.8$ mm, strongly recurved, translucent, whitish; staminodes linear, c. 1 mm long, white; stigmas strongly recurved, entire or slightly bifid, flattened, $2.2\text{--}3.2$ mm long, sparsely papillose, the papillae $60\text{--}100$ (– 110) μm long, sometimes purple. Male flowers with perianth sessile within the globose spathe, the whole flower breaking free at anthesis and floating; staminodes, stigmas and ovary absent; stamens 9, anthers bilocular. Flowering period June–September. Adventitious root-tips white or grey-green. $2n = c.48$.

Habitat and distribution (Fig. 6). *E. nuttallii* occurs in similar habitats to *E. canadensis*. Although widely distributed in England, it is still less common than *E. canadensis*, but is continuing to increase. In Wales it is known in v.cc. 35, 41, 42, 46 and 51, whilst in Scotland it has been recorded from widely separated localities in v.cc. 72, 83 and 106. In Ireland it has been found in L. Neagh at Drumenny, Co. Tyrone, v.c. H36, and has also been introduced into a pond at the National Botanic Gardens, Glasnevin, Co. Dublin, v.c. H21.

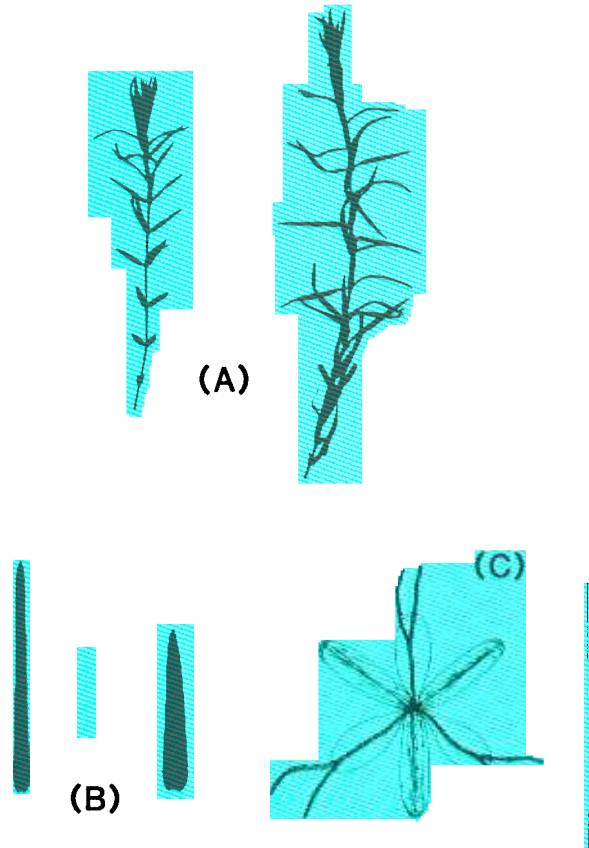


FIGURE 7. *E. callitrichoides*. A, silhouettes of plants. B, silhouettes of leaves. C, perianth of female flower. Scale bars = 1 cm.

3. *ELODEA CALLITRICHOIDES* (Rich.) Casp. in *Mber. kgl. Pruss. Akad. Wiss.*, 47-48 (1857). *Anacharis callitrichoides* Rich. in *Mem. Inst. France*, 12 (2): 7-8 (1814). TYPE: Montivideo, *Commerson* (holotype: P-JU). Fig. 7.
Elodea ernstiae H. St John in *Darwiniana*, 12: 644 (1963).

Dioecious. Lowermost leaves decussate, ovate to linear-lanceolate, 3.0-14.0 × 0.5-1.2 mm; median and upper leaves in whorls of 3, linear or rarely linear-lanceolate, rarely strongly twisted, 9-25 × 0.7-2.2 mm; leaf apices acuminate rarely narrowly acute, 0.2-0.6 mm wide c. 0.5 mm below apex; leaf posture (Fig. 3) spreading, patent, erecto-patent, arcuate-deflexed or slightly deflexed c. 2-4 mm from the leaf base, usually flaccid; leaf-margin teeth (80-)110-140 μm long. Female flowers with sepals linear-oblong, linear-elliptic, cucullate at the apex, 3.1-4.3 × 0.9-1.6

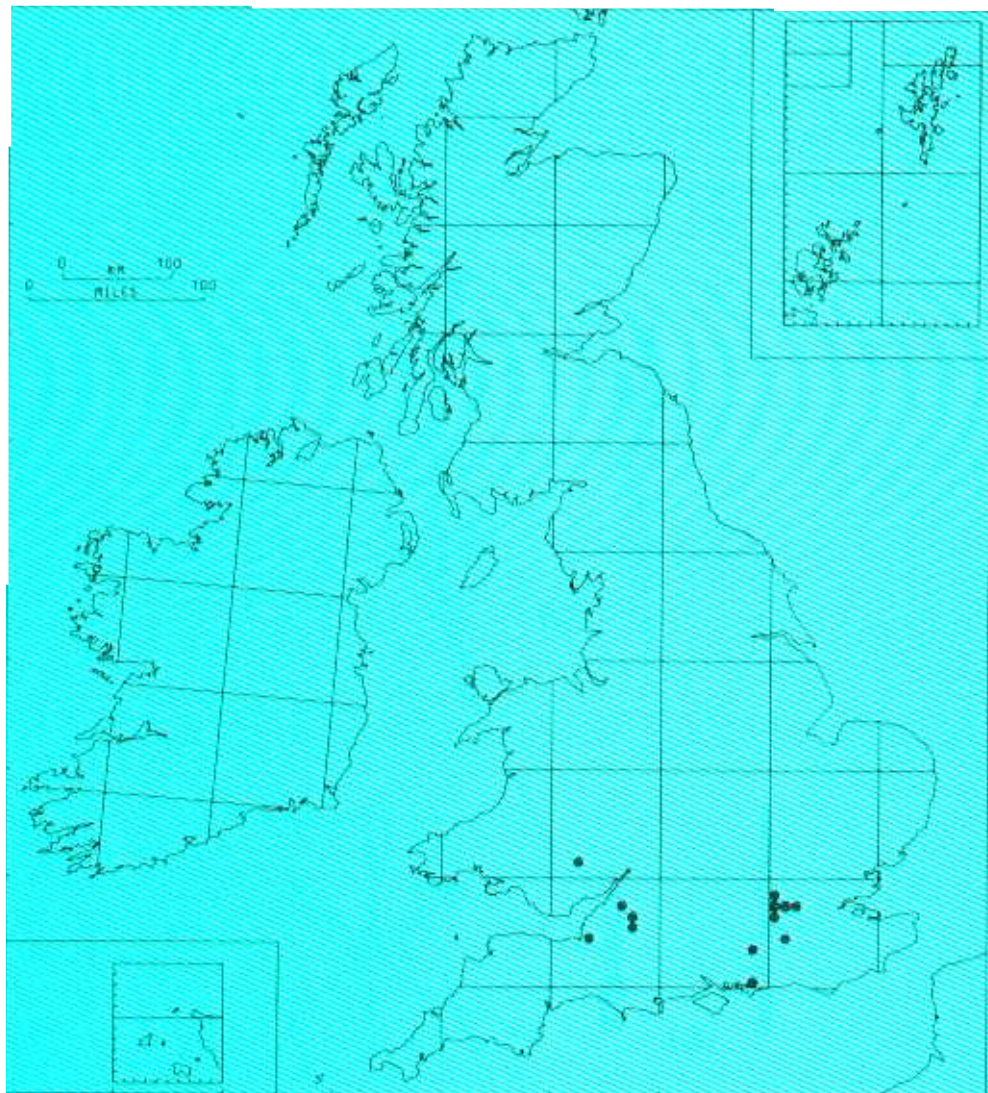


FIGURE 8. Distribution of *E. callitrichoides* in the British Isles. Map includes the 10 km squares from which the plant now appears to be extinct.

mm, spreading or slightly recurved, grey-green or greenish-white, heavily streaked with purple around the apex and midrib; petals oblong-elliptic, 2.9–3.8 × 1.0–1.8 mm, spreading or slightly recurved, translucent, whitish; staminodes linear, 1.5–3.8 mm long, white; stigmas spreading, deeply bifid, terete, 4.2–6.6 mm long, densely papillose, the papillae 120–215 µm long, purple. Male flowers similar to female but with staminodes, stigmas and ovary absent; stamens 9, anthers bilocular. Flowering period October–April. Adventitious root-tips red. $2n=c.32$.

Habitat and distribution (Fig. 8). *E. callitrichoides* has been found in canals, ponds and slow-moving rivers. It is, however, a casual species and is currently known to occur in only two localities in v.cc. 13 and 42. It has not been recorded from either Scotland or Ireland.

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