A pondweed, new to the European flora, from the Scottish Western Isles, with some remarks on the phytogeography of the island group

by

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MS. received November 14, 1949

The Scottish Western Isles, more generally known collectively as the Hebrides, are situated to the northwest of Great Britain. They must not, however, be regarded as constituting, either geographically or biogeographically, a single unit, for they are divided by the Minch into two groups. One of these, the Outer Hebrides, lies between latitudes 56° 48′ N. and 58° 32′ N., about 70 kilometres from the mainland, and approaches the margin of the continental shelf. The other, called by contrast the Inner Hebrides, comprises an irregular series of islands stretching down the west coast of Scotland at varying distances from it. Many of the larger and more important of the Inner Isles are so close to the mainland that the dates of their severance therefrom must be regarded, from the geological standpoint, as very recent indeed. In consequence, their floras and faunas bear a strong resemblance to those of the adjacent portions of Scotland. On the other hand, whilst there may have been land connections between the Outer Hebrides and the mainland during the Boreal period of postglacial times, the links did not last long enough to affect materially the composition of the biota of the Outer Group. Although some of the animals and plants now established in the Outer Isles may have dwelt there throughout the Glacial Period, the bulk reached the area during one of the periods of temporary climatic amelioration which interrupted the Upper Pleistocene Glaciation. Here, let it be emphasized that, to a considerable extent, the same remarks hold true of the Isles of Coll, Tiree, Rhum, Eigg, Canna and Muck in the Inner Group.

If, as is here postulated, the flora and fauna of the Outer Hebrides differ in time of entry, and in origin, from those of the majority of the Inner Isles, it appears likely that they will be built up of different elements. Inspired by this possibility, we instituted investigations in the more critical islands of both groups for three purposes: (1) to gain a full knowledge of the plants and animals concerned, (2) to use the facts so accumulated to determine the dates of the separation of the Outer Isles from the Inner Isles and the mainland and (3) to fix the times when the Inner Isles and Scotland parted company.

In the course of these explorations, special efforts were made to extend our acquaintance with two of the most important, biogeographically speaking, components of the British Flora, the so-called American and Lusitanian elements. In carrying out our aims, we had marked success, more especially with the American section.

Prior to our researches, this element in our flora was supposed to have its headquarters in Ireland, although it was recognized that the orchid *Spiranthes stricta* (RYDB.) A. NELS. and the pondweed *Naias flexilis* ROSTK. et SCHMIDT grew in the Hebridean Isle of Colonsay, and the pipewort *Eriocaulon septangulare* WITH. in the Isles of Skye and Coll, neither of these species having been found in the Outer Isles. In the Inner Isles, the ranks of the American element were increased in 1940 when my son J. Heslop HARRISON collected *Spiranthes stricta* in plenty on the Isle of Coll whilst, later, *Juncus tenuis* WILLD. (undoubtedly as a genuine native) and *Myriophyllum alterniflorum* var. *americanum* PUGSLEY were observed on the Isle of Tiree. *J. tenuis* was also noted on the Isles of Raasay and Rhum, but, almost certainly, it owes its presence on those two islands to human activities.

In the Outer Isles, although the sponge, *Heteromyenia ryderi*, had been known there previously, the existence of the American element amongst the plants was first demonstrated in 1938, when I dredged *Naias flexilis* from Loch Altabrug in the Isle of South Uist. Subsequently, it was procured from many lochs and lochans in the Isles of North Uist and Benbecula, both of which islands, when subjected to close examination, proving to support extremely rich pondweed floras. Thus, from Benbecula were obtained *Potamogeton coloratus* HORNEM., *P. alpinus* BALB., × *P. Billupsi* FRYER, × *P. sparganiifolius* LAESTAD. and × *P. Gessnacensis* FISCHER and from North Uist and Baleshare, *P. Friesii* RUPR. and the extremely rare *P. rutilus* WOLFG., hitherto only known in the British area from the Shetland Isles. The species listed from Benbecula were first placed on record by HARRISON 1941; this provided the first Outer Hebridean record of the plants concerned. As for *P. rutilus*, it was determined by me, and recorded for the first time by HARRISON 1942 : 28.

Work on the Hebridean pondweeds did not cease with the publication of these notes, for, in August, 1943, further investigations were made on South Uist to see how far *Naias flexilis* penetrated into lochs of moorland proclivities, and to discover whether the Benbecula and North Uist novelties existed there. *Naias flexilis* was shown to luxuriate in Lower Loch Ollay, but, more important still, a strange *Potamogeton*, utterly unlike any European species known to me, was dragged from an isolated backwater of Loch Ceann a'Bagh. This defied determination

until 1944, when the acquisition of new and more material from a lochan draining into Loch Ceann a'Bagh suggested that the plant might be American in its affinities. Recourse was therefore made to FERNALD 1932, after which it speedily became clear that the species to which the South Uist plants belonged was the common American species *Potamogeton epihydrus* RAF. Moreover, it could only be assigned to var. *Nuttallii* CHAM. et SCHLECHT. In this way, not only was an important addition made to the ranks of the American element in the British Flora, but also a new species of pondweed placed on record for Europe.

Curiously enough, this species was collected in 1907 by Miss A. VIGIERS in a canal at Salterhebble Bridge near Halifax, England and recorded by BENNETT 1908: 10 under the name *Potamogeton pensylvanicus* CHAM. et SCHLECHT. Occurring in a canal in a heavily industrialized area, the plant was undoubtedly an introduction brought in with imports of American origin. It has been suggested that the agents responsible for its presence were bales of cotton but, in the opinion of FERNALD, this is very unlikely, as although *P. epihydrus* is of free occurrence in the eastern seaboard States, it almost misses the cotton belt. Since the favoured habitats in South Uist are to be found far from human habitation of any sort on desolate moorlands, any suspicion of introduction in the Outer Hebrides is untenable.

In his early communications, BENNETT employed the name *Potamogeton pensylvanicus* to designate the Halifax plant, but, later, FERNALD demonstrated that the correct appellation of the typical plant was *P. epihydrus* RAF. It should be made clear that, whilst the Halifax plants seem referable to the typical form of the species, the South Uist examples must be regarded as belonging to the var. *Nuttallii* CHAM. et SCHLECHT., and as such they are now described:

Rhizomes slender and creeping far and near over the bottom of the lochan in such a way as to form a mat; stems, for the most part, simple and, on the average, 50 cm in height, although they may be considerably greater when growing in deep water; submersed leaves, thin, pellucid and ribbon-like, length 4—18 cm, breadth 2—8 mm, 3—7-nerved, strongly lacunate, especially in the space between the two nerves adjacent to the mid-rib; submersed leaves close together on non-fruiting stems, but remote on the fruiting shoots; floating leaves coriaceous, opposite, with petioles often as long as the blades, elliptic, blunt at tips, length 2—4.5 cm, breadth 0.6—1.2 cm, 7—13-nerved; leaves transitional in form between the floating and submersed leaves occur early in the season; ligules of submersed leaves, free, hyaline, obtuse, 2—3 cm long; peduncles 1.5—3 cm long lying in the axils of the floating leaves;

fruiting spikes, 1—2.2 cm long, 0.5—0.7 cm broad; fruits 3 mm × 2.5 mm, dorsal keel 0.2—0.8 mm broad, beak nearly absent.

This description was made from South Uist specimens, and, if comparisons are made with those discussed in FERNALDs account, it will be obvious that our plants are distinctly less robust on the average than those examined by him. Nevertheless, in my opinion, the divergence is not such as to warrant the application of a new racial or varietal name to British examples.

Anyone acquainted with the natural history of Hebridean pondweeds in the field will quickly realize that they are precocious in their development. Despite that fact, when both *Potamogeton natans* and *P. polygonifolius* have their floating systems well developed, and even possess flowers, the topmost leaves of *P. epihydrus* var. *Nuttallii* are well below the surface of the water. Thus, on June 14th, 1949, the developing shoots of the latter species were examined. These sprang from a mat of rhizomes threading their way, just below the surface, through dense peaty mud lying in the lochan at all depths between 0.3 and 1.5 metres. This was covered with masses of the moss *Fontinalis antipyretica*, through which the shoots of the pondweed had thrust their way to attain heights of 9—35 cm.

A curious observation in connection with these plants was made; the shoots and leaves were dimorphic in colour. Some were of a delicate pellucid green whilst others were heavily charged with an anthocyanin pigment. Examination showed that this peculiarity depended neither upon the depth of water nor upon shade, for it was observed in plants well shaded by shrubs like *Salix aurita* L. and *Sorbus Aucuparia* L., as well as in those growing in the lochan as far out as the eye could see. At the same time, the first coriaceous leaves were just commencing to unfold. In July, the plants begin to flower, and the fruits are ripe toward the end of August.

Unfortunately, the pH values of the lochan in which *P. epihydrus* grows were not determined, but those of the adjacent Loch Ceann a'Bagh were investigated, and found to be 7.52. Still, as the loch is tidal in its lower reaches, and receives accessions of water from very acid moorlands as well as from machair land heavily charged with shell sand, this figure may not be significant. Determinations made in the loch at other times have given figures as low as pH 6.2. Further, as the lochan with which we are equally concerned, cannot obtain water from the sea or machair, it is restricted for its water supply to the drainage of peaty moorlands. Its pH figures must, in consequence, be exceedingly low, an opinion confirmed by the plants, other than *P. epihydrus* var. *Nuttallii*, growing there. As was to be expected in a moorland pool, the flora was exceedingly poor in species. In addition to the pondweed and

the moss *Fontinalis antipyretica*, the only plants present were *Potamogeton natans* L. in small quantity, *Menyanthes trifoliata* L. and *Juncus* spp.

Finally, we must endeavour to find a date for the arrival of *Potamogeton epihydrus* and other members of the American group in the Hebrides, and likewise to ascertain the effects of the Glacial Period on their position. In the former task, we are aided by the presence of a corresponding European element, exemplified by *Calluna vulgaris* HULL in the Newfoundland Flora. Clearly, such an interchange of biota as these circumstances imply can have taken place only when a free passage over dry land was rendered possible by the existence of a land connection between the two continents. Almost inevitably, we are compelled to appeal to geographical conditions such as existed in Pliocene or earlier times to account for the biological facts. Coupled with the absence of the plants concerned from the continent of Europe, this definitely means (1) that their arrival in the Hebridean area cannot be regarded as having synchronized with that of the European forms which pressed into the island area during some favourable stage toward the close of the Ice Age, and (2) that they must have survived the Glacial Period not far from where they now exist. Whilst it is not excluded that they have come in at some period of high land levels during the Ice Age, the presence of *Eriocaulon septangulare* in Interglacial beds in the west of Ireland renders this idea unlikely.

Let us consider now the stations in which they may have survived. As I have shown elsewhere — HARRISON 1948 —, in spite of the fact that the Coll-Tiree group forms the headquarters of the American element in the Hebrides, no refugia were possible there inasmuch as those islands were reduced to mere skerries by the eustatic rise in sea levels which characterized the area at the close of the Glacial Period.

Fortunately, other possibilities, depending upon movements of the earth's crust remain open. In addition to eustatic changes in sea level which affect glaciated areas, other land movements, of the type known as isostatic, have occurred. As the ice sheets developed, and increased in thickness, their weights depressed the land surfaces immediately beneath them, thereby producing an outflow of the subcrustal magma to the periphery, which, in turn, caused a marginal bulge. Thus, beyond the present shores of the Hebrides and Ireland, land, if only a comparatively narrow strip, may have become available for refugia.

Here let us examine the biological evidence provided by other organisms. Of these, the famous moss, *Myurium Hebridarum* stands out pre-eminent. This plant is far from rare throughout the Outer Hebrides and in the Coll-Tiree, Rhum-Eigg groups, with an isolated station on the mainland of Scotland. Elsewhere, it is only known from the Azores, Madeira and the Canary Islands. Owing to its failure to fruit, it must

rely solely on vegetative means for reproduction and dispersal. Taking these facts into account, it is impossible to believe that chance dispersal has been responsible for its present-day peculiar, but orderly, distribution. Clearly, it, too, must have persisted from times when the Macaronesian islands were so placed in respect to the Hebridean area as to admit of some interchange of biota; again, we are compelled to date its arrival here in Tertiary times, and to demand refugia in which it passed the Glacial Period.

It is true that *Myurium Hebridarum* sometimes grows on South Uist alongside relict alpine and arctic species, but it is difficult to imagine its having survived on nunataks as these forms must have done. Judging from its stations in South Harris, it would be much more at home on loch edges located on the marginal bulge postulated above. Moreover, since the American element, as represented by *Potamogeton epihydrus, Naias flexilis* and *Eriocaulon septangulare*, includes a majority of water plants, such refuges as nunataks were quite unsuitable for them. If they survived at all, since long-distance random dispersal seems excluded, they must have overwintered in low-lying peripheral refugia from which, on the onset of favourable geographical and climatic conditions, they emerged to establish themselves in their present habitats. Moreover, the presence of *Potamogeton gramineus* L. and *P. filiformis* PERS. in Greenland today lends considerable support to these views.

Summary

1. An American *Potamogeton, P. epihydrus* RAF. var. *Nuttallii* CHAM. et SCHLECHT. has been discovered on the Isle of South Uist in the Outer Hebrides, a group of islands lying off the west coast of Scotland.
2. This makes an important addition to the ranks of the socalled American element in the British Flora.
3. In my opinion, *Potamogeton epihydrus* var. *Nuttallii*, with the rest of the American element in our Flora, persisted throughout the Pleistocene Glaciations in ice-free refugia situated on the western fringes of a greatly extended Hebridean area.

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