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HYBRIDS IN THE GENUS *EQUISETUM* IN EUROPE: AN UPDATED ANNOTATION

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Summary.
A list of authenticated hybrids in the genus *Equisetum* in Europe is given. This includes two hybrids in subgenus *Hippochaete* and six in subgenus *Equisetum*. Brief notes on the morphology, ecology and distribution in Europe of each of the hybrids is given.

Key words: *Equisetum*, "Horsetails", hybrids, geography, ecology, phylogeny.

Resumen.
Se presenta una lista de híbridos autentificados del género *Equisetum* en Europa, que incluye dos híbridos del subgénero *Hippochaete* y seis del subgénero *Equisetum*. Asimismo, se presentan unas breves notas sobre la morfología, ecología y distribución en Europa de cada uno de los híbridos citados.

Palabras clave: Equisetum, híbridos, geografía, ecología, filogenia.

INTRODUCTION.

The genus *Equisetum* (the 'Horsetails') is largely North Temperate in distribution, with a total of 10 species in Europe including members of both subgenera:

Subgenus *Hippochaete*:

E. ramosissimum Desf., *E. hyemale* L., *E. variegatum* Schleich. ex Weber & Mohr, *E. scirpoides* Michx.

Subgenus *Equisetum*:

E. fluviatile L., *E. arvense* L., *E. pratense* Ehrh., *E. sylvaticum* L., *E. palustre* L., *E. telmateia* Ehrh.

The European distribution of these species is mapped in Jalas & Suominen (1972). Further, at least three varieties of *E. variegatum* occur in Europe (Page, 1982, 1988a)
Between these species, eight authenticated hybrids occur, which are presented with brief notes on their morphology, ecology and distribution in Europe, in the following list. In addition, at least four other possible hybrids have been reported in Europe (see 'Discussion'), and are in need of further research and confirmation. This list updates that of Rothmaler (1944), Manton (1950) and Duckett & Page (1975).

SUBGENUS *HIPPOCHAETE.*

Equisetum* x *moorei Newm. (*E. hyemale* L. x *E. ramosissimum* Desf.).

This hybrid is intermediate between its putative parents in stem-diameter, ridge-number, sheath-length and appression to stem, sheath-tooth persistence, stem persistence in winter, stomatal length, and stem anatomy, but similar to *E. hyemale* in stomatal width and to *E. ramosissimum* in sheath-width. The plant is, however, very variable in overall size and morphology, and can closely approach either parent in appearance. In many colonies, cones are produced in some abundance from May to November but the spores are very variable in size and appear to be completely abortive. It is a fairly vigorous hybrid, which is widely but infrequently spread throughout Europe in the sympatric portions of its parental ranges, as far north as Poland and Russia and as far south as Italy. Colonies may however be locally extensive, mainly on sandy river banks, lake shores and occasionally on railway lines. In south-eastern Ireland, it is widespread in coastal sand-dunes to the tide-line, and local reproduction and spread by sea-borne vegetative fragment dispersal is suspected (PAGE & BARKER, 1985).

Equisetum* x *trachyodon A. Braun (*E. hyemale* L. x *E. variegatum* Schleich. ex Weber & Mohr).

This hybrid is intermediate between its putative parents in all characters except the length/width ratio of the leaf-sheath (which exceeds that of both parents) and stomatal size (almost identical with *E. variegatum*). Confusion with *E. hyemale* is unlikely but small plants may easily be mistaken for *E. variegatum*. Separation from the latter is usually possible in the field by the long narrow, black teeth with narrow membranous margins in the hybrid. Cones are produced from June to October but usually fail to open and hence to shed their spores, which are usually described as completely abortive. However, some sporangia may contain spores of widely assorted size, and occasionally a few of these look relatively well-formed.

This is a very vigorous hybrid which is widely but infrequently spread throughout Europe in the sympatric portions of its parental ranges, as far north as Greenland, Iceland and Sweden and as far south as France. It is especially characteristic of damp sandy river and stream banks, where constant erosion maintains ecological openness of the habitats. In Ireland it is also widespread in open sandy lake-margin habitats, and in western England and western Scotland, also in sand-dune slacks. Much of its local reproduction is by subterranean rhizome growth, but in Britain and Ireland, some reproduction of established colonies by freshwater-borne or saltwater-borne vegetative stem fragments is suspected (PAGE & BARKER, 1985). The abundant Irish stations for this hybrid probably involve a different and more vigorous variety of *Equisetum variegatum* (var. *majus* Syme) in their parentage from those elsewhere in Europe (PAGE, 1982, 1988).

SUBGENUS *EQUISETUM*.

Equisetum* x *dycei C.N. Page (*E. fluviatile* L. x *E. palustre* L.).

This hybrid is intermediate between the two supposed parents in the number and depth of ridges and furrows on the shoot internode, and in the ratio of the central hollow to the diameter of the stem. Shoots are semi-prostrate and simple or sparingly branched, typically with a long unbranched, terminal portion. The rhizomes of the hybrid bear tubers as do those of *E. palustre*. Individual endodermises around each vascular bundle in both shoot and rhizome, and the presence of a central hollow in the rhizome, affirm that *E. fluviatile* is one parent (PAGE, 1963).

This appears to be a relatively weak hybrid, the occurrence of which has been recognized only throughout Scotland and Ireland (PAGE, 1982, 1988), but which could occur much more widely in Atlantic Europe throughout the extensively sympatric portions of its parental ranges.

Despite its lack of vigour, its Scottish and Irish station are relatively numerous, especially in low-competition ditch, stream bank and lake shore habitats, usually where both parents are present nearby. Most colonies are, however, of small size and of very local occurrence. Its presence in several recently dug man-made ditches, but less so in older ones, suggests that it may be a pioneer which is usually ecologically seral and hence often ephemeral, becoming later displaced by more vigorous colonizing vegetation (PAGE, 1973, 1988). Each colony presumably represents a separate cross between its very widespread parents.

Equisetum* x *litorale Kuhlew. ex Rupr. (*E. arvense* L. x *E. fluviatile* L.).

Shoots of this hybrid are generally intermediate between the parents in most characters but are also extremely variable and may sometimes very closely resemble either parent (e.g. in drier habitats they approach *E. arvense* and in wet ones *E. fluviatile*). Experimental cultivation shows that this variability is a plastic one, totally induced by environmental conditions. Hybrids can usually be distinguished from the parents by external features (e.g. length of first internodes of branches, shape of upper part of stem, number of ridges, number, length and direction of branches) but in some cases (e.g. separation from unbranched forms of *E. fluviatile*) anatomical characters (e.g. size of the central hollow and vallecular canals) are also needed. In the field, a good initial diagnostic character is that the internode of the main stem yields more easily to light squeezing between finger and thumb than does that of the *E. arvense* parent, but much less so than that of *E. fluviatile*. Colonies are typically totally sterile. Occasionally small cones are sometimes sporadically produced from June to July, but their spores appear to be completely abortive.

E. x *litorale* is probably the second most vigorous hybrid horsetail in Europe, after *E.* x *font-queri* (q.v.). It is probably very widespread in northern Europe, though is almost certainly greatly under-recorded. Within Britain and Ireland, well over 100 stations are known for this plant. Its sites occur in a wide range of semi-natural and artificial wetlands: in ditches, stream banks, lake margins, marshes, fens, swamps and sea shorelines. It typically forms large and dense colonies. The size of many of its colonies and the frequency of their occurrence almost certainly reflect the considerable vegetative vigour of this hybrid, which usually appears to persist well against other vegetational competition. Although most of its distantly-separated sites must represent independent hybridizations between its very widespread parents, there is also evidence of establishment of dispersed shoot fragment material around lakes and along streams (PAGE & BARKER, 1985).

Equisetum* x *rothmaleri C.N. Page (*E. arvense* L. x *E. palustre* L.).

Colonies of this hybrid are closely intermediate in morphology between those of the parents, and give the appearance of somewhat yellow-green shoots of *E. palustre* with a broader

outline and more conspicuously angled, more slender, branches. The monomorphic habit of *E. palustre* is inherited in the hybrid, which bears scattered small black cones on the tips of some of the shoots. Its spores appear to be entirely abortive.

This hybrid, which is not very vigorous, seems to occur fairly widely in the wetter, western Atlantic fringes of Scotland and Ireland, as small and sometimes diffuse colonies in ditches, along stream banks, in marshes and in lake-margin reedswamp habitats. It usually occurs in the presence of both parents, as well as often with *E. fluviatile*, and in some sites in Ireland and western Scotland also with *E.* x *litorale* and *E.* x *dycei* (PAGE, 1988a).

Its parents are very widespread, and this hybrid may well yet be found elsewhere in Europe.

Equisetum* x *mildeanum Rothm. (*E. pratense* Ehrh. x *E. sylvaticum* L.).

Colonies of this hybrid are closely intermediate in morphology between the parents, with sparsely branched branches and main shoot sheath-teeth which are longer and blacker than those of *E. sylvaticum*.

It has been reported from Russia, Germany and Sweden, and has recently been found in at least three localities in Scotland (PAGE, 1988b), and could well occur elsewhere in the more mountainous parts of central and northern Europe. In Scotland its habitats are all on steep rocky, mountain slopes, in regions where the two parents each occur in some abundance.

Equisetum* x *bowmanii C.N. Page (*E. sylvaticum* L. x *E. telmateia* Ehrh.).

This somewhat unlikely-sounding hybrid has the thick, mostly ivory-white main shoot internodes of *E. telmateia*, with the thin, drooping, branches of *E. sylvaticum*, with branch internode features and main shoot teeth strongly intermediate between the two very different parents.

It has been recorded only recently, in southern England, on a man-made roadside embankment and adjacent ditches. Here it grows in the vicinity of colonies of both parents, between which its morphological intermediacy is specially striking. Its site marks one of the few parts of Europe in which its two parents are both sympatric and frequent (PAGE, 1988b).

Equisetum* x *font-queri Rothm. (*E. palustre* L. x *E. telmateia* Ehrh.).

Shoots of this hybrid are intermediate in morphology between those of the parents, and give the appearance of overgrown shoots of *E. palustre* with the conspicuous ivory-white internodes of *E. telmateia*. The hybrid has the shallowly biangulate branch-ridges and 2-ribbed teeth of *E. telmateia*, but inherits the monomorphic habit of *E. palustre*. It is vegetatively prolific. Cones are produced in abundance, and some of its spores appear to be well-formed.

This hybrid is one of exceptional vegetative vigour. It has been reported from Spain and France (BADRÉ & PRELLI, 1980), and I have authenticated material from each of its known sites. It has also been found in three localities in Britain. It occurs in a variety of base-rich, wet, flushed habitats, and its two English records are on a railway embankment and on a canal side. Its most extensive locality anywhere is that on the Isle of Skye, western Scotland, where its shoots are abundant over an area of approximately two square miles. Here it occupies a wide range of moist, mostly flushed, habitats, becoming particularly abundant in damp depressions, irrigated slopes, seepage lines, scree banks, drainage channels, ditches, stream banks, roadside verges and rubble. It appears to have ecologically displaced one of its parents, *E. palustre*, from most of its area, and perhaps other species and hybrids. Most of its spread in this locality may be rhizome growth, but the occurrence of a percentage of good-looking spores in many of its cones in some seasons suggest that some limited spread also by this means cannot be ruled out (PAGE, 1973, 1982).

All its localities occur within the limited sympatric portions of the parental ranges in Europe.

DISCUSSION.

Four other hybrids additional to those listed above have been reported in Europe (e.g. Rothmaler, 1944; Derrick, Jermy & Paul, 1987); these are excluded from the above annotated part of this list through my not having been able to find and authenticate material of them. These are *E. scirpoides* x *E. variegatum*, *E. ramosissimum* x *E. variegatum*, *E. arvense* x *E. pratense*, and *E. arvense* x *E. telmateia*. All however, are taxonomically possible combinations and might well exist. All could be sought in the sympatric parts of their parental ranges.

Four aspects stand out as especially notable from the annotated parts of this list.

One is the occurrence at all of hybrids in a genus of plants as old as *Equisetum*.

A second is the restriction of hybrids to combinations between members of the same subgenus. I have never been able to confirm any inter-subgeneric hybrid in *Equisetum* on a Eurasian or even world scale (PAGE, 1974; PAGE & BARKER, 1985).

A third is the notable frequency of these hybrids in the wetter parts of the extreme Atlantic periphery of Europe, and for this reason, Britain and Ireland contain both an exceptionally high number of hybrids and an exceptionally high number of stations for most.

The fourth is the varying degrees of vigour of the hybrids formed (and hence their wild 'survivability') in relation to the phylogeny and ecology of their parents established on independent grounds (PAGE, 1972). This led to the proposal (PAGE & BARKER, 1985), for the hybrids in this genus, of "Page's rule". This states that the weakest hybrids are those between phylogenetically distant but ecologically similar pairs of parents, while the most vigorous hybrids result from crossing between phylogenetically close but ecologically most divergent parental pairs.

The genus *Equisetum* is probably the oldest vascular plant genus on Earth. It still, however, probably has a lot to teach us!

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