

A new hybrid horsetail, *Equisetum arvense* × *E. telmateia* (*E.* × *robertsii*) in Britain

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ABSTRACT

An extensive colony of *E.* × *robertsii* T. D. Dines **hybr. nov.** (*E. arvense* L. × *E. telmateia* Ehrh., Equisetaceae) was discovered on sand and boulder-clay cliffs at Traeth Lligwy on the N.E. coast of Anglesey (v.c. 52), close to a known colony of *E.* × *font-queri* Rothm. (*E. palustre* L. × *E. telmateia*). *E.* × *robertsii* is intermediate between its parents in all respects. The morphology, stem anatomy and stomatal characters of the hybrid and its parents are described and illustrated, and its habitat is also outlined. This hybrid has previously been reported from Suffolk, where its identity was never confirmed, and from the Czech Republic, where the record was apparently based on material of *E. arvense*. The distribution and ecology of other hybrids involving *E. arvense* and *E. telmateia* are discussed.

KEYWORDS: Morphology, anatomy, stomata, Anglesey.

INTRODUCTION

Britain and Ireland provide particularly rich hunting grounds for hybrids between the eight native and one alien species of *Equisetum* known from this area. Nine hybrid combinations have currently been recorded, with all nine species being involved to varying degrees.

The genus *Equisetum* is divided into two subgenera, *Hippochaetae* and *Equisetum*, and hybrids are only formed between species from the same subgenus (Hauke 1963 & 1978; Page & Barker 1985). Two hybrids are known between the three species (*E. variegatum* Schleich. ex F. Weber & D. Mohr, *E. hyemale* L. and *E. ramosissimum* Desf.) in subgenus *Hippochaetae*, and seven have been recorded between the six species in subgenus *Equisetum*.

All *Equisetum* hybrids, except *E.* × *litorale* Kühlew. ex Rupr. (*E. arvense* L. × *E. fluviatile* L.) and *E.* × *trachyodon* A. Braun (*E. hyemale* × *E. variegatum*), can be regarded as rare, and they usually exist in small, isolated populations. Given the morphological variability displayed by the species, hybrid horsetails can be difficult to identify, and all are probably under-recorded.

One species, *E. telmateia* Ehrh., has a particular propensity to hybridise. It is currently known to have formed hybrids with three of the most common species in Britain and Ireland (with *E. palustre* L. to give *E.* × *font-queri* Rothm., with *E. fluviatile* to give *E.* × *willmotii* C. N. Page and with *E. sylvaticum* L. to give *E.* × *bowmanii* C. N. Page). Missing from this list is the hybrid with the most frequent species in Britain, *E. arvense*. Although *E. arvense* and *E. telmateia* are abundant in suitable habitats across Britain and Ireland, the hybrid between them has remained elusive and undescribed.

In July 2000 we visited Traeth Lligwy (SH48) on Anglesey (v.c. 52) to examine the population of *E.* × *font-queri* that was discovered there in 1989 (Roberts 1990). At the south-eastern end of the bay, while making our way towards the *E.* × *font-queri* site, we passed an area of sand and boulder-clay cliffs and noticed plants of an *Equisetum* of unusual appearance. They were stout and well-branched, possessed pale green internodes, and many were decumbent with declined or

horizontal branches. Our initial impression was one of plants intermediate between *E. arvense* and *E. telmateia*. Specimens were collected and subsequent examination has confirmed the presence of the hybrid between these species.

We can trace only two earlier reports of hybrids between *E. arvense* × *E. telmateia*. The first is that of Dostal (1950), who collected putative plants of the hybrid from near Nový Jičín in Moravia (Czech Republic) in 1948. He provisionally named the hybrid *E. × dubium*, but no formal description was published and no herbarium specimens appear to exist. Moreover Hrouda (1988), in agreement with Novak (1971), considers the record to be a mistake, the plants in question being robust forms of *E. arvense*. The name *E. × dubium* (nom. nud.) is therefore placed in synonymy with *E. arvense*.

There are also references to *E. arvense* × *E. telmateia* from E. Suffolk (v.c. 25), where an old, established colony was recorded and determined by F.W. Simpson from a shady marsh at Foxhall (TM24) in 1974, and another from Belton (TG40) in 1977 (Simpson 1982). Unfortunately, no specimens exist of these plants (Simpson, pers. comm., 2000) and no formal description was published. There is no mention of the Suffolk populations in Stace (1975, 1997), Page & Barker (1985) or Page (1997).

The population described here is therefore the first confirmed and fully documented occurrence of this hybrid. It is given here a formal name, and specimens have been placed in **BM**, **E** and **NMW**. This discovery brings the number of confirmed *Equisetum* hybrids recorded for Britain to ten, and those involving *E. telmateia* to four.

TAXONOMIC DESCRIPTION

Equisetum × robertsii T. D. Dines, **hybr. nov.**
(*Equisetum arvense* L. × *E. telmateia* Ehrh.) (Fig. 1)

HOLOTYPE: Growing on wet sand and boulder-clay cliffs, Traeth Lligwy, Anglesey, v.c. 52, SH498871, 6th July 2000, T. D. Dines (**BM**).

An erect or decumbent herb, with rhizomes black or brown-black, glossy, 2–(2.2)–3 mm in diameter. Stem to 60 cm, terete, moderately thick, 2.5–(4)–5 mm in diameter; stem internodes green or pale green when young, whitish green or white when mature, always paler towards the base of the stem, minutely rough, with central hollow 0.25–0.5 of diameter of stem and 12–(20)–30, shallow, rounded ridges; stem sheaths 3–(4)–6 mm long (excluding teeth), appressed, dull greenish brown when young, brown or blackish when mature; sheath teeth numerous, about as many as the ridges, 3–(4)–5 mm long, appressed, with a single rib, slender, acute, occasionally with a fine, hairlike apex, uniformly brown, lacking a scarious margin or with a very narrow scarious margin at the base, two or three sometimes adhering laterally by their margins. Branches numerous, arranged in regular and numerous whorls, 9–(11)–14 per whorl, 60–(117)–190 mm long, distributed evenly around the stem or arranged bilaterally (particularly on decumbent stems), slightly ascendent when young, later ascendent to declined when stem erect but declined when stem decumbent, slender, 1.5–2 mm in diameter, green or yellow-green; first internode of branches equal in length to or slightly longer than stem sheath; branch sheaths appressed to branch, yellow-green, with teeth 2–3 mm long, with a green base and a narrowly triangular brown point; branch internodes with 4–6 flattened or slightly rounded ridges and an equal number of rounded furrows, the ridges sometimes slightly biangled where they enter the subtending sheath. Cones unknown, not seen and not to be expected on vegetative stems; spores unknown.

Herba erecta vel decumbens, rhizomatibus nigris vel brunneonigris, nitidis, 2–(2.2)–3 mm diametro, praedita. Caulis ad 60 cm, teres, modice crassus, 2.5–(4)–5 mm diametro; caulis internodia viridia vel subviridia ubi juvenilia, albiviridia vel alba ubi matura, caulis basin versus semper pallidiora, minute aspera, cavo centrali 0.25–0.5 diametri caulis metiente, porcis 12–(20)–30 non profundis rotundatis instructa; caulis vaginae 3–(4)–6 mm longae (dentibus exclusis), appressae, obscure viridibrunneae ubi juveniles, brunneae vel nigricantes ubi maturae; vaginae dentes numerosi, circiter tot quot porcae, 3–(4)–5 mm longi, appressi, costa singula praediti, graciles, acuti, apice tenui capilliformi aliquando muniti, uniformiter brunnei, marginem scariosum

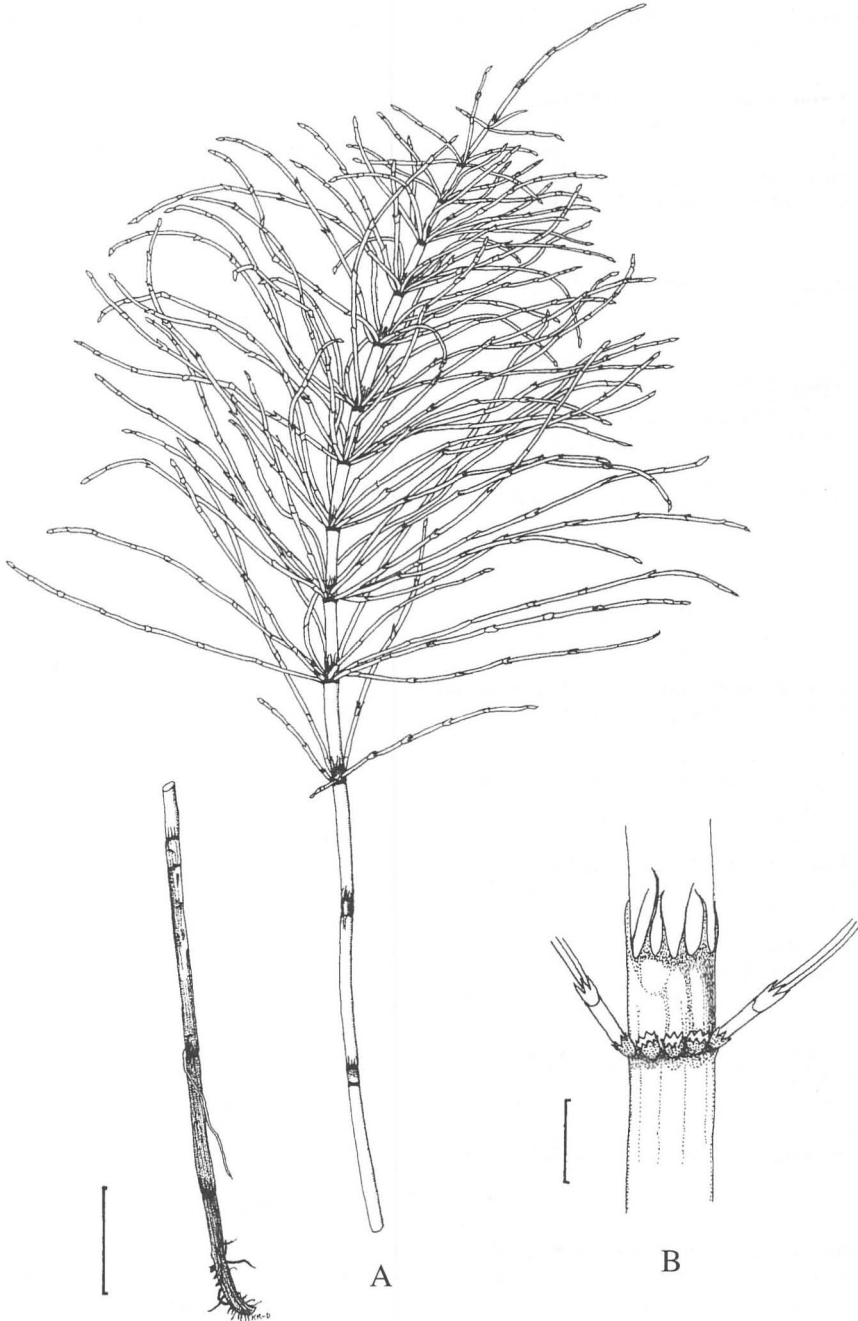


FIGURE 1. *Equisetum × robertsii* T. D. Dines. del. K. Rees-Davies.

A. Habit of whole plant growing upright; when growing from the cliff-face, the stem is decumbent and the branches are declined (scale bar = 5 cm); B. Detail of stem node, showing sheath, sheath-teeth, and mode of insertion of branches (scale bar = 4 mm).

carentes vel margine scarioso perangusto basi praediti, duo tresve lateraliter marginibus interdum adhaerentes. Rami numerosi, in verticillis regularibus numerosis dispositi, 9–(11)–14 in quoque verticillo, 60–(117)–190 mm longi, aequaliter circum caulem distributi vel bilateraliter ordinati (praecipue in ramis decumbentibus), ubi juveniles leniter ascendentes, postea ramo erecto ascendentes vel declinati sed ramo decumbente declinati, graciles, 1.5–2 mm diametro, virides vel flavovirentes; ramorum internodium primum caulis vaginam aequans vel paulo excedens; ramorum vaginae ad ramum appressae, flavovirentes, dentibus 2–3 mm longis praeditae, base viridi et apice brunneo anguste triangulari; ramorum internodia porcis 4–6 complanatis vel leniter rotundatis sulcisque totidem canaliculatis instructa, porcis aliquando leniter biangularibus ubi vaginam subtenentem intrant. Strobili ignoti, nec visi nec in ramis vegetativis exspectandi; sporae ignotae.

The hybrid is named in honour of R. H. Roberts for his outstanding contribution to our knowledge of the Anglesey flora and its conservation; his work, particularly with *Polypodium* and *Dactylorhiza*, has influenced many British and Irish botanists. He received the H. H. Bloomer Award of the Linnean Society in 1999. Dick also found and described the population of *E. × fontqueri* at Traeth Lligwy (Roberts 1990). If an English name is required, Anglesey Horsetail may be appropriate, or Marchrawn Môn in Welsh.

MORPHOLOGICAL DESCRIPTION

Morphologically, most plants of *E. × robertsii* are reassuringly intermediate between the parent species. This is shown in Table 1, where various characters of the hybrid and its parents are compared. The hybrid itself is illustrated in Fig. 1.

Because typical plants of *E. arvense* and *E. telmateia* differ widely in appearance, plants of *E. × robertsii* are readily identified without resorting to detailed examination and measurement. They differ most markedly from *E. arvense* in having thicker stems with paler internodes, these contrasting markedly against the longer, darker stem sheath and sheath teeth. They also possess more branches per whorl, these branches being longer than *E. arvense* and tending to be curved downwards or horizontal if the stem is decumbent. The plants have the look of a robust, more yellow-green *E. arvense* with pale stem internodes and less erect branches.

E. arvense and *E. × robertsii* sometimes grow together, especially along the base of the cliff. In such situations, main stems are often decumbent and they can instantly be distinguished by observation of their branches; those of *E. arvense* are always ascendent while those of *E. × robertsii* are always curved downwards. When growing on top of one another, the effect of this contrast is most striking.

E. × robertsii differs markedly from *E. telmateia* in having shorter, more slender stems with greener internodes, especially when young; fewer and shorter branches, but these being slightly thicker than in normal *E. telmateia*; and in frequently being prostrate, a character we have never observed in *E. telmateia*. The shoots also lack the distinct 'bottle-brush' appearance of *E. telmateia*. The overall impression therefore, is of a depauperate, slender-stemmed and less branched *E. telmateia* with greener internodes.

E. arvense is a very variable species, however, and sometimes has thicker, paler stems than normal, giving plants that closely resemble this hybrid. If a more detailed examination is required to determine the identity of doubtful plants, the morphology of the branch internodes provides the best evidence. Very distinctive, knife-edge branch angles are diagnostic of *E. arvense* (Page 1997). In cross-section, they resemble a Maltese cross, usually having 4 ridges, although 3 or 5 are not uncommon. They also bear a shallow groove along the base of each ridge. These characters can be seen with the naked eye, and are clearly visible with a $\times 10$ lens. The branch internodes of *E. telmateia* are very different, being shallowly lobed into 4 or 5 angles. Each of these angles bears a groove along distinct ridges its apex, producing a double-ridge effect which is characteristic of this species (Page 1997). Furthermore, the edges of these ridges are armed with a row of minute teeth, giving it a saw-edged appearance, also unique to *E. telmateia*. These characters are readily observed with a $\times 10$ lens. In *E. × robertsii*, the internodes are intermediate between the parents. They have 4–6 that are usually rounded or flat-topped at their apex. They lack both the 'knife-

TABLE 1. MORPHOLOGICAL CHARACTERS OF *E. × ROBERTSII* AND ITS PARENTS

	<i>E. telmateia</i>	<i>E. × robertsii</i>	<i>E. arvense</i>
Shoot colour	Yellow-green.	Bright green or yellow-green.	Dull green.
Shoot apex	Flat-topped, squared off.	Tapering, usually with a flagellate tip.	Tapering, often with a flagellate tip.
Stem	Erect.	Decumbent to erect; if decumbent, branches horizontal to declined.	Decumbent to erect; if decumbent, branches ascendent.
Stem stomata	Absent.	Present, but not frequent.	Present, frequent.
Stem height	58–(86)–108 cm.	25–(45)–60 cm.	28–(41)–61 cm.
Stem diameter	5–(8)–9 mm.	2.5–(4)–5 mm.	2–(3)–4 mm.
Stem cavity diameter	2/3 or more.	1/4 to 1/2.	1/4 to 1/2.
Stem internode colour	White.	Green or pale green when young, whitish green or white when mature.	Green.
Stem surface	Smooth, 20–30 indistinct ridges.	Indistinctly ridged, 12–(20)–30 ridges.	Distinctly ridged, 6–(13)–18 ridges.
Stem sheath length	5–(7)–9 mm.	3–(4)–6 mm.	2–(4)–5 mm.
Stem sheath colour	White or very pale green.	Green when young, brown or blackish when mature.	Green.
Stem sheath teeth length	4–(6)–8 mm.	3–(4)–5 mm.	1–(2)–2.5 mm.
Stem sheath teeth colour	Brown.	Brown.	Green or green with brown tip.
Stem sheath teeth shape	Narrowly triangular, with finely pointed tip.	Triangular (not narrow or broad), some with short fine point.	Shortly triangular.
Stem sheath teeth margins	With a narrow basal scarious margin.	No scarious margin, or rarely with a very narrow basal margin.	No scarious margin.
Branch length	120–(153)–247 mm.	60–(117)–190 mm.	92–(132)–170 mm.
Length of first branch internode in relation to stem sheath	Much shorter.	Equal to or, usually, slightly longer.	Longer.
Number of branches per whorl	16–(22)–30.	9–(11)–14.	7–(9)–13.
Branch internodes	4–5 shallow, biangled ridges bearing saw-edged teeth.	4–6 distinct rounded or flat-topped ridges, sometimes slightly biangled basally, lacking both saw-edged teeth and groove at base.	3–5 very prominent knife-edge ridges, with groove along base between ridges.
Branch teeth length	2–(2.5)–3 mm.	2–(2.5)–3 mm.	1.7–(2)–2.2 mm.
Branch teeth	Green base with slender, brown point; adpressed.	Green base, narrowly triangular with brown point; adpressed.	Green, bluntly triangular; curving outwards.

Measurements given are based on samples of 20 from populations of all three taxa at Traeth Lligwy, Anglesey (v.c. 52). Where appropriate, averages are given in brackets along with the maximum and minimum range encountered.

edge' ridges and the groove along the ridge base found in *E. arvense*. The saw-edge teeth and double-ridge of *E. telmateia* are absent in the hybrid, although a trace of the double-ridge can sometimes be seen, especially where a branch internode enters its subtending sheath.

As mentioned previously, a large population of *E. × font-queri* (*E. telmateia* × *E. palustre*) also grows at Traeth Lligwy, approximately 400 metres away from *E. × robertsii*. *E. × font-queri* differs from *E. × robertsii* in being much larger (many plants being over 90 cm tall), being completely smooth to the touch, having longer branches and longer stem sheaths, the sheath teeth and branch teeth having a distinct scarios margin, and the first branch internode being much shorter than the sheath. These are all characters derived from the *E. palustre* parent. Also, *E. × font-queri* produces terminal cones on vegetative shoots, and these were numerous in the Lligwy population in July, a character again derived from *E. palustre*. *E. × robertsii* does not appear to produce cones; since both *E. arvense* and *E. telmateia* produce cones on achlorophyllous stems in early spring, the hybrid may have been expected to do the same, but no such cones could be found despite extensive searches between March and June 2001, and neither have cones been found on any vegetative shoots.

ANATOMICAL AND STOMATAL CHARACTERS

METHODS

Details of stem anatomy and the micromorphology of stomata are important in *Equisetum* identification, and material from Traeth Lligwy was therefore examined. For stem transverse sections, fresh material was sectioned by hand and stained with 0.01% toluidine blue in distilled water. For scanning electron microscopy (SEM) of stem stomata, fresh sections of stem 5 mm in length were fixed in 3% gluteraldehyde in 0.1 M phosphate buffer, dehydrated in an ethanol and acetone series, and critical-point dried using a Polaron CPD. Samples were then mounted on aluminium stubs with double-sided tape and sputter-coated with gold using a Polaron SEM coating unit. Specimens were examined on a Hitachi S-520 scanning electron microscope at 10 kv, and photographs taken using 50 ASA Ilford PAN-F film.

ANATOMICAL CHARACTERS

The arrangement of cell types within *Equisetum* stems is frequently used to identify different taxa, especially hybrids. Transverse sections of the stem internodes of *E. arvense*, *E. telmateia* and *E. × robertsii* are illustrated in Fig. 2.

The internal anatomy of *E. × robertsii* is clearly intermediate between that of its parents, although its overall appearance is closer to *E. arvense* than *E. telmateia*. The most important differences are in the arrangement of the green, chloroplast-bearing chlorenchyma tissue and the supportive and strengthening collenchyma tissue. In *E. telmateia*, chlorenchyma is absent (hence the white colour of the internodes), and the collenchyma forms a continuous ring around the whole stem, being located immediately under the epidermis. The collenchyma of *E. arvense* is distinctively arranged into discrete bundles at the apex of each ridge, and at the base of each furrow separating them. The chlorenchyma is arranged in a broad band around and beneath each bundle of ridge collenchyma. This almost continuous distribution of chlorenchyma gives the stem of *E. arvense* its more or less uniform green colour. In *E. × robertsii*, the collenchyma forms broader, shallower bundles beneath the ridges and in the valleys, and the chlorenchyma is confined to two discrete bundles on either side of the ridge collenchyma. When viewed externally, each furrow on the stem of *E. × robertsii* can be seen to possess a pair of narrow green lines, and this is explained by the distribution of chlorenchyma.

The central canal of *E. × robertsii* is more similar to *E. arvense*, and it is perhaps surprising that the hybrid has inherited so little of the characteristically large canal of *E. telmateia*; another *E. telmateia* hybrid, *E. × wilmottii* (Page 1995), does exhibit this feature. The vallecular canals (which are associated with the vascular tissue) of *E. × robertsii*, however, are intermediate between the parents, being smaller than those of *E. telmateia*, but larger than in *E. arvense*. The size and arrangement of the endodermis, the carinal canals, and the vascular tissue is similar in all three taxa.

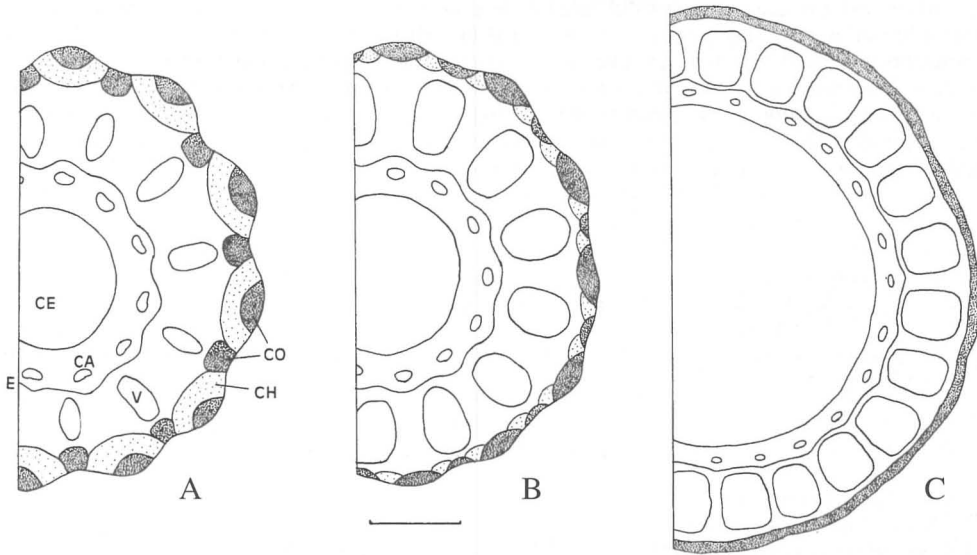


FIGURE 2. Transverse sections of stem internodes (all material from Treath Lligwy, Anglesey, v.c. 52). A. *Equisetum arvense*; B. *E. × robertsii*; C. *E. telmateia*. CO = collenchyma (shaded), CH = chlorenchyma (stippled), V = vallicular canal, E = endodermis, CA = carinal canal and vascular tissue, CE = central canal (scale bar = 0.9 mm, all section at same scale).

STOMATAL CHARACTERS

The micromorphology of stomata in *Equisetum* is highly diverse between species, and has been used as both an aid to identification and a basis for taxonomic classification (Hauke 1963, 1978; Page 1972). In *Equisetum*, true guard cells (which form part of the epidermis) are not present, although the paired cells that surround the stomatal aperture perform the same function. These cells are termed subsidiary cells (Hauke 1957), and are, for their most part, hidden beneath the surface epidermis. Only the periphery of each cell that actually borders the edge of the stomatal pore is visible. The visible part of the cells on either side of the pore are together termed the stomatal cell area (Page 1972). This area is highly variable in shape, and the cells themselves are richly ornamented with numerous hemispherical or globose bead-like projections from the cell surface, which are termed pilulae (Page 1972).

Two extremes in form can be recognised. In the first (Fig. 3, A and B), the stomatal cell area is nearly circular in outline and has a highly convex profile. The surface of the cells are sparsely covered in short, globose pilulae, and a ring of such pilulae delimit the outer edge of the stomatal cell area. Beyond this, there is also a trench-like depression. The stomatal pore itself is often open and clearly visible. In the second type (Fig 3, E and F), the stomatal cell area is highly elongated longitudinally, and low and flat in profile. The actual surface of the subsidiary cells is often invisible, being completely covered in drumstick or rod-shaped pilulae which are arranged in regular rows and point inwards towards the stomatal pore, usually intermeshing and obscuring the pore itself. The stomatal cell area therefore appears like an elongated sunken pore filled with opposing and interlocking rods. In this type, there is no trench-like border.

The first type of stomatal cell area is seen in *E. arvense* from Traeth Lligwy (Fig. 3, A and B), thus confirming the observations of Page (1972) and Hauke (1978) for this species. The second type is seen in *E. telmateia* and *E. palustre* (Page 1972; Hauke 1978), and in the hybrid between these species, *E. × font-queri* (Fig. 3, E and F). Because *E. arvense* possesses stomata of the first type, and *E. telmateia*, *E. palustre* and *E. × font-queri* of the second type, stomatal morphology is a useful tool for the technical confirmation of *E. × robertsii*. Stomata of this hybrid are illustrated in Fig. 3 (C and D), and are clearly intermediate between those of *E. arvense* and *E. × font-queri*

(which illustrates the *E. telmateia* and *E. palustre* type). They differ from *E. arvense* in being more elongate in outline and less convex in profile, and in having more frequent, longer pilulae. Also, the stomatal pore is closed and the edge of the stomatal cell area is less well defined. They differ from *E. × font-queri* in being much more rounded in outline and more convex in profile, having shorter, more globose pilulae (especially towards the outer edge of the cell), and in the edges of the cell area being more clearly defined. The stomata of *E. × robertsii* therefore confirm its hybrid parentage, and also clearly separate it from *E. × font-queri*.

CONFIRMATION OF THE HYBRID

Taking into account the morphological, anatomical and stomatal characters, it can be concluded with certainty that *E. arvense* and *E. telmateia* are the parents of *E. × robertsii*. The presence of abortive spores would provide further evidence, and these will be examined if such material becomes available, but the current evidence is so compelling that we do not feel these are needed to confirm the hybrid. Some hybrids, such as *E. × font-queri* and *E. × trachyodon* (Hauke 1978), are known to occasionally produce a small proportion of fertile spores, and these will also be looked for in *E. × robertsii*. Both *E. arvense* and *E. telmateia* have the same chromosome number, $2n = 216$ (Stace 1997).

Material from Traeth Lligwy has been examined by Mr P. Acock, Miss A. Paul and Dr C. N. Page, all of whom have agreed that it is the hybrid between *E. arvense* and *E. telmateia*. Dr Page has examined other putative British material which may be this hybrid, but reports that specimens from Anglesey are "... the most convincing, in that they appear to be the most exactly intermediate". His observations suggest that the hybrid is probably overlooked elsewhere and should be searched for more widely, especially where the parents grow together in disturbed, wet habitats.

HABITAT DESCRIPTION

The population of *E. × robertsii* at Traeth Lligwy grows on an area of sand and boulder-clay cliffs with a N.E. aspect. These deposits overly Carboniferous conglomerates and, in one place, Carboniferous limestone. At the S.E. end of the site, the cliffs reach a maximum height of approximately 16 m, and slope down to a sand, gravel and boulder beach, where the conglomerate and limestone is frequently exposed. There is a zone of erosion up to 2.5 m high at their base. Towards the N.W., the rocks are not exposed and the overlying clay and sand cliffs are lower, sloping down to a sandy beach.

Plants of *E. × robertsii* are found over an area of approximately 400 m² (200 m long by 20 m wide). Throughout the length of the site, they grow in a variety of substrates, including pure sand, well-drained, humus-rich sandy loam, and pure clay. The cliffs are damp, with obvious areas where seepage of fresh water occurs, and some sections are slumped. Plants of the hybrid occur from the top of the cliff down to the beach, onto which they extend in a few places. They rarely form a dense colony in any one area, but their strongly rhizomatous growth means that plants are loosely clumped in many areas on the cliffs. They are most frequent towards the base of the cliff, particularly in the otherwise unvegetated zone of erosion and on sections of slumped clay.

The sand and boulder clay are derived from a variety of sources (calcareous beach sand, local limestone and conglomerate rocks), and the soil is therefore very variable in pH, ranging from a highly calcareous 8.9 (at the base of the limestone cliff) to an acidic 5.1 (at the top of the sandy conglomerate cliff), the average of twelve samples being 8.1. Such high soil pHs may partly result from enrichment by salt-laden sea-spray. With such a range in pH, it is not surprising to find that a diverse list of 102 associated species have been recorded from the cliff, including both calcicole and calcifuge species, occasional halophytes and species typical of both rank and heavily rabbit-grazed coastal grassland. These taxa are listed in Appendix 1. Although most abundant on the eroded cliff base, where competition is minimal, *E. × robertsii* is not infrequent in the more densely vegetated areas higher up, and competes successfully in stands of *Cirsium arvense*, *Eupatorium cannabinum*, *Hedera helix*, *Heracleum sphondylium*, *Pteridium aquilinum*, *Rubus fruticosus* agg., *Ulex europaeus* and *Urtica dioica* that dominate this area.

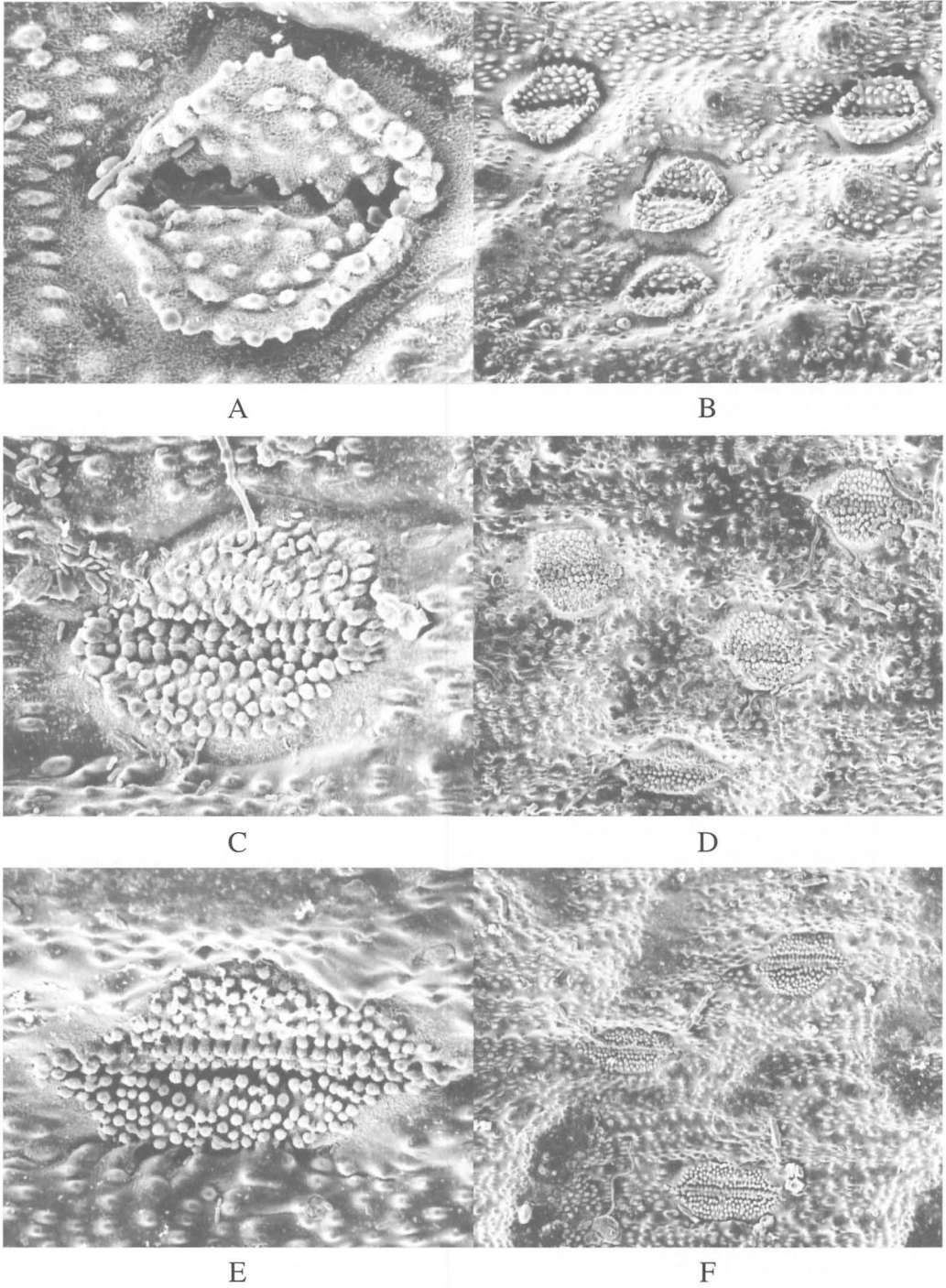


FIGURE 3. Photomicrographs of stem stomata (all material from Treath Lligwy, Anglesey, v.c. 52). A–B. *Equisetum arvense*; C–D. *E. × robertsii*; E–F. *E. × font-queri* (*E. telmateia* × *E. palustre*). A, C and E, individual stomata (×2200); B, D and F, stomatal groups (×660).

In contrast to *E. × robertsii*, *E. × font-queri* at Traeth Lligwy grows at the back of a small area of sand dunes (Roberts 1990). This site is more scrubby, being dominated by bushes of *Salix cinerea* subsp. *oleifolia* and *Rubus fruticosus* agg. It is also flatter and less open to erosion. The population of *E. × font-queri* is much smaller than that of *E. × robertsii*, but the plants are much more densely spaced within this area.

Throughout the entire extent of the *E. × robertsii* population, plants of the hybrid often grow in close proximity to *E. arvense*. Specimens of this species show considerable variation at Traeth Lligwy, ranging from weak, narrow-stemmed and sparsely-branched plants to very robust specimens with thick stems, dense branches, and even frequent secondary branching. The closest population of *E. telmateia* is on the top of the cliff at the eastern edge of the sand dune hybrid population (approximately 15 m from the nearest hybrid plants), where a typically dense colony grows interspersed with robust plants of *E. arvense*. Both parents therefore grow in very close proximity to the hybrid.

Although Traeth Lligwy is a popular and heavily used beach, the main cliffs on which *E. × robertsii* grows separate the beach from the Anglesey coastal footpath, and are too steep, overgrown and wet to be developed. Little threat is currently posed to the population, although plants on the lower cliffs to the N.W. may be at risk from trampling.

DISCUSSION

DISTRIBUTION AND ECOLOGY OF PARENTS

E. arvense has a Circumpolar Wide-boreal distribution (Preston & Hill 1997); it is found throughout much of central, western and northern Europe (Jalas & Souminen 1972). In contrast, *E. telmateia* has a European Southern-temperate distribution (Preston & Hill 1997), being most frequent in southern, western and central Europe, north to the British Isles. It is also present in western N. America (Jalas & Souminen 1972), although the taxon there is currently regarded as a separate subspecies, *E. telmateia* subsp. *braunii* (Milde) Hauke (Hauke 1978).

In Britain, *E. arvense* (like many Wide-boreal species) is extremely widespread, being absent only from upland areas in the most north-westerly parts. It is similarly widespread in Ireland, but not quite as frequent, being unrecorded from a number of 10-km squares throughout its range (Jermy *et al.* 1978). *E. telmateia* is a more restricted species, being absent from parts of south-west and eastern England, central Wales and much of Scotland. In Ireland, it is most frequent in the north and the south-east (Jermy *et al.* 1978).

Throughout its British and Irish range, *E. arvense* can be encountered in a very wide range of natural, semi-natural and man-made habitats (Page 1997). Its natural habitats include river banks, fixed dune-pastures, sea-cliffs and montane flushes. It has, however, become closely associated with human activity, and is now commonly found in cultivated ground, road-verges, paths, quarries, waste ground and railway embankments. It tolerates a wide range of soil pH and substrate, and its only requirement is for constantly moist or damp soil, at least around its potentially deep rhizomes, a feature common to all *Equisetum* species (Hauke 1978; Page 1997). *E. telmateia* is more exacting in its requirements, preferring calcareous substrates that are constantly wet. It is most frequently found along spring lines and open flushes on deep clay soils, and is particularly common on eroding sea and river cliffs, but is also found in marshes, and has also colonised roadside verges and railway embankments.

Given the ubiquitousness of *E. arvense* and the similarity in their habitat requirements, it is unusual to encounter *E. telmateia* in the absence of *E. arvense*. The most recent data available from the Biological Records Centre (Monks Wood) indicate that of the 10-km squares in which *E. telmateia* occurs there are only two in Britain and five in Ireland in which *E. arvense* is not also recorded. Although their presence in the same 10-km square does not necessarily mean that the species are actually growing together, *E. arvense* is able to grow well in the same habitats as *E. telmateia*, and it is likely that the species co-exist extremely frequently.

There is therefore a widespread sympatric occurrence of *E. arvense* and *E. telmateia* in Britain, Ireland and Europe, but their hybrid appears to be rare. This apparent anomaly is discussed below in the context of other *Equisetum* hybrids.

OCCURRENCE OF HYBRIDS IN *EQUISETUM*

The coincidence between hybrids and parents in *Equisetum* is very variable. Some hybrids occur in the apparent absence of both their parents, particularly where species of subgenus *Hippochaete* (*E. hyemale*, *E. variegatum* and *E. ramosissimum* Desf.) are involved. At its most extreme, this is illustrated by the presence in Ireland of *E. × moorei* Newman (*E. ramosissimum* × *E. hyemale*). *E. ramosissimum* is absent from Ireland and found only in Britain as an alien. It has been suggested that the presence of *E. × moorei* in Ireland could indicate the former presence of *E. ramosissimum* here as a native (Page & Barker 1985). The second most frequent *Equisetum* hybrid in our area, *E. × trachyodon* (*E. variegatum* × *E. hyemale*) is also commonly encountered in Britain and Ireland in the absence of both its parents (Page 1997).

Most species of subgenus *Equisetum* are more widespread in Britain and Ireland than those of subgenus *Hippochaete*, and one would therefore expect hybrids between these species to occur in the vicinity of their parents. This is certainly true. The two most common hybrids in the subgenus, *E. × litorale* (*E. fluviatile* × *E. arvense*) and *E. × dycei* C.N. Page (*E. fluviatile* × *E. palustre*) are usually closely associated with their parents (Page 1997), and this is also true of many of the rarer hybrids, for example *E. × mildeanum* Rothm. (*E. pratense* Ehrh. × *E. sylvaticum*), *E. × bowmanii* (*E. telmateia* × *E. sylvaticum*) and *E. × font-queri* (Page 1973 & 1988). An exception is *E. × willmotii* (*E. fluviatile* × *E. telmateia*), which is known from one site in Co. Cavan, Ireland, in the absence of both parents (Page 1995).

The frequency of a hybrid, however, is no reflection of parental frequency. This is shown by the hybrids *E. × robertsii*, *E. × font-queri*, *E. × willmotii* and, particularly, *E. × rothmaleri* C. N. Page (*E. arvense* × *E. palustre*), all of which are apparently rare despite the abundance of the parents in suitable habitat across Britain and Ireland. The first three of these, in particular, form robust hybrids which occur in large, probably long-lived colonies.

In attempting to reconcile these differences, Page & Barker (1985) suggest that several factors are involved in the formation of, and subsequent success of, particular hybrid combinations. These include the availability of a disturbed soil surface for gametophyte germination and subsequent colonisation of a bare area by the hybrid, the availability of a habitat intermediate between that required by the parents, the presence of an oceanic microclimate which promotes gametophyte growth and longevity, and, finally, the possibility of vegetative spread by rhizome or stem fragmentation.

All these requirements are met at Traeth Lligwy for the formation and successful growth of *E. × robertsii*. The slumping clay cliffs provide regular bare surfaces for hybrid formation and subsequent colonisation. It is not possible to say if the hybrid has arisen at Lligwy once or several times, although once is probably the more likely scenario. If it has arisen only once, the sheer size of the population indicates that it arose many years ago, and has been successfully spreading vegetatively for some time - although the possibility of fertile hybrid spores cannot be ruled out as there is evidence of the production of well-formed spores in both *E. × font-queri* and *E. × trachyodon* (Hauke 1978; Page & Barker 1985). Anglesey also has an oceanic climate, characterised by mild winter and cool summer temperatures, and relatively high rainfall of 90–100 cm per year (Roberts 1982).

E. × robertsii appears to be a successful plant at Traeth Lligwy; it forms a very large and probably very long-lived population, and competes well with vigorous tall herbs. Given this, and the abundance of its parents in suitable habitat across Europe, why is it apparently so rare elsewhere? One factor may lie in the taxonomic relationship between the parents. Page (1972) proposes a simple rule for the success (in terms of frequency) of hybrids, "In *Equisetum*, the least successful hybrids in the field are those which arise between pairs of species which are ecologically similar but taxonomically distant. The most successful regularly arise between parents which are ecologically diverse but taxonomically near".

Although there is much disagreement over the precise phylogenetic relationship between the various species in subgenus *Equisetum* (see Hauke 1978 for a comprehensive review), it is generally agreed that *E. telmateia* and *E. arvense* are taxonomically distant. Indeed, both Hauke (1978) and Page (1972) place them in separate sections within the subgenus. They are, however, similar in their ecological needs, although *E. telmateia* is more demanding in its habitat requirements. The rarity shown by *E. × robertsii* therefore supports Page's rule, and fits in with the other uncommon hybrids between ecologically similar but taxonomically distant species

(particularly *E. × willmotii* and *E. × bowmanii*). However, the size and vigour of the *E. × robertsii* population suggests that it is a successful hybrid that can compete well; the limiting factor appears to be the formation of the hybrid, which may be governed by either ecological or genetical factors. Page's rule suggests the latter may be the case, and this might also be supported by the presence of *E. × font-queri* at the same site - perhaps the gametophytes of *E. telmateia* at Treath Ligwy are particularly liable to hybridisation.

ACKNOWLEDGMENTS

We would like to thank P. Acock, A. Paul, A. C. Jermy and C. N. Page for determining the original material. N. Brown helped in compiling the species lists and with determining soil pH values, and R. Walls also helped in thoroughly surveying the site. The preparation for the SEM and anatomical work was undertaken by A. Bell, to whom we are very grateful. A. Paul and C. D. Preston assisted in obtaining papers, and we are especially grateful to J. Cerovský and L. Radford for their help in translating extracts from various Czech floras. We also thank the Biological Records Centre (Monks Wood) for providing data on the current distribution of the parent species in Britain and Ireland. The Latin diagnosis, and comments on the morphological description, were very kindly supplied by P. H. Oswald, and we also thank P. D. Sell for advice on taxonomic matters. A draft version of the paper was extensively commented on by C. D. Preston, to whom we are most grateful. Finally, but perhaps most importantly, we must thank K. Rees-Davies for her superb illustration.

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(Accepted January 2002)

APPENDIX 1. ASSOCIATED SPECIES

The following taxa have been recorded in the same area as *E. × robertsii* (r = rare, 1 or 2 plants seen; o = occasional, 3 to 7 plants seen; sd = in sand-dune areas only). Nomenclature follows Stace (1997).

Anthoxanthum odoratum, *Acer pseudoplatanus* (r), *Achillea millefolium*, *Agrimonia eupatoria* (o), *Agrostis capillaris*, *A. stolonifera*, *Arrhenatherum elatius*, *Athyrium filix-femina* (o), *Brachypodium sylvaticum*, *Bromus hordeaceus* subsp. *hordeaceus* (sd), *Carex arenaria* (sd), *C. caryophylla* (sd), *C. flacca*, *Centaureum erythraea* (sd), *Centaurea nigra* (sd), *Cerastium fontanum* (sd), *Chaerophyllum temulum* (o), *Chamerion angustifolium*, *Cirsium arvense*, *C. palustre*, *C. vulgare*, *Cochlearia officinalis*, *Crataegus monogyna*, *Crepis capillaris*, *Dactylis glomerata*, *Dactylorhiza fuchsii*, *D. purpurella* (sd), *Deschampsia cespitosa* subsp. *cespitosa*, *Dryopteris affinis* subsp. *affinis* (r), *D. dilatata*, *D. filix-mas*, *Elytrigia juncea* (sd), *Epilobium hirsutum* (sd), *E. montanum*, *Equisetum arvense*, *E. palustre* (sd), *Eupatorium cannabinum*, *Festuca rubra*, *Filipendula ulmaria*, *Fragaria vesca*, *Galium aparine*, *G. verum*, *Geranium robertianum*, *Glechoma hederacea*, *Hedera helix* subsp. *helix*, *Heracleum sphondylium*, *Holcus lanatus*, *Hypericum androsaemum* (o), *H. tetrapterum* (r), *Hypochaeris radicata*, *Juncus acutiflorus* (sd), *J. bulbosus* (sd), *J. inflexus* (sd), *Lathyrus pratensis*, *Leymus arenarius* (sd), *Lolium perenne* (sd), *Lonicera periclymenum*, *Lotus corniculatus*, *L. pedunculatus*, *Ononis repens*, *Phyllitis scolopendrium* (o), *Pimpinella saxifraga*, *Plantago lanceolata*, *P. maritima*, *Poa humilis*, *Potentilla anglica*, *P. anserina*, *P. erecta* subsp. *erecta*, *P. reptans*, *Primula vulgaris*, *Prunella vulgaris*, *Pteridium aquilinum*, *Pulicaria dysenterica* (sd), *Ranunculus acris*, *Rhinanthus minor*, *Rosa canina* agg., *R. pimpinellifolia*, *Rumex crispus* subsp. *littoreus* (sd), *Rubus fruticosus* agg., *Sagina procumbens*, *Salix cinerea* subsp. *oleifolia*, *S. repens* (r), *Sanguisorba minor* subsp. *minor*, *Sanicula europaea* (o), *Senecio jacobaea*, *Silene dioica*, *Solidago virgaurea*, *Sonchus oleraceus* (sd), *Tamus communis*, *Taraxacum* sp. (sd), *Torilis japonica*, *Trifolium dubium* (sd), *T. medium*, *T. pratense*, *T. repens*, *Tussilago farfara*, *Ulex europaeus*, *Urtica dioica*, *Veronica chamaedrys*, *Vicia cracca*, *Viola riviniana*.