

A reassessment of the hybrid *Potamogeton* × *gessnacensis* G. Fisch. (*P. natans* × *P. polygonifolius*, Potamogetonaceae) in Britain

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ABSTRACT

Potamogeton × *gessnacensis* G. Fisch. (*P. natans* L. × *P. polygonifolius* Pourr.), hitherto known in Britain from Caernarvonshire (v.c. 49) and East Ross (v.c. 106), was discovered in 1996 in Shetland (v.c. 112). Cytological examination of plants from Caernarvonshire and Shetland shows that they are similar, with a chromosome number of $2n = c. 39$. This is intermediate between *P. natans* ($2n = 52$) and *P. polygonifolius* ($2n = 28$), both counts previously reported from British material. Populations of *P.* × *gessnacensis* are variously intermediate in morphology between the putative parents, the Caernarvonshire plants being closer to *P. natans* than the others; they are highly sterile. The habitat of *P.* × *gessnacensis* at its British sites is described. *P. natans* has not been recorded from any of the sites, which suggests that it may have been eliminated by competition with the hybrid.

KEYWORDS: *Potamogeton coloratus*, *P. epihydrus*, cytology.

INTRODUCTION

Potamogeton natans L. (Broad-leaved Pondweed) and *P. polygonifolius* Pourr. (Bog Pondweed) are the most frequent broad-leaved species of *Potamogeton* in the British Isles (Preston & Croft 1997). However, the hybrid between them appears to be very rare. Dandy (1975) reported “British plants which appear to be this hybrid” from two localities, Llyn Anafon, Caernarvonshire (v.c. 49) and Hill of Nigg, E. Ross (v.c. 106). Dandy’s cautious wording contrasts with his normally confident phraseology (other hybrids in the same account are described as “clearly intermediate”, “obviously intermediate”, “manifestly intermediate” and “strikingly intermediate” between the parental species) and suggests that he regarded the identification as in need of confirmation. Preston (1995a) also described *P.* × *gessnacensis* as a hybrid requiring further research, pointing out that plants in the two British populations differed in morphology, with those at Llyn Anafon approaching *P. natans* very closely.

In August 1996 P.M.H. and C.D.P. discovered a further population of plants (at Loch of Gards, Shetland v.c. 112) which were morphologically intermediate between *P. natans* and *P. polygonifolius* and appeared to be highly sterile. As *P. natans* and *P. polygonifolius* differ in chromosome number, fresh material was sent to J.P.B. for cytological study. His results supported the provisional identification of the Shetland plant as the hybrid *P.* × *gessnacensis*. The plant from Llyn Anafon was also examined cytologically and proved to be similar. The results of these cytological studies are presented in this paper, and discussed in relation to the morphology of the plants.

CYTOLOGICAL STUDIES

Fresh material of putative *Potamogeton* × *gessnacensis* collected at Loch of Gards, Shetland (v.c. 112) on 1 August 1996 and Llyn Anafon, Caernarvonshire (v.c. 49) on 2 September 1996 was cultivated at the University of Leicester. Roots were pretreated in 8 hydroxyquinoline at 4°C for 8 hours, then fixed in fresh 3:1 ethyl alcohol:glacial acetic acid. The roots were then hydrolysed for 10 minutes at room temperature in 5N hydrochloric acid. The meristem was then dissected out in a drop of aceto-orcein using fine tungsten needles and tapped, flamed and squashed. Voucher specimens from both populations have been deposited in CGE.

Chromosome counts of $2n = c. 39$ were obtained from plants from Llyn Anafon (Fig. 1) and Loch of Gards (Fig. 2). The material is rather difficult cytologically. The chromosomes are rather numerous, very small (most are less than 1 μm long) and there is considerable variation in size between chromosomes within the complement. Another difficulty is that the chromosomes seem to be of two types (possibly the complements of the two parental taxa). One complement has a quadripartite appearance and resembles the textbook chromosome; it is clearly comprised of two chromatids, a centromere and four ends. The other sort of chromosome appears diffuse, without an obvious centromeric constriction and with only two ends apparent. The quadripartite chromosomes are easy to interpret even when adjacent, but this is not the case with the diffuse ones. In Fig. 1b (hollow arrow), the torpedo-shaped "body" has been interpreted as two adjacent chromosomes, though a case could be made for interpreting it as a single chromosome. However, other preparations from the same plant do not have a similarly shaped large chromosome. In Fig. 2b the V-shaped chromosome has been interpreted as a single chromosome with the chromatids splitting apart, rather than two small abutting chromosomes. The presence of a homologous chromosome is often useful in interpreting cases like this, but homologues need not be present in a hybrid (see the single strongly satellited chromosome arrowed in Figs 1a and 2a). A more certain count might be obtained by looking at the size and range of morphology of the chromosomes of the two parental taxa and checking the interpretation of the metaphase squashes in the light of this information. These interpretative difficulties are reflected in the fact that only approximate counts are presented here.

Interpretative difficulties apart, the Llyn Anafon and Shetland karyotypes of *P.* × *gessnacensis* have a number of features in common. Both have a single very distinctive satellited chromosome (arrowed in Figs 1a and 2a), and the same mixture of "quadripartite" and "diffuse" chromosomes.

Potamogeton natans has a chromosome number of $2n = 52$. This statement is based on eight

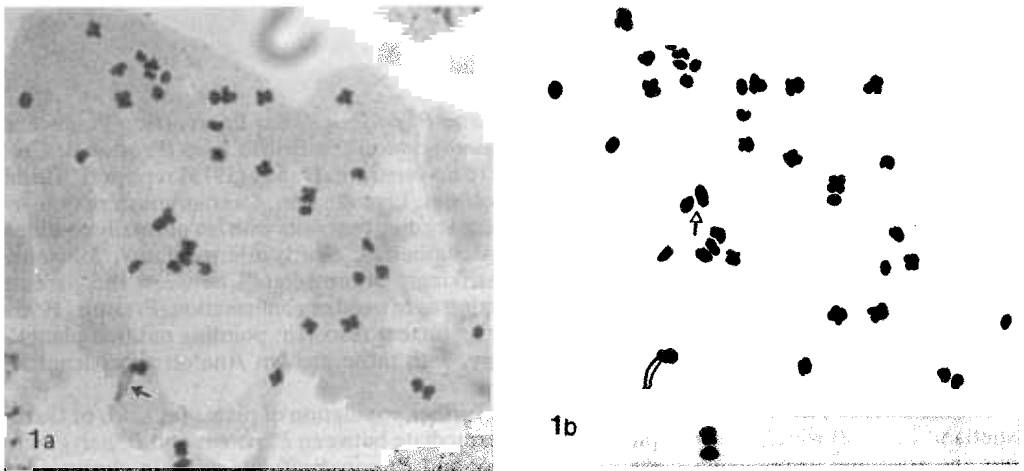


FIGURE 1. Cytological preparation of *Potamogeton* × *gessnacensis* from Llyn Anafon, Caernarvonshire (Fig. 1a) and the interpretation of this preparation as $2n = c. 39$ (Fig. 1b). The solid arrows in Fig. 1a indicates a conspicuous satellited chromosome. The hollow arrow in Fig. 1b indicates an area which is difficult to interpret (see text). Scale: as Fig. 2.

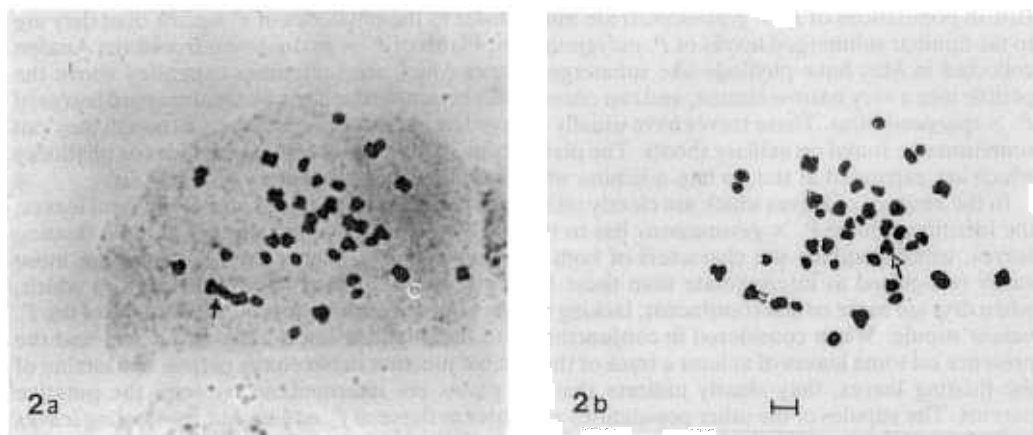


FIGURE 2. Cytological preparation of *Potamogeton* × *gessnacensis* from Loch of Gards, Shetland (Fig. 2a) and the interpretation of this preparation as $2n = c. 39$ (Fig. 2b). The solid arrow in Fig. 2a indicates a conspicuous satellited chromosome. The hollow arrow in Fig. 2b indicates an area which is difficult to interpret (see text). Scale bar = $2 \mu\text{m}$.

separate counts, one (as $2n = c. 52$) from English material (Hollingsworth *et al.* 1995; Hollingsworth *et al.* submitted). In this paper we have adopted, for convenience, the usual assumption that this represents the tetraploid level in *Potamogeton*. A count of $2n = 42$ has also been reported for *P. natans* from two localities, in N. America (Stern 1961, as $n = 21$) and eastern Asia (Probatova & Sokolovskaya 1984, as $2n = c. 42$). *P. polygonifolius* is a diploid species: $2n = 26$ is reported for this species by Palmgren (1939, as $n = 13$), Fernandes (1950) and Ficini *et al.* (1980). However, the three English counts of this species all unambiguously gave a count of $2n = 28$ (Hollingsworth 1995; Hollingsworth *et al.* submitted). In his summary of the chromosome numbers of *Potamogeton*, Les (1983) attributed the chromosome number $2n = 52$ to *P. polygonifolius* on the basis of two (uncited) counts. We have only been able to trace a single apparent count of $2n = 52$ for this species, by Takusagawa (1961). Although this count has been cited by abstracters (e.g. Moore 1973), a close reading of the text reveals that this count was never made, but was merely the chromosome number which Takusagawa would expect this species to have on the basis of the chromosome number of similar species.

Judging by the chromosome counts cited above, one would expect the hybrid *P.* × *gessnacensis* to be a triploid with $2n = 39$ or $2n = 40$. The cytological results show that the plants from Llyn Anafon and Shetland are indeed triploid, with a number which is certainly close to the expected number. They are therefore almost certainly a hybrid between a diploid and a tetraploid species. The tetraploid species is clearly *P. natans*, on morphological grounds. Although the morphological evidence for the involvement of *P. polygonifolius* is less strong, this is almost certainly the diploid parent. The only other broad-leaved pondweeds in the British flora which are diploids are *P. coloratus* and *P. epihydrus*, neither of which are likely parents of a hybrid which grows in upland N. Wales and Shetland.

RECOGNITION OF *P.* × *GESSNACENSIS*

One of the features which distinguishes the hybrids of *P. natans* with the broad-leaved species *P. gramineus* (*P.* × *sparganiiifolius*), *P. lucens* (*P.* × *fluitans*) and *P. nodosus* (*P.* × *schreberi*) is the presence of narrow, laminar submerged leaves intermediate between the phyllodes of *P. natans* and the laminar leaves of the other parent (Preston 1995a, b). Similar leaves might be expected to occur in the hybrid between *P. natans* and *P. polygonifolius*. However, the submerged leaves of the

British populations of *P. × gessnacensis* are much closer to the phyllodes of *P. natans* than they are to the laminar submerged leaves of *P. polygonifolius*. Plants of *P. × gessnacensis* from Llyn Anafon collected in May have phyllode-like submerged leaves which are sometimes expanded above the petiole into a very narrow lamina, and can occasionally resemble the narrowest submerged leaves of *P. × sparganiiifolius*. These leaves have usually decayed by August or September, although they can sometimes be found on axillary shoots. The plants from Scotland have either phyllodes or phyllodes which are expanded at the tip into a lamina which resembles a rudimentary floating leaf.

In the absence of leaves which are clearly intermediate between phyllodes and submerged leaves, the identification of *P. × gessnacensis* has to be based on features of the stipules and the floating leaves, which combine the characters of both parents (Table 1). Plants from Shetland are more easily recognised as intermediate than those from elsewhere, as they have short stipules which, when dry, are more or less translucent, lacking the very opaque, buff-coloured appearance of the *P. natans* stipule. When considered in conjunction with the phyllode-like submerged leaves and the presence on some leaves of at least a trace of the flexible junction between the petiole and lamina of the floating leaves, they clearly indicate that the plants are intermediate between the putative parents. The stipules of the other populations are closer to those of *P. natans*, but the floating leaves have longitudinal veins which are less markedly translucent than in that species. The flexible junction between the petiole and the lamina is also absent or poorly developed in these populations, but this character has to be used with caution as it is not always present in *P. natans*.

The inflorescences of *P. × gessnacensis* are usually shorter than those of *P. natans* and even in the field it is possible to obtain some indication that it is a sterile hybrid. The perianth segments of plants at Llyn Anafon and Loch of Gards remain closed and the stigmas protrude through them. This behaviour is typical of sterile hybrids (Preston 1995a, p. 46) and contrasts with that of fertile species where the perianth segments open to expose anthers which shed copious amounts of pollen. At Llyn Anafon on 2 September 1996 the old inflorescences of the hybrid were rotting, and being replaced by newly developed inflorescences. Examination of the pollen of plants from Llyn Anafon has shown that it is sterile (G. C. S. Clarke, in litt. to J. E. Dandy, 10 July 1973, BM). Plants from Llyn Anafon sometimes produce easily detached fascicles of short phyllodes or phyllode-like leaves in the leaf axils: these were first noted by A. Fryer on a specimen collected by C. Bailey on 29 September 1884 (BM). Similar structures are occasionally produced by *P. natans* and may act as vegetative propagules.

Material from Llyn Anafon is illustrated by Preston (1995a) and plants from Shetland are drawn as Fig. 3.

BRITISH POPULATIONS OF *P. × GESSNACENSIS*

Potamogeton × gessnacensis is now known from three sites in Britain. It has been collected at Llyn Anafon, Caernarvonshire, since 1884, the early specimens being originally named *P. natans*, *P. polygonifolius* or (in the case of plants collected by E. F. Cooper in 1890) *P. natans × polygonifolius*. At Llyn Anafon *P. × gessnacensis* grows in water from 0.3 to at least 0.8 m deep around the edge of the lake. The stands of the hybrid are extensive, especially in relatively sheltered bays, typically occupying several square metres in area. They flower freely, but the inflorescences rot rather than set fruit. Llyn Anafon is a base-poor upland lake (altitude 500 m), although there may be slight base-enrichment from a small outcrop of dolerite and a larger outcrop of less basic andesite south of the lake. Its flora includes *Callitriche hamulata*, *Isoetes lacustris*, the aquatic variant of *Juncus bulbosus*, *Littorella uniflora*, *Lobelia dortmanna*, *Menyanthes trifoliata*, *Myriophyllum alterniflorum*, *Potamogeton berchtoldii*, *Ranunculus omiophyllus*, *Sparganium angustifolium*, *Subularia aquatica*, *Utricularia vulgaris* sensu lato and *Chara globularis* var. *virgata*. *Potamogeton polygonifolius* occurs in runnels leading into the lake and in water up to 0.5 m deep near the edge, but *P. natans* is apparently absent. A second rare *Potamogeton* hybrid, *P. × griffithii*, also occurs at Llyn Anafon with one parent (*P. alpinus*) but not the other (*P. praelongus*).

The record of *P. × gessnacensis* from a small stream on the Hill of Nigg, East Ross, is based on a single collection made by U. K. Duncan on 10 August 1970. In a letter to J. E. Dandy dated 5 November 1970 and now kept with the specimen in BM, she commented "I noted at the time that there was no typical *natans* to be seen in the vicinity on the Hill of Nigg. In fact I thought this must be

TABLE 1. A COMPARISON OF SOME CHARACTERS OF *POTAMOGETON NATANS*, *P. POLYGONIFOLIUS* AND THE THREE BRITISH POPULATIONS OF THEIR HYBRID *P. × GESSNACENSIS*

	<i>P. natans</i>	<i>P. × gessnacensis</i>		Loch of Gards	<i>P. polygonifolius</i>
		Llyn Anafon			
Stipules					
Length (mm)	40–170	30–85	32–88	20–42	10–50
Colour (when dry)	Green or buff, opaque	Brown or buff, ± opaque	Green or brownish green, ± opaque	Brown, ± translucent	Brown, translucent
Floating leaves					
Longitudinal veins of fresh leaves (when held up to light)	Translucent	Opaque or translucent (if translucent usually very narrow)		Opaque (sometimes paler than lamina but not translucent)	Opaque
Discoloured junction between petiole and lamina	Usually present, rarely absent	Absent or trace visible	Absent or trace visible	Absent or trace visible	Absent
Inflorescences					
Length (mm)	20–60	11–28		8–20	10–42
Capacity to produce well-formed fruits	Present	Absent		Absent	Present

* Observations based on a single dried specimen consisting of two vegetative plants (BM).



FIGURE 3. *Potamogeton* × *gessnacensis*, drawn by L. T. Ellis from herbarium specimens collected at Loch of Gards, Shetland, by C.D.P. & P.M.H. on 1 August 1996 (Preston 96/145, 146, CGE). Scale bars = 3 cm.

a form of that species . . . there were only four plants, all nearly the same, growing in a colony in the small streamlet at GR 28/828708. I had followed up the stream from the coast expecting to find the loch at approximately that locality, but to my disappointment it had completely disappeared, having become a “bog” full of moss, rushes etc., without even a pool of water left . . .”

The third site, Loch of Gards, Shetland, is a shallow coastal lake. *P.* × *gessnacensis* grows in water 0.2–0.3 m deep, forming small patches over a sandy substrate around the edge of the lake, and larger stands by a wall which crosses the lake at the south end. The plants were flowering when first discovered on 1 August 1996 and still flowering when W. Scott revisited the site on 4 September 1996. There was no sign of fruit developing on either date. Loch of Gards is a relatively eutrophic lake which (judging by its situation) must receive some input of salt-spray. Few aquatic plants grow with the *P.* × *gessnacensis*, but the deeper water in the centre of the lake is dominated by *Potamogeton pusillus* and *Ranunculus baudotii*. Other species present include *Littorella uniflora*,

POTAMOGETON × GESSNACENSIS

Myriophyllum alterniflorum, *Persicaria amphibia*, *Potamogeton filiformis* and *P. perfoliatus*. Neither *P. natans* nor *P. polygonifolius* was recorded at Loch of Gards in 1996.

It is remarkable that *P. natans* has not been recorded from any of the British *P. × gessnacensis* sites. At Llyn Anafon and Loch of Gards the habitat which appears to be suitable for this species is occupied by the hybrid, suggesting that if *P. natans* was formerly present it may have been out-competed by the hybrid. *P. polygonifolius* is present at Llyn Anafon in a different habitat.

DISCUSSION

The results of the cytological studies outlined above support the conclusion that the plants from Llyn Anafon and Loch of Gards are *P. × gessnacensis*. However, the evidence is not yet absolutely conclusive, and more detailed cytological study, or isozyme or other molecular studies, would be worthwhile.

P. × gessnacensis is a difficult hybrid to detect in the field. In order to identify it one needs to recognise that it is intermediate between the parents, and resist the temptation to ascribe it to one parent or the other. It is unlikely that a population such as that at Llyn Anafon, which has a close resemblance to *P. natans*, could be identified on a single visit to a site, as the characteristic features of the submerged leaves are apparent only in the early season whereas the sterility of the plants can be established only later in the summer. The hybrid is more difficult to detect as a herbarium specimen, and the fact that J. E. Dandy was able to identify the plant from Llyn Anafon as *P. × gessnacensis* provides remarkable testimony to his knowledge of the genus. In view of these difficulties of identification, it seems likely that there are further populations of the hybrid in Britain that have hitherto escaped detection; the hybrid is also likely to occur in Ireland.

The variation between the British populations of *Potamogeton × gessnacensis* is apparently paralleled by variation in the type locality, the Gessnach stream in Germany. In his initial description of the hybrid as *P. × gessnacensis*, Fischer (1907) recognised three varieties, one variety closer to *P. natans*, one closer to *P. polygonifolius* and one intermediate between the other two.

SPECIMENS EXAMINED

The above account is based on the following specimens of *P. × gessnacensis*. Determinations attributed to J. E. Dandy (J.E.D.) were made in 1973 unless otherwise stated.

BRITISH ISLES

WALES: Caernarvonshire, v.c. 49: Llyn Anafon, SH/69.69., 29 September 1884, *C. Bailey*, **BM**, det. J.E.D.; August 1890, *E. F. Cooper*, **BM**, det. J.E.D.; 5 July 1905, *H. W. Pugsley*, **BM**, det. J.E.D.; 1 October 1906, *J. F. Dutton*, **BM**, det. J.E.D.; 30 July 1910, *G. Goode*, **LTR**, det. J.E.D., 1975; 4 August 1928, *A. Wilson*, **YRK**, det. C.D.P., 1997; 4 July 1946, *R. Ross*, **BM**, det. J.E.D.; 4 July 1984, *M. Wade*, **UTLH**; 28 May 1988, *C. D. Preston & N. F. Stewart*, *Preston 88/35, 37, 38*, **BM**, **CGE**, **NMW**; 27 August 1989, *C.D.P. & N. F. Stewart*, *Preston 89/462, 464, 465*, **CGE**, **NMW**; 2 September 1996, *T. D. Dines & C.D.P.*, *Preston 86/231, 232, 233*, **BM**, **CGE**, **NMW**.

SCOTLAND: East Ross, v.c. 106: N. side of Hill of Nigg, NH/828.708, 10 August 1970, *U. K. Duncan*, **BM**, det. J. E. D. Shetland, v.c. 112: Loch of Gards, Scat Ness, HU/38.09., 1 August 1996, *P.M.H. & C.D.P.*, *Preston 96/145, 146, 147*, **BM**, **CGE**, **E**; 4 September 1996, *W. Scott*, *Scott 3527*, **CGE**, **E**, det. C.D.P., 1996.

GERMANY

In der Gessnach zwischen Ödhof und Schaufing b. Deggendorf (Bayer. Wald), 17 August 1921, *L. Oberneder*. **BM**.

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