

Two hybrids in *Equisetum* new to the British flora

C. N. PAGE

Royal Botanic Garden, Edinburgh

ABSTRACT

Two hybrids in *Equisetum* subgenus *Equisetum* are reported as new to the British flora. These are *E. palustre* L. × *E. telmateia* Ehrh. (= *E. × font-queri* Rothm.) and *E. arvense* L. × *E. palustre* L. (= *E. × rothmaleri* hybr. nov.).

Descriptions and diagnoses of these hybrids are given, and the significance of their occurrence in Britain is discussed.

INTRODUCTION

Within the British flora two hybrids in *Equisetum* subgenus *Equisetum* (the deciduous horsetails) have previously been known. One of these, *Equisetum palustre* L. × *E. fluviatile* L., has been recorded only from a single station in the Outer Hebrides (Page 1963). The other, *E. arvense* L. × *E. fluviatile* L. (*E. × litorale* Kühlew.), has long been familiar to botanists and is widespread. This paper reports the presence in Britain of two further interspecific hybrids in the subgenus. These are *Equisetum arvense* L. × *E. palustre* L. (*E. × rothmaleri* hybr. nov.) and *E. palustre* L. × *E. telmateia* Ehrh. (*E. × font-queri* Rothm.).

E. × font-queri has been previously recorded from two stations in the Mediterranean area, but earlier reports of hybrids between *E. arvense* and *E. palustre* (as *E. × torgesianum* Rothm.) (Rothmaler 1944) are, I think, incorrect. Good examples of both these hybrids have been found recently by the author on the Isle of Skye (v.c. 104, North Ebudes). Although both represent significant additions to the British flora, the find of *E. × font-queri* is in several ways of special interest. Its shoots are large and exactly intermediate in morphology between its two rather dissimilar parents (Fig. 1A, D, E); it has colonised nearly two square miles (c 5 km²) of native moorland, possibly displacing one of its parent species from most of this area; and it cones vigorously and produces spores which may not be entirely abortive.

Descriptions and diagnoses of the new hybrids are detailed below, with notes on their ecology and biology. For ease of comparison the descriptions follow the format of Warburg (1962).

EQUISETUM × ROTHMALERI

DESCRIPTION AND DIAGNOSIS

Equisetum × rothmaleri C. N. Page, hybr. nov. (*E. arvense* L. × *E. palustre* L.).
Fig. 1B

Caules 25-50 cm alti, 2-3 mm diam., virides, alte 5-8 sulcati; vaginae (dentibus exclusis) 6-7 mm, virides; dentes tot quot sulci, subulati, nigrescentes, marginibus

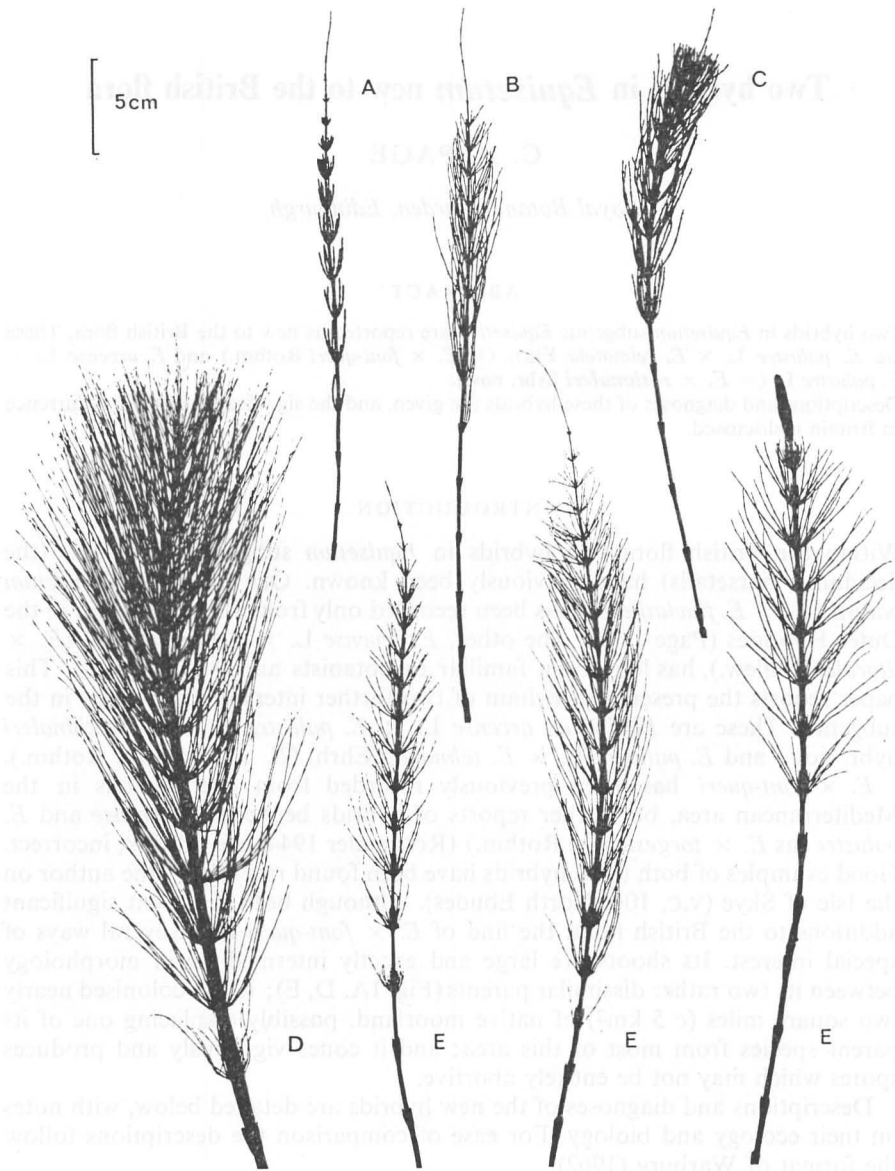


FIGURE 1. Silhouettes of typical aerial shoots of *Equisetum* × *rothmaleri* and *E.* × *font-queri* and their putative parents taken from material collected on Skye in early July. A, *E. palustre*; B, *E.* × *rothmaleri* (*E. arvense* × *palustre*); C, *E. arvense*; D, *E. telmateia*; E, *E. font-queri* (*E. palustre* × *telmateia*), two vegetative shoots and one fertile shoot.

angustis scariosis, 1-costati; cavitas centralis $\frac{1}{4}$ – $\frac{1}{2}$ caulis diam. Ramuli patentes vel suberecti, \pm regularites verticillati, simplices, plerumque tetragoni; internodium infimum vaginam caulis proximam aequans vel duplo superans; vaginae pallidae, dentibus triangularibus-acuminatis patulis minute nigro. Strobilus 4–9 mm longus; sporae abortivae.

Stems 25–50 cm, erect, 2–3 mm diameter, green; grooves 5–8, deep; sheaths (excluding teeth) 6–7 mm, green; teeth as many as the grooves, subulate, blackish with narrow scarious margins, 1-ribbed; central hollow $\frac{1}{4}$ – $\frac{1}{2}$ diameter of stem. Branches spreading to suberect, in \pm regular whorls, simple, usually 4-angled; the lowest internode 1–2 times length of adjacent stem-sheath; sheaths pale, teeth triangular-acuminate, somewhat spreading, with minute black tips. Cone 4–9 mm long; spores abortive.

HOLOTYPE: Kilmaluag, near Rubha Hunish, Trotternish Peninsula, Isle of Skye, Scotland, GR 18/427.742, July 1971, C. N. Page no. C 7902 (E; isotypi BM, K)

Shoots of this hybrid are clearly intermediate in general morphology between those of the putative parents *E. palustre* and *E. arvense*. The three are compared in Table 1. The hybrid resembles *E. arvense* in having the teeth of the sheaths on the main shoot with only narrow scarious margins, the longest branches typically near the middle of the shoot, the first internode of the branch about as long as or longer than the adjacent stem-sheath, the branches with prominent acute ridges separated by deep furrows (usually not more than four), and spreading teeth to the branch-sheaths. It resembles *E. palustre* in typically having a rather long branchless terminal portion to the stem, branches which are mostly ascending, a gradually tapering outline to the upper part of the shoot, black-tipped teeth on the branch-sheaths, and small vallicular canals and central cavity and a single common endodermis in the stem. The combination of these characters distinguishes *E. × rothmaleri* from either parent. The appearance of the entire colony is thus one of somewhat yellow-green shoots of *E. palustre* with a broader outline and more conspicuously angled branches.

The monomorphic habit of *E. palustre* is inherited in the hybrid, whose cone-bearing shoots thus differ from the sterile shoots only in being slightly shorter (25–35 cm) and in terminating in a small ovoid cone (4–9 mm long, 2–3 mm broad) which is black in colour when mature in July. Only about 5% of the shoots found bore cones, and these shoots were widely scattered amongst the vegetative ones. The cones were all small and the spores entirely mis-shapen, colourless, lacking all but the most rudimentary elaters and obviously abortive.

E. × rothmaleri can be distinguished from *E. × litorale* (*E. arvense* \times *E. fluviatile*) by its smaller size, more ascending branches, darker ochreolae, and by the transverse section of the stem, which shows a much smaller central cavity and a single common endodermis. *E. × rothmaleri* is distinct from *E. × font-queri* (*E. palustre* \times *E. telmateia*) in its smaller size, green stem-internodes, stem and branches with simple ridges and single ribs to the teeth. It is less easy to distinguish from *E. fluviatile* \times *E. palustre* but it can be separated by its smaller size, more abundant and more regular branching, more deeply furrowed branches with more prominent ridges and a longer first internode, a single common endodermis in the stem, and the lack of any orange-brown tinge to the internodes or sheaths of the main stem (a characteristic of only *E. fluviatile* and its hybrids).

TABLE 1. COMPARISON OF *EQUISETUM* HYBRIDS AND THEIR PUTATIVE PARENTS
(all data based on material from Skye)

	<i>E. telmateia</i>	<i>E. palustre</i> × <i>E. telmateia</i> (<i>E. × font-queri</i>)	<i>E. palustre</i>	<i>E. arvense</i> × <i>E. palustre</i> (<i>E. × rothmaleri</i>)	<i>E. arvense</i>
height (cm)	40-80	30-65	25-30	35-50	20-55
stem-width* (mm)	5.0-8.0	2.5-4.0	1.5-2.5	2.0-3.0	2.0-3.0
stem-internode colour	ivory white	mostly ivory white	green	green	green
proportion of upper unbranched part of shoot	$\frac{1}{10}$	$\frac{1}{8}$	$> \frac{1}{4}$	$\frac{1}{6}-\frac{1}{4}$	$< \frac{1}{10}$
length of sheath of main stem (excluding leaves)* (mm)	13-18	12-15	6-8	6-7	5-8
number of teeth of main stem-sheath (= internodal ridges)*	14-18	8-12	5-8	6-10	7-15
usual number of branch ridges	4-5	4-6	5-6	mostly 4	3-4
shape of branch ridges	prominent, biangulate	moderate, shallowly biangulate	low, rounded, simple	prominent, simple	prominent, simple
position of longest branches on main stem	upper $\frac{1}{2}$	near middle	lower $\frac{2}{3}$	near middle	middle-upper $\frac{1}{3}$
ratio of length of first branch internode to adjacent stem-sheath	$\frac{1}{2}-1$	$\frac{1}{3}-\frac{3}{4}$	$\frac{1}{4}-\frac{1}{2}$	$< 1-2$	2-3
endodermal pattern of main stem	single common	single common	single common	single common	single common
ratio of width of central hollow of stem to stem diameter*	$> \frac{1}{2}$	$c \frac{1}{4}$	$< \frac{1}{4}$	$\frac{1}{4}-\frac{1}{2}$	$c \frac{1}{2}$
ratio of width of vallecular canals to stem diameter*	$< \frac{1}{8}$	$c \frac{1}{6}$	$\frac{1}{5}-\frac{1}{4}$	$c \frac{1}{6}$	$c \frac{1}{8}$
fertile shoot-type	dimorphic	monomorphic	monomorphic	monomorphic	dimorphic

* Measured $\frac{1}{3}$ of the way up the stem.

LOCAL DISTRIBUTION AND ECOLOGY

A single colony of this plant was found in July 1971 at Kilmaluag near Rubha Hunish on the Trotternish Peninsula, Isle of Skye (v.c. 104) (GR 18/427.742). It is locally abundant in roadside ditches which drain flat marshy ground. It occurs for about 50 yards (*c.* 46m) along either side of a small road and it spreads for a short distance into the adjacent marshy fields. In the ditches it is locally dominant but becomes less abundant in the fields where it occurs with *Equisetum palustre*, *E. fluviatile*, *Filipendula ulmaria*, *Ranunculus flammula*, *Potentilla palustris*, *Caltha palustris* and other marsh species.

EQUISETUM × *FONT-QUERI*

DESCRIPTION AND DIAGNOSIS

Equisetum × *font-queri* Rothm. (*E. palustre* L. × *E. telmateia* Ehrh.) Fig. 1E

Stems 30–65 cm, erect, 2.5–4.0 mm diameter, mostly ivory-white, smooth; grooves 8–12, shallow; sheaths (excluding teeth) 12–15 mm, ± appressed, greenish, sometimes blackish above; teeth as many as the grooves, blackish with scarious margins, subulate, 2-ribbed; central hollow about $\frac{1}{4}$ diameter of stem. Branches spreading, usually in regular whorls, numerous, simple, 4–6-angled; the lowest internode $\frac{1}{3}$ – $\frac{3}{4}$ the length of adjacent stem-sheath; sheaths pale, teeth triangular-acuminate, brownish, appressed. Cone 8–42 mm long; spores at least partially abortive.

SPECIMENS: *c.* $\frac{1}{2}$ mile north of Loch Leathan, 1 mile WSW of the Storr, Trotternish Peninsula, Isle of Skye, Scotland, GR 18/511.534, July 1971, C. N. Page no. C7880 (BM, E, K)

Shoots of this hybrid are strikingly intermediate in size and morphology between those of *E. palustre* and *E. telmateia* (Table 1). They resemble *E. telmateia* in their large size, thick stems, stem internodes which are mostly ivory-white, biangulate branch ridges, stem- and branch-sheaths with 2-ribbed teeth, and relatively long somewhat flexuous teeth on the main stem-sheaths. They can be clearly linked with *E. palustre*, however, by their comparatively slender overall outline, long terminal branchless portion, spreading to subsending branches which are more robust than those of *E. telmateia*, stems with relatively small vallicular canals and central cavity, and stomata on the stem internodes (absent in *E. telmateia*). Indeed, the overall appearance of stands of the hybrid is one of overgrown shoots of *E. palustre* with the conspicuous ivory-white internodes and long teeth on the sheaths of the main stem as in *E. telmateia*. Although the monomorphic habit of *E. palustre* is inherited in the hybrid, a few cone-bearing shoots of *E. × font-queri* were found in which whorled branches were absent from the vegetative nodes. However, these shoots were tall (25–50 cm) with long vegetative internodes and resembled the occasional unbranched shoots also to be found from time to time in local *E. palustre* colonies; they are very different therefore from the thick, short, spring cone-shoots characteristic of *E. telmateia*. Most cone-bearing shoots of *E. × font-queri*, then, closely resemble the vegetative ones with profuse whorls of green branches. Nearly half of all the shoots seen in July 1971 bore cones. These mature in July and are ovoid in shape, slimmer than those of *E. telmateia* (8–42 × 3–9 mm) and pale green in colour with chestnut-

brown tips. They are thus intermediate between the relatively small, markedly cylindrical and usually blackish cones of *E. palustre* and the large, broad, ovoid-ellipsoid cones of *E. telmateia*, which are whitish or pale green with small brown tips. In the field, cones of the hybrid appear well-filled and seem to open and dehisce normally. Examination of the fresh spores showed that a proportion (varying from 5% to 50% in different sporangia and different cones) were relatively well-formed, green in colour, and possessed well-developed elaters. The remainder of the spores were small, mis-shapen, lacked good elaters, and were obviously abortive as in other hybrids.

Equisetum × *font-queri* can be readily distinguished from the other known *E. palustre* hybrids (*E. × rothmaleri* and *E. fluviatile* × *E. palustre*) as well as from *E. × litorale* (*E. arvense* × *E. fluviatile*) by its more robust shoots with ivory-white internodes, typically more abundant branches, and 2-ribbed teeth to the stem- and branch-sheaths.

LOCAL DISTRIBUTION AND ECOLOGY

It was found in July 1971 locally abundant and sometimes dominant over a distance of about two miles (*c.* 3.5 km) by the road along the east side of the Storr on the Trotternish peninsula, Isle of Skye (v.c. 104) (GR 18/511.532–516.614). It was present on both sides of the road and up to half a mile (*c.* 0.8 km) from it, the altitude varying from 150–525 ft (45–160 m). It extended from just north of Loch Leathan in the south to about half a mile north of Rigg Burn. Between these two points the hybrid forms a nearly continuous stand, becoming particularly abundant in most damp depressions, irrigated slopes, flushes, seepage lines, screebanks, drainage channels, ditches and streambanks; it is also vigorously colonising roadside verges and rubble along most of the two-mile stretch of road. The plant was not found in the immediate vicinity of the Storr itself (J. C. Gardiner *pers. comm.*).

DISCUSSION

MORPHOLOGY AND PARENTAGE OF THE HYBRIDS

It has been shown in Table 1 that the two hybrids are almost exactly intermediate between two pairs of British species in a large number of distinct morphological characters; the parentage of each can therefore be deduced with reasonable certainty. The only morphological trait not found to be intermediate in the hybrids is the inheritance (from *E. palustre* in each case) of monomorphic aerial shoots. It is worth noting that in *E. × litorale* the monomorphic condition of one parent (*E. fluviatile*) is similarly dominant over the dimorphic condition of the other (*E. arvense*).

All three putative parent species of the two hybrids are present on Skye, and at least one of these (*E. palustre*—the parent common to each of the hybrids) is locally extremely abundant. It colonises a wide range of wet boggy and marshy habitats, flushes, ditches, and even roadside banks and verges, and in most places cones vigorously. Both the other two parent species occur near the hybrids. The withered remains of the ephemeral spring fertile shoots of *E. telmateia* were found and it is probable that *E. arvense* is also fertile in this area.

The hybrids occupy habitats intermediate between those of the putative

parents; in the case of *E. × font-queri* the hybrid also occupies virtually the whole range of habitats of both.

EXTRA-BRITISH DISTRIBUTION

Putative hybrids between *E. arvense* and *E. palustre* have been reported by Rothmaler (1944) under the name *E. × torgesianum* from about five localities in north-central Europe, although these stations are poorly documented. I am not aware of any further published records and I have found no material of this hybrid in herbaria. I have examined the material from the north-central European localities (six sheets from five stations) at Jena (**JE**) attributed by Rothmaler to hybrids between *E. arvense* and *E. palustre*. Specimens from four of these localities, including the holotype of *E. × torgesianum*, appear to be robust plants of *E. palustre* with a superficial resemblance to *E. arvense*. I can, however, find no good characters to link any of the specimens firmly with *E. arvense* (or any other species). I am not convinced, therefore, that they are hybrids and in my opinion they all belong to *E. palustre*. The specimen from the fifth locality is equally clearly *E. arvense*. My material from Skye is easily distinguished from all of these plants. The name *E. × torgesianum* cannot, therefore, be used for the Skye hybrid, which has accordingly been described above (p. 229) as *E. × rothmaleri*. The Skye locality is thus the only one known for this hybrid.*

Putative hybrids between *E. palustre* and *E. telmateia* have been recorded previously from two Mediterranean stations. The type locality of *Equisetum × font-queri* is given by Rothmaler (1944) as 'Hispania, Gerona, Martorella de la Selva . . . Solum in loco classico observatum, sed frequens', where the plant occurred in damp alder woodland. I have examined Rothmaler's material (8 sheets bearing 45 shoots) at **JE** collected at various times from the Gerona locality, including the holotype of *E. × font-queri* collected on 29th April 1934 by Font Quer. In size and morphology all Rothmaler's specimens are distinctly intermediate between *E. palustre* and *E. telmateia*, and are, without doubt, the hybrid between them. My Skye material of *E. palustre × E. telmateia* corresponds extremely closely with these Spanish specimens, and there is little doubt that they are the same hybrid.

The second and, as far as I am aware, only other known station for this hybrid was detected by Hauke (1966) in herbarium material at Stockholm (**S-PA**) from 'Entre le pont du Var et la mer (Alpes maritimes)' collected by Emile Burnat, 20th May 1872. The locality is near Nice, southern France. I have examined this material and agree with Hauke's determination. These specimens are somewhat smaller than my Skye plants (averaging about 30–45 cm) but otherwise they compare very closely with them, and small specimens of the Skye plants can be distinguished from them only with difficulty. The habitat is given as alluvial riverside sand several feet above the river water; about half the shoots seen bear cones. Further sheets from this same locality are at Kew (**K**), and most of these are also fertile. Judging by the size of these collections (4 sheets containing 17 specimens at **S-PA**, 4 sheets with 22 specimens at **K**) the hybrid must also have once been reasonably abundant in the Nice locality, and further search for this plant both at Gerona and Nice is greatly to be desired.

A retrospective search for other herbarium material also revealed a specimen which is clearly this taxon in London (**BM**) collected from Rigg Burn, Skye, by

* This updates and re-inforces information already published (Page 1972, p. 366).

Patricia A. Sims, on 19th August, 1960. This record pre-dates my own find of this plant on Skye in the same locality and provides evidence that *E. × font-queri* has been in this area for over 10 years. These specimens were also bearing cones.

EXCEPTIONAL FEATURES OF *E. × FONT-QUERI* ON SKYE

The very large size of the area occupied by *E. × font-queri* on Skye cannot fail to impress even a casual observer. Further, over the whole of this area, with the exception of the immediate vicinity of the road, *E. × font-queri* appears to have invaded previously closed habitats. Many of the habitats it occupies are elsewhere colonised vigorously by *Equisetum palustre*, but in the area of the hybrid this species is almost absent, giving the impression that *E. × font-queri* has largely ousted and replaced this parent.

The abundance of fertile shoots and the large size of the cones of *E. × font-queri* are also exceptional features for a hybrid horsetail. The presence of a proportion of spores in these cones which appear to be not entirely abortive is possibly unique, although it is not known whether any of these spores are viable.

These features all contrast markedly with the colony of *E. × rothmaleri* described here as well as with the only known colony of *E. fluviatile × E. palustre*, which is in the Outer Hebrides. The colonies of each of these two hybrids are small and appear to be hardly, if at all, more vigorous than their parent species. Indeed, the only hybrids in *Equisetum* subgenus *Equisetum* seen by the author which approach the vigour of *E. × font-queri* are certain colonies of *E. × litorale* in other parts of the British Isles. Cases where *E. × litorale* has invaded closed communities must also be rare. The weakness of the colonies of *E. × rothmaleri* and *E. fluviatile × E. palustre* when compared with the relative vigour of those of *E. × litorale* and *E. × font-queri* is especially significant in the light of the inter-relationships of the parent-species that have been suggested on micromorphological grounds (Page 1972). These data indicate that *E. palustre* and *E. telmateia* are closely related, similarly *E. arvense* and *E. fluviatile*. It appears, therefore, that the most vigorous and successful hybrids in the subgenus *Equisetum* are those between the most closely related (yet ecologically diverse) pairs of species, whilst hybrids between more distantly related species (which may be ecologically more similar) are scarcely, if at all, more vigorous than their parents.

DISTRIBUTION AND ORIGIN OF THE HYBRIDS

During this survey several stations for *E. × litorale* were also detected on Skye, making a total of four interspecific hybrids in *Equisetum* subgenus *Equisetum* in the Hebrides. This high local concentration of hybrids in this subgenus contrasts with the certain occurrence elsewhere in the British Isles of only *E. × litorale*.

Despite the extensive total ranges of the *E. telmateia* complex (temperate western Eurasia and western North America) and of *E. arvense* and *E. palustre* (chiefly North Temperate regions of both the Old and New Worlds), the recorded interspecific hybrids among this trio are all from western Europe. Furthermore, the number of known stations for these hybrids is surprisingly small when compared with the relatively large number for the hybrid between *E. arvense* and *E. fluviatile*—90 stations for *E. × litorale* are known in Fennoscandia (Borg 1967) and nearly 100 in the British Isles.

The isolation of the Skye colony of *E. × font-queri* from its two Mediterranean stations suggests that, as with *E. × rothmaleri* and *E. fluviatile × E. palustre*,

this hybrid has arisen independently in the Hebridean area, and implies that the local environment must be particularly favourable for hybridisation. Conditions that are conducive to hybridisation in *Equisetum* are as yet poorly understood and clearly deserve further study. Reports of *Equisetum prothalli* in the wild are extremely few, and are only from habitats which are damp, recently-exposed and free, at least initially, from much competition (Matzke 1941, Feigley 1949, Hauke 1967, Page 1967). The occurrence of all three Hebridean *E. palustre* hybrids near to or in roadside ditches suggests an association between the digging or clearing of the ditch by man and the formation of the hybrid. Any damp mud surface exposed at an appropriate season would probably form an ideal substrate for rapid prothallial growth. Manton (1950 p. 223), commenting upon the number of interspecific hybrids in *Equisetum* known at that time from Ireland, states that the mild, oceanic Irish climate seems likely to favour their production. This view is strengthened by the subsequent discovery of *Equisetum fluviatile* × *E. palustre* in the Outer Hebrides and the presence of these two new hybrids on Skye—both in areas where the rainfall is high and spread liberally throughout the year.

ACKNOWLEDGMENTS

It is a pleasure to record my thanks to Messrs J. W. Dyce, J. C. Gardiner and A. C. Jermy for useful discussion in the field, to Mr B. L. Burt, Mr D. M. Henderson and Dr T. G. Walker for helpful comments on the manuscript, and to Mr Burt for preparing the Latin description.

REFERENCES

- BORG, P. (1967). Studies on *Equisetum* hybrids in Fennoscandia. *Ann. Bot. Fenn.*, 4: 35–50.
FEIGLEY, M. (1949). An occurrence of gametophytes of *Equisetum* in Cheboygan County, Michigan. *Am. Fern. J.*, 39: 106–109.
HAUKE, R. L. (1966). A systematic study of *Equisetum arvense*. *Nova Hedwigia*, 13: 81–109.
HAUKE, R. L. (1967). Sexuality in a wild population of *Equisetum arvense* gametophytes. *Am. Fern. J.*, 57: 59–66.
MANTON, I. (1950). *Problems of Cytology and Evolution in the Pteridophyta*. Cambridge.
MATZKE, E. B. (1941). Gametophytes of *Equisetum arvense* L. *Torreyia*, 41: 181–187.
PAGE, C. N. (1963). A hybrid horsetail from the Hebrides. *Br. Fern. Gaz.*, 9: 117–119.
PAGE, C. N. (1967). Sporelings of *Equisetum arvense* in the wild. *Br. Fern. Gaz.*, 9: 335–338.
PAGE, C. N. (1972). An assessment of inter-specific relationships in *Equisetum* subgenus *Equisetum*. *New Phytol.*, 71: 355–369.
ROTHMALER, W. (1944). Pteridophyten-Studien I. *Reprum nov. Spec. Regni veg.*, 54: 55–82.
WARBURG, E. F. (1962). *Equisetum*, in CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. *Flora of the British Isles*, 2nd ed., pp. 6–11. Cambridge.

(Accepted June 1972)