The history and distribution of the bulbil-bearing *Ficaria verna* subsp. *verna* (Ranunculaceae) in Britain

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This pdf constitutes the Version of Record published on 31st August 2020

**Abstract**
The distributions of the subspecies of *Ficaria verna* Huds. are under-recorded in Britain, but published county Floras indicate that subsp. *verna* is an introduction in some areas and is increasing in many areas. This evidence is examined and a hypothesis to account for the observed patterns is tested against an analogy with *Allium paradoxum* (M. Bieb.) G. Don in Berwickshire where the author has personally observed colonisation over forty years. The results suggest a link between the recent increase in *Ficaria verna* subsp. *verna* and the nineteenth century expansion of the horticultural trade. Earlier waves of colonisation are suspected but not substantiated.

**Key words:** archaeophyte; native; neophyte; Berwickshire; distribution; horticulture.

**Introduction**
I have been intrigued by circumstantial evidence in published county Floras that, in some parts of Britain, *Ficaria verna* subsp. *verna* is increasing and may be an introduction, unlike the native subsp. *fertilis*.

My home is a former farmhouse at Clarilaw, Roxburghshire (v.c.81) which was built in about 1860 on the site of earlier farmhouses, in a sequence which may date back to around 600 AD. The naturalised plant introductions that are thought to have been deliberately introduced at an early date include *Chenopodium bonus-henricus* as a pot-herb and *Myrrhis odorata* as a flavouring. Unintentional introductions include *Allium paradoxum*, probably brought in with herbaceous plants about 1970 (before my wife and I bought the property). Unsurprisingly there is *Ficaria verna* in the garden and I was aware, when weeding, that at least some of the plants produced bulbils, but I had never given the matter further thought.

I have now found that all the *Ficaria verna* in my garden and nearby is subsp. *verna* and suspect that it is an introduction here, so I have set out to investigate whether this is likely and, if so, how and when it came to be introduced.

**History**
The earliest record known to me of bulbils in British *Ficaria* is in Gigi Crompton’s historical Cambridgeshire online-flora (Crompton, 2001) as ‘subsp. *bulbifer*, Cambridge, CC Babington, 26.5.1839, det. PD Sell, CGE’. This is picked up in Babington’s *Manual of British Botany* (Babington, 1843) as ‘St[ems] 3-8 in, long,
weak, often producing bulbs in the axils of its leaves’. Despite the Manual being widely used, British botanists were slow to record the presence of bulbils, perhaps because Babington did not give the bulbil-producing plants any separate taxonomic rank.

Babington was such a discerning botanist that I do not believe he would have omitted to suggest the possibility of the bulbil-producing plants being an introduction if he had not been familiar with them over a wider area than the city of Cambridge. Similarly at least some other discerning botanists in Britain would have drawn attention to the bulbils had they considered them unusual. One botanist who did comment on the bulbils was James White in his *The Flora of Bristol* (White, 1912). He noted that ‘axillary bulbils are not of very rare occurrence with us’ and goes on to describe in exemplary detail a luxuriant plant gathered in a sheltered lane.

The situation in Britain contrasts with that on the continent of Europe where subsp. *verna*, a tetraploid, is much more widespread than subsp. *fertilis*, a diploid, which is found mainly across a broad strip along the Atlantic fringe. Indeed subsp. *fertilis*, but not subsp. *verna*, is very rare as close to Britain as Belgium, so, before proposing subsp. *verna* as an introduction everywhere in Britain, it would be necessary to discuss its likely history in Belgium and adjacent countries.

**Hypothesis to account for colonisation**

Before turning to the Floras, I set out a hypothesis as to how subsp. *verna* might have come to be increasing. I suggest that some of the plant nurseries cultivating recent plant introductions, and marketing them as choice garden plants, were contaminated with subsp. *verna* as a weed. It might have colonised them recently, or have been a long-established plant in the area. The plant nurseries inadvertently dispersed subsp. *verna* to the gardens of the mansion houses that were their prime customers from about 1750. With the coming of the railways, the horticultural trade expanded very rapidly and plants were distributed throughout Britain to gardens of all descriptions, including relatively outlying farmhouses. By 1920, subsp. *verna* could have come to be widely distributed in gardens, including those in areas in which it had previously been absent.

If *Ficaria* bulbils were dispersed in plant containers, might they not have also been dispersed with the bare-rooted hedging plants (chiefly *Crataegus*) that were despatched by the thousand from plant nurseries to enable the massive hedge-planting programme that was integral with the enclosures of the Agricultural Revolution from around 1750? It is certainly possible, but there is no evidence from various Floras (see below) to support it.

It is evident that if *Ficaria verna* subsp. *verna* is brought to a garden, it can propagate itself freely and be dispersed within a confined area by soil disturbance. It is another matter for it to disperse more widely. In considering such dispersal, I have sought an analogy with a more closely-studied species.

**Testing the hypotheses against the colonisation of Berwickshire by *Allium paradoxum***

I have chosen the bulbil-bearing *Allium paradoxum* in Berwickshire to test the hypothesis because I have witnessed its ongoing colonisation there over forty years and because a 1 km distribution map (Fig. 1) is available (albeit based on sample surveys).
Allium paradoxum has very much the same ability to propagate, by bulbils in the inflorescence and bulb offsets underground, as Ficaria verna subsp. verna has with its leaf-bulbils and root-tubers. Moreover, both taxa are shade-loving and occupy similar habitats. After fifty years the Allium in my garden has only colonised an area of about 0.25 hectares, though it is dominant under trees. It has failed to cross the drive to another wooded strip. Footwear seems very ineffective as a means of dispersal. This year, 2020, it has for the first time appeared under a hedge 100 m down the road, probably from a bulbil picked up by the tread on a car tyre and soon ejected. It must now be expected to colonise that hedge bottom.

Figure 1. The distribution of Allium paradoxum in Berwickshire has two elements, a notably thin scatter around habitation and a continuous strip along the lower sections of the river system, where it is now abundant. Its bulbils are known to have been dispersed along the rivers by floods. It is absent from all the hill country and most of the coastline.

In Berwickshire, following its presumed introduction as a weed with garden plants a little before 1950, it has been spread only slowly along roads by bulbils caught in the treads of car tyres, colonising hedge bottoms, and as a weed in herbaceous plants passed from garden to garden, so that colonisation of these habitats remains modest. Meanwhile, slowly but inevitably, the bulbils have reached the rivers in a number of places and have been spread down their flood plains by winter floods. This has enabled massive colonisation of riverside woodland. In about 70 years the colonisation of the rivers is almost complete and a number of burns have also been colonised. I used to think that only the parts of the woodlands on
the flood plain itself would be colonised. I was wrong. The cloven feet of roe deer have proved to be effective in distributing bulbils along their tracks up the woodland banks, though it takes decades for a bank to be fully colonised. Badgers may also play a role. Timber extraction can lead to much wider dispersal.

There is every reason to suppose that *Ficaria verna* subsp. *verna* can colonise in very much the same way as *Allium paradoxum*.

**Evidence from the Floras**

I have found circumstantial evidence for recent spread in subsp. *verna* in several Floras and in the BSBI Distribution Database (https://database.bsbi.org/). I consider here in detail Mary McCallum Webster’s *Flora of Moray, Nairn and East Inverness* (McCallum Webster, 1977), Arthur Chater’s *Flora of Cardiganshire* (Chater, 2010), Paul Green’s *Flora of County Waterford* (Green, 2008), Geoffrey Halliday’s *A Flora of Cumbria* (Halliday, 1997) and BSBI database records for North Northumberland and elsewhere.

Mary McCallum Webster is exemplary in giving localities for the scarcer members of the flora. Thus for subsp. *verna* (as subsp. *bulbifera*) she states: ‘probably introduced. Shady places generally near habitations’. Her Inverness records are: ‘Abundant by the burn and in the Hotel garden, Kingussie, 1954; bank of the Big Burn Glen Cottage, Inverness, 1970; Calcabock and Dunain, 1970; bank at Inshriach Nursery; ditch by the farm of Viewhill, Gollanfield; by the potting sheds at Fitchity House; beneath the garden wall at Culloden House; banks of the burn at Farr House, and by the River Beauly below Lovat Bridge’ (there are further records for Moray and Nairn). Inshriach Nursery was an enterprise specialising in Himalayan plants established in 1938 in a natural birch wood and the record from there is a neat example of a likely link to the horticultural trade.

Ian Green has commented to me on the current distribution of *Ficaria verna* in nearby Nairn. He considers that the two subspecies are now equally common. Subsp. *fertilis* is more often found in natural habitats like river banks, while subsp. *verna* is more often found about habitation. This seems to indicate much colonisation by subsp. *verna* over the fifty years since 1970, very much along the lines my working hypothesis would suggest.

Arthur Chater has written an extensive account of *Ficaria verna* in his *Flora of Cardiganshire*. He has acquired the enviable ability to distinguish the two subspecies vegetatively from a distance, utilising differences in leaf texture and mat-forming capability. He considers both subspecies to have increased between 1995 and 2005 in two urban and suburban areas around Aberystwyth, but that subsp. *verna* has increased much more than subsp. *fertilis*. He estimates a thousand-fold increase at these localities. This suggests a particular dispersal event (such as the contamination of council grass-cutting machinery) followed by bulking up. I have observed such a phenomenon with *Allium paradoxum* where bulbils have been sparsely scattered over an area of riverside woodland by floods and have bulked up over a decade. Chater (2010) found subsp. *verna* to be much more localised than subsp. *fertilis* and to be found chiefly near habitation and along river systems but to be rare in ancient woodland and other wild sites and to be quite absent from the coastal slopes. This contrasts with the situation on the continent where subsp. *verna* is especially characteristic of ancient woodland. Thus the distribution pattern in Cardiganshire is again consistent with my hypothesis.
Paul Green’s *Flora of County Waterford* is also informative. He finds subsp. *verna* (as *Ranunculus ficaria* subsp. *bulbifera*) to be much the rarer of the two subspecies though he observes that it can often form dense patches under trees. He states that it is often found on dumped soil, which is aiding its spread to some of the more remote parts of the county. Once again there is evidence of ongoing colonisation.

The North Northumberland records are interesting. There Professor George Swan made meticulous records of *Ficaria verna* in the period 1960-1963 as a contribution to the Critical Supplement to the Atlas of the British Flora (Perring & Sell, 1968). Most of the records were made with 100 m grid references on the Individual Record Cards used for the Atlas survey. A review of these records on the map shows subsp. *verna* to have been found close to habitation and along river systems, while subsp. *fertilis* was found both in these habitats and also in natural habitats along the coastal strip, in native grassland on basalt outcrops and to 350 m in the Cheviot Hills.

Recent survey at tetrad scale by Chris Metherell suggests recent spread of subsp. *verna* in North Northumberland and has confirmed its scarcity along the coast (C. Metherell, pers. comm. 2020). Thus, although at 10 km scale both subspecies were widespread in the 1960’s and in the 2010s, there is compelling evidence at finer scales of habitat differences between the subspecies and a strong suggestion of recent spread in subsp. *verna* with its more anthropomorphic habitats. There is, however, no evidence as to whether or not subsp. *verna* had been present in the vice-county for centuries, albeit as the less widespread of the two subspecies.

Geoffrey Halliday’s *A Flora of Cumbria* (Halliday, 1997) has remarkably complete distribution maps of the subspecies at 2 km scale based on a survey 1974-1997 that show both subsp. *fertilis* and subsp. *verna* to be widespread. The caption for subsp. *verna* (as subsp. *bulbifera*) notes that it is ‘locally common in damp, shaded habitats, chiefly in the east’ [and thus away from the coast]. These are usually, but certainly not always, anthropogenic, for example gardens, where it can be a pernicious weed, and by woodland paths’. The distributions in Cumbria are strikingly similar to those for North Northumberland, though, in the absence of historical records, no comment is made on any apparent increase.

It has also been instructive to search for pre-1950 herbarium records of both subspecies in the BSBI database and the herbaria@home website (http://herbariaunited.org/atHome/). There are records in the database of twenty such specimens of subsp. *verna* from BM (the Natural History Museum). While most are from the south and east of England, there are specimens from Northwest Yorkshire, East Perthshire and the settlement of Tarbert on the island of Harris in the Outer Hebrides. There are a similar number of specimens for subsp. *fertilis*. The specimens retained in the herbarium are presumably a selection aimed to cover morphological variation and geographical distribution, so I do not think any conclusions can be drawn of the relative frequencies of the two subspecies. There are very many specimens for *Ficaria verna* in herbaria@home but only two are determined to subspecies. I have examined a selection of the others and find most to be indeterminate at subspecies level, often because they were collected early in the season. I did notice two more subsp. *verna* specimens as they are much easier to identify than subsp. *fertilis*, for which I did not notice any further examples,
though my best guess was that most of the remaining specimens were subsp. fertilis.

I largely ignored the two subspecies when recording *Ficaria verna* in my surveys of Berwickshire. I discovered that one had to wait till May to be certain that a particular plant had produced bulbils if it was subsp. *verna*, or a full head of viable achenes if it was subsp. *fertilis*. Early season records could not be identified with confidence, which was most inconvenient. I satisfied my conscience by making a single record of each subspecies in each hectad. In effect I assumed that the two subspecies were more or less equally widespread, like those of *Veronica hederifolia*, and not worthy of much attention.

To test my suspicion that subsp. *verna* was more widespread here in the Scottish Borders than recorders have realised, on 14 May 2020 Luke Gaskell, at my suggestion, searched for *Ficaria verna* around his home at Kittyfield farmhouse, Roxburghshire, and down a lane to the River Tweed, 100 m below. To his surprise virtually all the plants encountered were subsp. *verna*. They were found in a variety of shaded habitats. At the same time Robin Cowe searched around his home in Chirnside, Berwickshire, and on a walk down to the Whiteadder Water, 50 m below. He found much more subsp. *verna* than subsp. *fertilis*. Subsp. *verna* was mostly in shaded habitats, while subsp. *fertilis* showed a tolerance for more open habitats. He too was surprised by the relative frequencies of the two subspecies.

I have little field experience of the south of England, but the BSBI database maps and a review of a sample of the Floras, with the assistance of David Pearman, confirm that both subspecies are very widespread and abundant, though very variably recorded at subspecies level. In Suffolk, Francis Simpson’s *Simpson’s Flora of Suffolk* (Simpson, 1982) considers subsp. *verna* (as subsp. *bulbifera*) as the less frequent subspecies favouring shady habitats, while Martin Sanford’s *A Flora of Suffolk* (Sanford & Fisk, 2010) also considers it the less frequent subspecies but states that it is usually found in more disturbed sites, often associated with habitation or churchyards. This suggests recent expansion of the subsp. *verna* population in anthropomorphic habitats. In Hampshire, however, Martin Rand (pers. comm.) states that ‘I thought a long while ago that it might be possible to make some distinction between habitats [of the subspecies], but the more I’ve looked, the less convinced I’ve become’ (pers. comm.-).

**Discussion**

It is as well to remember just how widespread and abundant both subspecies are across almost all of England and some parts of Scotland and Wales, and to reflect that this severely limits any attempt to trace distributional or habitat changes over time. There does seem however to be agreement that subsp. *verna* is the less-frequent subspecies and to be the one that is increasing in many areas. This might reflect the increasing level of human activity, but it might possibly indicate a later date of arrival in Britain, with subsp. *fertilis* a native taxon and subsp. *verna* an archaeophyte which is still in the process of colonising Britain.

While the horticultural trade is proposed as a key driver of colonisation since 1800, there are likely to have been earlier waves of colonisation, at least in England. The medicinal herb gardens of the monasteries and medieval hospitals are possible sources of introduction, especially as the root-tubers of *Ficaria verna* were commonly used medicinally. Indeed, I have recorded subsp. *verna* by the walkway along the
massive stone-faced ramparts that are the Elizabethan town walls of Berwick upon Tweed and abundantly in a tiny dean adjacent to the site of a medieval hospital at Dalcove (Berwickshire NT63) destroyed by the English in 1544, where *Hyoscyamus niger* still grows on an eroding bank.

It is not necessarily a bar to native status to suppose subsp. *verna* to have had a southern and eastern distribution until recently. Its bulbils do not favour long-distance dispersal (in the absence of human assistance) and it would be but one of a considerable number of native species that have never managed to colonise all the parts of Britain that have suitable habitat and climate. Thus the Cheviot Hills proved a barrier to the colonisation of Berwickshire by *Glyceria maxima* and *Lysimachia vulgaris*, but both colonised strongly after their introduction from England a little over a century ago. For short-distance dispersal the bulbils of subsp. *verna* are probably dispersed in mud by animals as effectively as the achenes of subsp. *fertilis*. For long-distance dispersal the achenes have the advantage of being smaller and more robust. In open grassland, particularly on the coast, they may be dispersed by wind. It is to be expected that they are occasionally swallowed by birds, pass through their intestines unharmed and are evacuated at a distance. Such events, though rare, play a key role in the dispersal of many species.

**Conclusion**

While the early history of the subspecies of *Ficaria verna* remain ambiguous, there is circumstantial evidence of an increase in the range and abundance of subsp. *verna* since about 1800. The hypothesis that subsp. *verna* was dispersed as a weed with garden plants marketed by plant nurseries and gradually colonised more widely is supported by the observations of Flora writers and by analogy to the observed recent colonisation of the similarly-dispersed *Allium paradoxum* in Berwickshire.

It is not suggested that the association between subsp. *verna* and garden plants has been the only cause of an increase in its range. Rather, it may well be but one of a series of associations with human activity over an undefined period of time. In view of the long history of my own garden, it follows that the date of arrival of *Ficaria verna* subsp. *verna* remains unknown.

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ISSN: 2632-4970

https://doi.org/10.33928/bib.2020.02.215