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British hybrids involving *Epilobium tetragonum* subsp. *tournefortii* (Onagraceae), Tournefort's Willowherb

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Abstract
A study of populations of Tournefort's Willowherb, *Epilobium tetragonum* L. subsp. *tournefortii* (Michalet) Lév., a non-native taxon naturalised in Cambridgeshire, revealed the presence of plants which on the basis of their morphology were attributed to hybrids with native willowherbs *Epilobium parviflorum* Schreb. (Hoary Willowherb), *Epilobium tetragonum* L. subsp. *tetragonum* (Square-stalked Willowherb) and *Epilobium hirsutum* L. (Great Willowherb). Details of distinguishing characters are given. The hybrid taxa have not previously been recorded as such in the British Isles.

Keywords: hybridisation; Cambridgeshire; non-native subspecies

Introduction

Tournefort's Willowherb, *Epilobium tetragonum* L. subsp. *tournefortii* (Michalet) Lév., was first found naturalised in the British Isles in 2007 (Kitchener & Leslie, 2008). This conspicuously large-flowered taxon was spreading in two sites on the banks of the A505 Royston by-pass (TL34) in Cambridgeshire, v.c.29. It has since appeared in Bedfordshire, v.c.30 and well as in other v.c.29 locations (Fig. 1). Spread may be attributable to a combination of vehicular traffic and the prevailing winds, although it is not impossible that there has been more than one introduction via aircraft (Squires, 2018).

The purpose of this paper is to draw attention to hybridisation arising from contact with native British taxa.

Field investigations

Visits by Alan Leslie and Peter Leonard on 20 and 28 July 2021 to the Royston populations found that, where *E. tetragonum* subsp. *tournefortii* had spread across the A505 at one of its sites, to its south-western side, amongst the large-flowered plants there was a scattering of willowherbs with somewhat smaller flowers. These were, however, not as small-flowered as the most frequent other willowherbs present, *E. parviflorum* Schreb. (Hoary Willowherb) and *E. tetragonum* subsp. *tetragonum* (Square-stalked Willowherb).

Closer examination showed that the scattering fell into two groups, exhibiting characteristics of hybridisation by *E. tetragonum* subsp. *tournefortii* with each of these other taxa. The only other willowherbs noted, *E. montanum* L. (Broad-leaved

Willowherb) and *E. obscurum* Schreb. (Short-fruited Willowherb), were apparently not involved. *E. ciliatum* Raf. (American Willowherb), which is a ready hybridiser with our native willowherbs, was not seen.

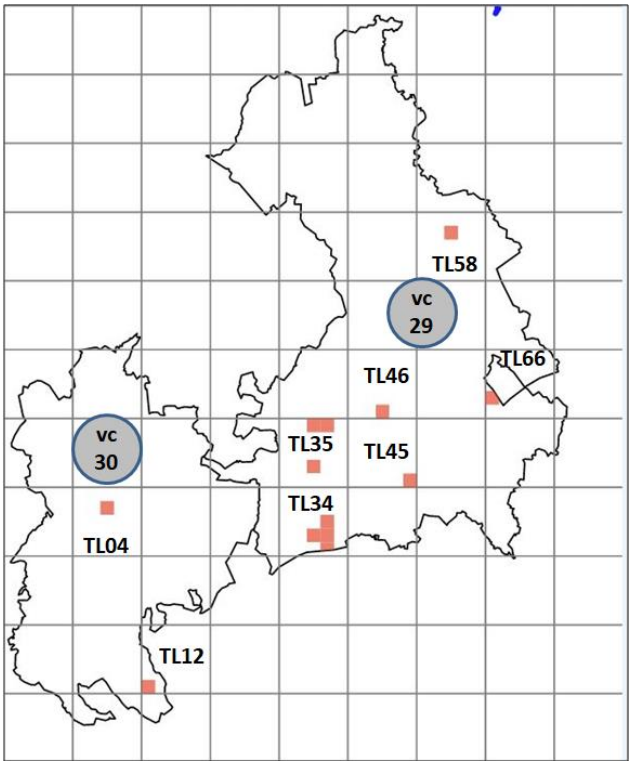

Figure 1. Records of *Epilobium tetragonum* subsp. *tournefortii*, 2008-21
© BSBI Distribution Maps 2021.

This discovery prompted a visit on 16 August 2021 to the A428 corridor near Hardwick (TL35), where Jonathan Shanklin had recorded *E. tetragonum* subsp. *tournefortii* in 2018. Here, not only was another specimen of *E. parviflorum* × *E. tetragonum* subsp. *tournefortii* found, but also plants which were apparently hybrids between subsp. *tournefortii* and *E. hirsutum* L. (Great Willowherb).

The *Epilobium parviflorum* cross

Epilobium parviflorum is particularly plastic in its response to different environmental conditions, e.g. as between dry, open habitats and damp shade; Geoffrey Kitchener's experience as BSBI *Epilobium* referee is that there are more enquiries about supposed hybrids which turn out to be this species than any other. Its hybrids (which have been recorded as crosses with nine other species in the British Isles) generally show as partly or fully sterile, and this helps differentiate from the effects of the variability of the species. At the A505 site, Royston, several plants were found which demonstrated partial sterility and otherwise possessed characteristics of intermediacy between *E. parviflorum* and *E. tetragonum* subsp. *tournefortii.* These were taken to be hybrids, and their relationship with the putative parents is summarised in Table 1. Further hybrid examples were found by Geoffrey Kitchener on 11 August 2021 about 1.2 km away with *E. tetragonum* subsp. *tournefortii* in a weedy, uncultivated field (TL3741) which is allocated for the Meridian Gate housing

development. The possibility that these might in both locations have been hybrids between *E. parviflorum* and *E. tetragonum* subsp. *tetragonum* is excluded most obviously by their larger flower size. Indeed, this was clear from a single plant at Meridian Gate which corresponded well with normal *E. parviflorum* × *E. tetragonum* subsp. *tetragonum*, with small flowers and a more delicate, willowy form of growth.

Table 1. Comparison of characteristics: *E. parviflorum* × *E. tetragonum* subsp. *tournefortii*

	Epilobium parviflorum	**Royston hybrids**	***Epilobium tetragonum* subsp. *tournefortii* (Royston plants)**
Fertility	Full seed set	Most seeds abortive, few developing fully	Full seed set
Stigma shape	4-lobed, with the lobes borne upright	Capitate, essentially entire, but often with a suggestion of 4-lobing at the apex	Entire, long and broadening at apex
Leaf indumentum	Numerous short, eglandular hairs on upper surface, often appearing felted; lower surface hairy, not just on veins	Variable amounts of short eglandular hairs on upper surface; lower surface hairy, not just on veins	Glabrous, except for hairs sometimes present on midrib below
Upper stem indumentum	Long, spreading, eglandular hairs mixed (increasingly towards top) with shorter glandular hairs	Longish eglandular hairs, some spreading but most flexed upwards (not appressed); rarely an occasional patent glandular hair	Short, curved, eglandular hairs, appressed upwards
Stem	Terete	More or less terete, although 2 slight ridges may be felt if the stem is rolled between finger and thumb	(2-)4 raised lines decurrent from the leaves
Petal length	6-9 mm	8.5-10 mm	(10)11-13(15) mm
Style hairs	Hairs not seen	Hairs not seen	Hairs present, extending up to ¾ of the length of the style

Figure 2. *Epilobium. parviflorum* × *E. tetragonum* subsp. *tournefortii* showing long hairs flexed upwards (images P. Leonard).

Epilobium parviflorum hybrids with *E. tetragonum* subsp. *tetragonum* are not uncommon in southern Britain, being mapped by Stace *et al.* (2015) from north Norfolk southwards. (The hybrid has been claimed further north and may be increasingly so, with the spread of subsp*. tetragonum* northwards; it should be noted also that the mapping overall does not differentiate hybrids with the enigmatic taxon *E. tetragonum* subsp. *lamyi* (F.W. Schultz) Nyman*,* if there are any.) The Royston plants, however, are the first records in the British Isles involving Tournefort's Willowherb.

Within the native range of *E. tetragonum* subsp. *tournefortii*, the cross is little mentioned. Haussknecht (1884) refers to it as collected in Syria, and gives a description, translated here:

'It has almost entirely the appearance of a hairy, small-flowered E. Tournefortii, from which it is distinguished by the leaves with a rounded base, with fewer and smaller marginal teeth and short patent hairs on the margins and veins, by the capsules that appear white-gray with appressed and patent hairs, as well as by the short patent hairs all around the stem. From E. parviflorum it is immediately recognizable by the stem, which is clearly covered with raised lines. The stigma is capitate and thickened, with 4 pointed lobes at the tip'.

Haussknecht's description clearly captures elements of intermediacy between the parents, although the Royston plants would lead us to emphasise somewhat different hair characteristics, and greater indistinctness of any stem lines. The characters given in Table 1 may not represent the only manner in which hybridity may be manifested, and German genetic research into *Epilobium* in the first half of the twentieth century provided many examples of differences between reciprocal hybrids. The absence of published research into reciprocal crosses between *E.*

parviflorum and *E. tetragonum* subsp. *tournefortii* means that we cannot with full confidence make any supposition about the direction of crossing involved in the Royston plants examined. Data for crosses between *E. parviflorum* and *E. tetragonum* subsp. *tetragonum* ought to have offered a degree of comparison, but the results of different workers, e.g. Geith (1924), Lehmann & Schwemmle (1927) and Köhler (1929), are not identical, although they generally found greater sterility where *E. parviflorum* was the female parent. Geith (1924), for example, found indehiscent anthers with sterile pollen grains and capsules with poor, or no seed-set in crosses with that parentage; whereas, with *E. tetragonum* as female parent, pollen was good-looking and seed-set was comparatively 'good', albeit only 18%. Thakur (1965) also found that crossing with *E. parviflorum* as female parent produced a plant with malformed anthers and capsules with only 2-3 fully formed seeds. The Royston plants (of course involving a different *E. tetragonum* subspecies and so not directly comparable) included specimens with the '2-3 seed' level of fertility, but also material with *c.*30 fully formed seeds per capsule, still a low level of fertility, but possibly indicating a different direction of crossing.

The *Epilobium tetragonum intermediates*

Several plants were found which carried characteristics of *E. tetragonum* subsp. *tournefortii*, but which did not appear to be this, or the cross with *E. parviflorum*. Instead, they were intermediate between *E. tetragonum* subsp. *tournefortii* and subsp. *tetragonum*, in a context where both were growing together. At the A505 site on the south western side of the road, a rough estimate was made that up to 5% of the colony of *E. tetragonum* subsp. *tournefortii* consisted of scattered intermediates. They were also present at the Meridian Gate site, and a few more were found by Geoffrey Kitchener and Alan Leslie on 11 August 2021 adjoining Royston solar farm north of the A505 (TL3542 and TL3642). By the solar farm it was noticeable that the occurrence of subsp. *tetragonum* was limited and that the intermediate was relatively uncommon and was only noted in its presence. This, together with the morphological evidence of intermediacy, points towards these plants being hybrids between the two subspecies. The frequency of occurrence contrasts with that in 2008, when only one intermediate plant was detected.

The most obvious features of the intermediate plants related to their flowers. These were smaller than those of neighbouring subsp. *tournefortii*; they were more upright in stance (as with subsp. *tetragonum*) than the generally out-facing flowers of subsp. *tournefortii*; and were intermediate in colour (although this character is not easily photographed or described). A more detailed comparison is given in Table 2 and flowers are illustrated in Figs. 3 and 4.

The occurrence of intermediates is well known in the native range of subsp. *tournefortii*. Raven (1962) described subsp. *tournefortii* as having a typically Mediterranean distribution, reaching its eastern limit in Turkey: 'In the Near East and in N. Africa it appears to intergrade completely with subsp. *tetragonum*'. As regards N. Africa, Raven (1967) further commented 'It is always found in the same areas as subsp. *tetragonum*, and here intermediates between the two are frequent and apparently completely interfertile'. He considered that the peculiar, disjunct distribution of subsp. *tournefortii* (in this context, disjunct should presumably be taken as being scattered locally across the Mediterranean as a whole), coupled with the fact that it is one of the very few outcrossing entities in the genus, suggests

strongly that it may be a relic similar to the populations from which the autogamous subsp. *tetragonum* and subsp. *lamyi* were derived. While it may be that outcrossing is not a primitive character after all, and protandry, which promotes outcrossing, has evolved independently on several occasions (cf. Baum *et al.*, 1994), this suggested pattern of evolutionary derivation from outcrossing taxa in Onagraceae was explored further by Raven (1979), noting that it is accompanied by a tendency towards reduction in flower size.

Table 2. Comparison of characteristics: the Royston intermediates (*Epilobium tetragonum* subsp. *tetragonum* × *E. tetragonum* subsp. *tournefortii*). Note: asterisked measurements are taken from Wilcox (2011).

	Epilobium tetragonum* subsp. *tetragonum	**Royston intermediates**	***Epilobium tetragonum* subsp. *tournefortii* (Royston plants)**
Fertility	Full seed set	Full seed set	Full seed set
Stigma shape	Entire, cylindrical	Entire, cylindrical but somewhat swollen in upper half	Entire, long and broadening at apex
Style length (including stigma)	(4.5)5-6.8 mm	6.6-9 mm	9-11.7 mm*
Style hairs	Hairs absent	Hairs present, but usually confined to near the style base	Hairs present, extending up to ¾ of the length of the style
Sepal length	4.0-5.2 mm	4-6 mm	8-10 mm*
Anther length	0.7-1.2 mm	1.3-1.6 mm	1.5-2.5 mm*
Petal length	(4)5-7(9) mm	7-11 mm, may be variable on same plant	(10)11-13(15) mm
Seed length	(0.9)1.0-1.2 mm	1.0-1.1 mm	1.1-1.3 mm

Presumably self-fertilisation normally preserves the integrity of subsp. *tetragonum*; and in any event, any occasional cross-fertilisation affecting that subspecies would not be possible from some of the insect visitors to subsp. *tournefortii* – a honey bee was noted visiting the latter at the solar farm site mentioned above, which the much smaller flowers of subsp. *tetragonum* would have been unlikely to be able to support. However, once an exceptional cross-fertilisation has taken place, then the fertility of the resultant intermediate is likely to give it a continuing place in the willowherb population, in contrast with interspecific hybrids with subsp. *tournefortii* which carry very limited fertility.

Figure 3. *Epilobium tetragonum* subsp. *tournefortii* (left); intermediate (centre); subsp. *tetragonum* (right) – scale bars 7mm apart (image P. Leonard).

Figure 4. *Epilobium tetragonum* subsp. *tournefortii* (right); intermediate (left) (image P. Leonard).

While current usage generally supports treatment of Tournefort's Willowherb as a subspecies of *E. tetragonum*, it was described as a species by Michalet (1855) and treated as such by Haussknecht (1884). A case was made for retention of this rank by Wilcox (2011), based on the degree of difference in relation to subsp. *tetragonum*, especially flower size, anther size and stigma characters (including the presence in subsp. *tournefortii* of hairs extending part-way up the style). However, the intergrading and interfertility of the two taxa, mentioned by Raven (1962, 1967) is a strong pointer towards a closer relationship, such as subspecies, being an appropriate treatment. Despite a tentative suggestion by Kitchener & Leslie (2008) that the single intermediate found in 2008 may have had some reduced fertility, this has not received any support from the intermediates found in 2021, which carried a

full complement of developed seeds, except where insect-damaged. Normally, interspecific *Epilobium* hybrids show reduced fertility by the variable development of seeds, of which only a minority become fully formed and filled. Full fertility, at least in F_1 hybrids, may generally be regarded as suggesting that otherwise closely related parents are best not treated as separate species. (It also supports the British treatment of *lamyi* as a subspecies of *E. tetragonum*.)

The *Epilobium hirsutum* cross, *Epilobium* × *brevipilum* nothosubsp. *nebrodense* (Strobl ex Hausskn.) Deschâtres

The A428 corridor near Hardwick is one of a number of roadside sites for *E. tetragonum* subsp. *tournefortii*, which suggests that vehicles may currently be responsible for much of its spread, whatever the means by which the plant may have arrived in the first place. With subsp. *tournefortii* on rough ground on the north side of the main road at TL3730 5978 Alan Leslie and Peter Leonard found a number of other willowherbs**:** *E. tetragonum* subsp. *tetragonum*, *E. parviflorum*, *E. hirsutum* and some 15-20 plants which resembled *E. hirsutum*, but which had anomalous features which pointed towards their identity being hybrids between *E. hirsutum* and *E. tetragonum* subsp. *tournefortii*.

Figure 5. *Epilobium* × *brevipilum* nothosubsp. *nebrodense* (image P. Leonard).

The most obvious features of these plants were the large flowers (Fig. 5) bearing the large deep rose-purple colour of *E. hirsutum* but with stigma lobes which were not revolute; the limited seed-set and occasional indehiscence of the anthers showing partial sterility; and the stem hairs which were eglandular, medium-length and flexed upwards, not the usual *E hirsutum* mixture of long, flexuous eglandular hairs and short glandular hairs. A more extensive comparison is given in Table 3, but some elaboration of these features is warranted.

The size of the flowers is notable; petals are at least the length of those of *E. hirsutum* and, surprisingly, at times exceeding its normal range. This helps separate the hybrid plants from the cross between *E. hirsutum* and *E. tetragonum* subsp. *tetragonum*, where petal length tends to be 10-11mm (and is probably unaffected

by the direction of crossing; at any rate, Geith (1924) found no differences in reciprocals).

Concerning stigma lobes, these are lacking in *E. tetragonum* subsp. *tournefortii*, and in developing flowers of *E. hirsutum* they are held vertically, but at anthesis spread out and reflex so that they are coiled round some 2mm below the highest point of the style. The hybrids examined showed in mature flowers somewhat shorter stigma lobes than those of *E. hirsutum*, either spread horizontally with minimal curvature downwards or held semi-erect, so expressing varying degrees of intermediacy with the entire stigma of *E. tetragonum* subsp. *tournefortii*. It is possible, however, that some observed upright positioning of the stigma lobes may be attributable to their development stage before expanding fully. Nevertheless, Haussknecht (1884) noted that a capitate stigma in which the lobes were no more than a suggestion of tips could be found on cultivated plants bearing a close relationship with *E. tetragonum* subsp. *tournefortii*, derived from backcrossing.

The stem hairs of the cross — dense and swept upwards (Fig. 6) — are very characteristic of hybrids between *E. tetragonum* and the longer-haired species such as *E. hirsutum* and *E. parviflorum*. This applies to crosses involving subsp. *tetragonum* as well as subsp. *tournefortii*, and was well observed by Compton (1911), who was the first to synthesise the hybrid between subsp. *tetragonum* (as *E. adnatum*) and *E. hirsutum* ('There are no long erect hairs, such as are present in *hirsutum*; the hairs are longer than in *adnatum*, and are obliquely directed upwards, i.e. their position is intermediate between the closely appressed down of *adnatum* and the erect hairs of *hirsutum*').

Figure 6. Stem hairs of *Epilobium* × *brevipilum* nothosubsp. *nebrodense* (left); and *Epilobium hirsutum* (right) (image P. Leonard).

Comparing our plants with the descriptions given by Strobl (1903), Haussknecht (1884) and Sennen (1928), there is reasonable accord, although only Haussknecht mentions hybrid sterility. The description in Strobl (1903) is particularly useful in referring to it (translated here) as 'easily distinguishable from all varieties of *hirsutum* by the smaller, even more densely and considerably more sharply toothed,

almost bare stem-leaves, downy (not shaggy) stems and branches, capsules downy with densely appressed hairs (not patent, rough-haired)...'. Strobl (1903), however, also refers to 'notably smaller flowers' which is slightly misleading, since his measurement of the petals as one-third more than the sepals, and hence in the range 12-15mm, is comparable with the petal length of both parents.

Table 3. Comparison of characteristics: *E. hirsutum* × *E. tetragonum* subsp. *tournefortii*.

	Epilobium hirsutum	**Hardwick hybrids**	***Epilobium tetragonum* subsp. *tournefortii* (Royston plants)**
Fertility and seeds	Full seed set, seeds *c.*1.1 x 0.6 mm	Seed set variable: usually most seeds obviously abortive, few developing fully; occasionally most seeds developing but not all filling out. Fully developed seeds *c.* 1.2 x 0.5 mm	Full seed set, seeds 1.1-1.3 x 0.5 mm
Stigma shape	4-lobed, with long lobes, becoming revolute	4-lobed, with short lobes either spreading or borne upright	Entire, long and broadening at apex
Leaf shape and attachment	Oblong-lanceolate, with incurved marginal teeth, semi-amplexicaul with leaf base shortly decurrent onto stem	Oblong-lanceolate, but somewhat narrower and more attenuate at the apex than *hirsutum*; with margins bearing a mix of incurved and pointed (not incurved) teeth; semi-amplexicaul	Oblong-lanceolate, with margins bearing short, pointed (not incurved) teeth; sessile
Leaf indumentum	Moderate to dense covering of short to long eglandular hairs on upper surface; also on margins and underside, especially midrib and veins	Leaves near-glabrous on upper surface although some shortish eglandular hairs on younger ones especially around midrib; eglandular hairs on underside	Glabrous upper surface; on lower surface, hairs (where present) restricted to midrib

		midrib and veins, also margins	
Upper stem indumentum	Long, spreading, eglandular hairs mixed (increasingly towards top) with dense shorter glandular hairs	Dense cover of medium-length eglandular hairs, some spreading (especially in upper parts); but most flexed upwards (not appressed); rarely an occasional patent glandular hair	Dense cover of short, curved, eglandular hairs, appressed upwards
Stem	More or less terete, although 2(-4)slightly raised lines running down from leaves; and 2 ridges may be felt if the stem is rolled between finger and thumb	More or less terete, although 4 slightly raised lines running down from leaves; and 2 ridges may be felt if the stem is rolled between finger and thumb	(2-)4 distinct raised lines decurrent from the leaves
Petal length	(10)12-17(20) mm	13-17(19) mm	(10)11-13(15) mm
Style hairs	Hairs normally absent	Occasional hairs present at base	Hairs present, extending up to ¾ of the length of the style
Basal growths	Long (may be 50 cm or more), 5-8 mm thick, fleshy rhizomes (soboles) forming terminal leaf rosettes	At least in some cases producing long rhizomes *c.*5 mm thick. It is assumed that terminal rosettes from these have resulted in an observed small dispersed vegetative colony.	Basal sessile rosettes formed in autumn, at the end of short rhizomes up to 4 mm thick

Epilobium hybrids with *E. tetragonum* subsp. *tetragonum* are recorded in southern Britain, also mapped by Stace *et al*. (2015), but are less frequent than the equivalent *E. parviflorum* hybrids. The Hardwick plants, however, are the first records in the British Isles for *E. hirsutum* crosses involving *E. tetragonum* subsp. *tournefortii*.

The cross has been widely, but very infrequently, recorded within the native range of *E. tetragonum* subsp. *tournefortii*. It was first noted by Gabriel Strobl in the course of his explorations of the flora of the Nebrodi mountains in Sicily. He apparently at first considered it to be a species, placed between *E. hirsutum* and *E. parviflorum*, and which he named *E. nebrodense*, a name which he used in his Flora der Nebroden (Strobl, 1878, p.158), without a description. His account of this 'species', in manuscript, came to the attention of Haussknecht, who recognised it as a hybrid and synthesised it as well, so providing in Haussknecht (1884) both an extract from Strobl's manuscript and Haussknecht's observations of cultivated specimens. Strobl's account never appeared in his Flora der Nebroden, printed in instalments in *Flora oder allgemeine botanische Zeitung* 1878-1887, but was eventually published by him in revised form referring to '*Ep. Nebrodense* mihi (*hirsutum* X *Tournefortii*, teste Hausskn.)' in Strobl (1903).

It was subsequently collected near Foncea and Burgos in north Spain by Frère Sennen, who purported to name his plants *Epilobium eliasii* and *E. eliasii* var. *adnatiformis* respectively (Sennen, 1928) and attributed a hybrid origin to them. Nieto Feliner (1995) also notes more recent records north west of Cordoba and from the Sierra de Aracena (south west Spain). It has also been recorded in Corsica by Jeanmonod & Burdet (1995), including a note in which the combination *Epilobium* × *brevipilum* nothosubsp. *nebrodense* (Strobl ex Hausskn.) Deschâtres was made by Deschâtres. It may be supposed that this hybrid is more likely to occur than crosses between *E. tetragonum* subsp. *tournefortii* and other taxa within sect. *Epilobium*, as both *E. hirsutum* and *E. tetragonum* subsp. *tournefortii* are generally out-crossers, and most other such taxa are normally or commonly self-pollinated.

The occurrence of hybrids involving *E. tetragonum* subsp. *tournefortii*

The occurrence of the various hybrids with Tournefort's Willowherb in locations so far from its native distribution, some 14 years from its first discovery as an introduction in Britain, is in sharp contrast with the paucity of hybrid records from its native area, other than the intermediates between the subspecies of *E. tetragonum*. However, if one asks why, the answer is not obvious. It might perhaps be supposed that the general treatment of Tournefort's Willowherb as a subspecies rather than a species, and the fact that only one of the three hybrids considered here has been given a separate name, may have discouraged recording. But if hybrids between *E. tetragonum* subsp. *tournefortii* and *E. hirsutum* and *E. parviflorum* respectively have been found, and Tournefort's Willowherb's status as a subspecies of *E. tetragonum* has led to those hybrids being recorded as crosses with *E. tetragonum*, then these would be named as plain *E.* × *brevipilum* Hausskn. and *E.* × *palatinum* F.W. Schultz accordingly. Yet, so far as records go, these are primarily north European taxa, with little Mediterranean representation. Possible alternative explanations include a general lack of interest in *Epilobium* hybrids or the potential that the disturbed, open habitats where *E. tetragonum* subsp. *tournefortii* occurs in Britain offer more scope for the creation and establishment of hybrids than its Mediterranean habitats.

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