



# The distribution and host range of *Thecaphora melandrii*, with first records for Britain

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**Summary.** *Thecaphora melandrii* (Syd.) Vánky & M.Lutz infects species in the Caryophyllaceae forming sori with spore balls in the floral organs. We report new finds from Britain, supported by phylogenetic analysis, that confirm its occurrence on *Silene uniflora* Roth. We review published and web accessible records and note the relatively few records of this smut, its sparse distribution, confined to Europe but scattered predominantly from central to eastern Europe. Analysis of the rDNA *ITS* and *28S* sequences demonstrates little variability among specimens, even those parasitising different host genera, which suggests that the species has evolved relatively recently. Some *Microbotryum* species infect the same host plants, and we found two species, *M. lagerheimii* Denchev and *M. silenes-inflatae* (DC. ex Liro) G.Deml & Oberw., in the same locations as *T. melandrii*, identified by morphology and molecular phylogenetic analysis. These species may form a stable multi-species community of parasites of *Silene uniflora*.

**Key Words.** Caryophyllaceae, gall, Glomosporiaceae, *Microbotryum*, *Silene uniflora*, smut.

## Introduction

The Caryophyllaceae is a large family of dicotyledonous plants (Greenberg & Donoghue 2011), and its species are hosts for many plant-parasitic microfungi, among them at least 38 species of smut fungi assigned to the genera *Microbotryum* Lév. and *Thecaphora* Fingerh. (Vánky (2012), with additional species in Denchev *et al.* (2009); Denchev & Denchev (2011); Piątek *et al.* (2012, 2013); Denchev *et al.* (2019); Kemler *et al.* (2020)), which form their sori in the floral organs. Although there are similarities in the appearance of the infections and the affected hosts, these two genera are not closely related; *Microbotryum* is in the Microbotryaceae within the subphylum Pucciniomycotina, and *Thecaphora* is the only genus in the Glomosporiaceae within the Ustilaginomycotina.

The genus *Thecaphora* contains plant-parasitic microfungi infecting hosts belonging to a range of dicotyledonous families. The species and their current nomenclature are summarised by Vánky *et al.* (2008) and Vánky (2012). Recently, three new species were described in Crous *et al.* (2018), Kruse *et al.* (2018) and Piątek *et al.* (in press). *Thecaphora* species are characterised by having spores in balls (or rarely single), generally without sterile cells, and infections are found in a range of different organs of their host plants. Here we focus on species of *Thecaphora* infecting hosts in the

Caryophyllaceae, and specifically on *T. melandrii* (Syd.) Vánky & M.Lutz. Vánky (2012) lists five species of *Thecaphora* with hosts in this family, all destroying the inner floral organs; most remain within the outer floral envelope (the calyx), but *T. alsinearum* (Cif.) Vánky & M.Lutz also spreads to the uppermost leaves.

*Thecaphora melandrii* is known to infect *Silene latifolia* Poir., *S. nutans* L., *S. vulgaris* (Moench) Garcke and *Stellaria graminea* L. as confirmed by genetic analyses of smut specimens from the respective hosts (Vánky & Lutz 2007; Vánky 2012), and is tentatively reported from several other host species, based on morphological analyses only, although we have traced the sources of only some of these reports below. Some of these tentatively reported hosts are doubtful, and need confirmation. *Thecaphora melandrii* deforms and partially replaces the inner floral organs, and is therefore gall-forming. The infection remains within the calyx, but causes the buds to deform and remain closed, so that the infection is clearly detectable externally. Here we report recent finds which confirm its occurrence on a new host species (*Silene uniflora* Roth), based on molecular evidence of nuclear rDNA *ITS* and *28S* sequences, and evaluate its geographical distribution based on published records. Vánky (2012) reported *T. melandrii* on *S. vulgaris* subsp. *maritima* (With.) A.Löve & D.Löve (which is a synonym of *S. uniflora*)

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but the source of this report is unknown. This fungus-host combination was however not verified by molecular methods.

*Microbotryum* has been found to consist of many similar species, distinguished by DNA sequence analysis and in some cases by subtle morphological differences. Vánky (2012) lists 28 species in hosts of the Caryophyllaceae, including 20 species in the host's anthers. More segregates have been identified subsequently, thus there are now 33 species, including 23 species of so-called anther smuts. *Microbotryum* anther smut species have co-evolved with their hosts (Refrégier *et al.* 2008), and are generally strongly host species specific. Several species have been described in recent years throughout the world, but here we consider only some of the European taxa, which have been worked out by Lutz *et al.* (2005, 2008); Denchev (2007a, b); Le Gac *et al.* (2007); Denchev *et al.* (2009); Denchev & Denchev (2011) and Piątek *et al.* (2012, 2013).

## Materials and Methods

### Specimens

Specimens used for molecular analyses were of *Thecaphora* and *Microbotryum* species infecting *Silene uniflora* (= *S. maritima* With., *S. vulgaris* subsp. *maritima*), collected in 2019, and preserved by pressing. Specimens were photographed *in situ*. The collection details are given in Table 1 (*Thecaphora*) and Table 2 (*Microbotryum*). The voucher specimens are deposited in the fungarium at the Royal Botanic Gardens, Kew (K(M)) and in the herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków (KRAM). An example habitat of *Silene uniflora* where infected individuals were found is shown in Fig. 1.

### Morphological analyses

The morphology of *Thecaphora* and *Microbotryum* species were studied using dried specimens. The microscopic characters were analysed by light microscopy (LM), using a Nikon Eclipse 80i light microscope. For this purpose spore balls and spores were placed in 80% lactic acid, heated to boiling point, cooled and then examined under a light microscope. The spore sizes of *Microbotryum* specimens were measured using NIS-Elements BR 3.0 imaging software. 30 spores were counted for each collection and the extreme measurements were adjusted to the nearest 0.5 µm. The species descriptions include the combined values and standard deviation for all measured specimens of the respective species. LM micrographs were taken with a Nikon DS-Fi1 camera. The morphology of *Thecaphora* and *Microbotryum* species are depicted in Figs 2 and 3.

**Table 1.** Specimens used for the analysis of the ITS and 28S sequences of *Thecaphora melandrii*. vc = vice county, a system of classifying regions in Britain and Ireland; grid references follow the British national grid.

Host	Genbank accession no. (ITS/28S)	Reference specimen
<i>Silene uniflora</i>	MN922348/MN922341	England, Stokes Bay, vc11, SZ59844 98238, 25 May 2019, Paul A. Smith, K(M)
<i>Silene uniflora</i>	MN922349/MN922342	England, Hook with Warsash LNR, shingle, vc11, SU48940 04794, 1 June 2019, Paul A. Smith, KRAM F-59672
<i>Silene uniflora</i>	MN922350/MN922343	England, Hook with Warsash LNR, shingle, vc11, SU48896 04878, 1 June 2019, Paul A. Smith, KRAM F-59673
<i>Silene uniflora</i>	MN922351/MN922344	England, Hook with Warsash LNR, vc11, SU48890 04877, 1 June 2019, Paul A. Smith, KRAM F-59674 (this clump was also infected with <i>Microbotryum</i> )
<i>Silene uniflora</i>	MN922352/MN922345	England, Gilkicker Point, vc11, SZ60544 97556, 17 July 2019, Paul A. Smith, KRAM F-59675
<i>Silene uniflora</i>	MN922353/MN922346	England, Gilkicker Point, vc11, SZ60532 97528, 17 July 2019, Paul A. Smith, KRAM F-59676
<i>Silene latifolia</i> subsp. <i>alba</i>	MN922354/MN922347	England, Gilkicker Point, vc11, SZ60495 97557, 17 July 2019, Paul A. Smith, KRAM F-59677
<i>Silene latifolia</i> subsp. <i>alba</i>	EF200023/EF200048	Italy, Varese, 11 Oct. 1986, E. U. & K. Vánky, BRIP: HUV 13273
<i>Silene latifolia</i> subsp. <i>alba</i>	EF200024/EF200049	Hungary, Budapest, 26 June 1986, J. Gönczöl, A. Révay & K. Vánky, BRIP: HUV 12677
<i>Silene latifolia</i> subsp. <i>alba</i>	EF200027/EF200052	Slovenia, Lake Bohinj (=Wochein), Stara Fužina, 31 July 2006, M. Lutz, BRIP: HUV 21371, TUB 012795
<i>Silene latifolia</i> subsp. <i>alba</i>	EF200028/EF200053	Switzerland, Wallis, Lenk, Nov. 2005, M. Wältli, BRIP: HUV 21178
<i>Silene nutans</i>	EF200029/EF200054	Hungary, Bükk Mts, 23 June 1982, J. Gönczöl, A. Révay, S. Tóth & K. Vánky, BRIP: HUV 11255
<i>Silene vulgaris</i>	EF200030/EF200055	Hungary, Balatonberény, 23 June 1968, S. Tóth & K. Vánky, BRIP: HUV 1771
<i>Silene vulgaris</i>	EF200031/EF200056	Switzerland, Graubünden, Sur, Alp Fix, 12 July 2006, M. Lutz, BRIP: HUV 21368, TUB 012789
<i>Stellaria graminea</i>	EF200034/EF200059	Russia, Ulyanovsk, Raton Bazarmy Syzgan, 17 July 1990, L. Horowitz, BRIP: HUV 14971
<i>Stellaria graminea</i>	EF200035/EF200060	Hungary, Bükk Mts, 23 July 1979, S. Tóth, BRIP: HUV 10729

**Table 2.** *Microbotryum* specimens from the localities in England searched for *Thecaphora melandrii* during this study.

Species	Host	Genbank accession no. ( <i>ITS</i> )	Reference specimen
<i>M. lagerheimii</i>	<i>Silene uniflora</i>	MN922355	Gilkicker Point, vc11, SZ60334 97729, 17 July 2019, Paul A. Smith, KRAM F-59668
<i>M. silenes-inflatae</i>	<i>Silene uniflora</i>	MN922356	England, Hook with Warsash LNR, vc11, SU48890 04877, 1 June 2019, Paul A. Smith, KRAM F-59669 (this clump was also infected with <i>Thecaphora melandrii</i> )
<i>M. silenes-inflatae</i>	<i>Silene uniflora</i>	MN922357	Hayling Island, vc11, SZ71649 98757, 20 July 2019, Paul A. Smith, KRAM F-59670
<i>M. silenes-inflatae</i>	<i>Silene uniflora</i>	N/A	Hayling Island, vc11, SZ71760 98741, 20 July 2019, Paul A. Smith, KRAM F-59671

### Phylogenetic analyses

Methods of DNA extraction, PCR, and sequencing of the nuclear rDNA *ITS1-5.8S-ITS2* region (*ITS*) and the nuclear rDNA *28S D1-D2* region (*28S*) followed Lutz *et al.* (2004) and Vasighzadeh *et al.* (2014), and molecular phylogenetic analyses followed the techniques used in Ziegler *et al.* (2018). To elucidate the phylogenetic position of the *Thecaphora* specimens their concatenated *ITS+28S* sequences were analysed along with all the available sequences of *T. alsinearum* and *T. melandrii* from GenBank, and three representative specimens of *T. saponariae* (Syd.) Vánky & M.Lutz. To clarify the relationship of the *Microbotryum* specimens within the genus *Microbotryum*, their concatenated *ITS+28S* sequences were analysed within datasets covering all the *Microbotryum* species available in GenBank (data not shown). The GenBank accession numbers of the *Thecaphora* sequences used and generated in this study are given in Table 1 and Fig. 4, the GenBank accession numbers of the *Microbotryum* sequences generated in this study are given in Table 2.

A Bayesian inference of the phylogenetic relationships within the sampled *Thecaphora* specimens was undertaken using Markov chain Monte Carlo analysis of an alignment of the concatenated *ITS+28S* sequences using the GTR+I+G model of DNA substitution with gamma distributed substitution rates and an estimation of invariant sites, random starting trees and default starting parameters of the DNA substitution model. To illustrate the results, the consensus tree of one run of the Bayesian Approach is presented in Fig. 4. A 50% majority-rule consensus tree is shown computed from 75,000 trees that were sampled after the process had become stationary. The topology was rooted with the *Thecaphora saponariae* specimens. Numbers on branches before slashes are estimates for a posteriori probabilities, numbers on branches after slashes are ML bootstrap support values. Branch lengths were averaged over the sampled trees. They are scaled in terms of expected numbers of nucleotide substitutions per site.

### Distribution and hosts

Records of *Thecaphora melandrii* were sought through an extensive review of the online accessible literature

and a selection of European smut floras and checklists, also considering the synonyms (taken from Vánky & Lutz (2007)) *Sorosporium melandrii*, *So. silenes-inflatae* and *So. stellariae*, and also *So. saponariae* or *T. saponariae* only where the host was in *Silene* L. or *Stellaria* L. Other online sources (such as online fungarium information, including records from Herbarium Ustilaginales Vánky (HUV; <https://collections.daff.qld.gov.au/>) and the Solheim Mycological Herbarium) were also investigated. Details of the locations and hosts were abstracted. The distribution of *Thecaphora melandrii* is shown in Map 1.

### *Thecaphora melandrii* in Britain

There are many records of *Microbotryum* spp. from Britain and Ireland recorded in the Fungal Records Database of Britain & Ireland (FRDBI; <http://www.frdbi.info/>). They (almost) all infect only the anthers (among species known in Britain & Ireland (Legon & Henrici 2005), only *M. major* on *Silene otites* (L.) Wibel deforms other floral parts too). So the first author (PAS) was surprised to find several plants of *Silene uniflora* on the shingle beach at Stokes Bay, Hampshire (see Table 1 for full record details) with deformed, unopened flowers (Fig. 2A, B, D) inside which most of the floral parts were swollen, and there were copious smut spores. The spores were in balls, although held together very loosely and disintegrating easily when mounted on microscope slides. The individual spores were verrucose (Fig. 2C), without the reticulate sculpturing characteristic of most *Microbotryum* species. This was clearly *Thecaphora melandrii*, which is not included in Legon & Henrici (2005) or its updates, and is therefore the first record for Britain & Ireland. Infected plants were present along approx. 1 km of the beach.

Further searching showed *Thecaphora melandrii* to be frequent infecting *Silene uniflora* on shingle at Hook with Warsash (SU4804), approx. 11 km from the Stokes Bay location, but it could not be found in searches on Hayling Island to the east of Stokes Bay. Nevertheless, it seems possible that *T. melandrii* may be in further suitable places along the south coast of England. All the searched locations had *S. uniflora*





**Fig. 1.** Habitat of *Silene uniflora* (in the foreground) infected with *Thecaphora melandrii* at Hook with Warsash; the large plants in the background are *Crambe maritima*.

plants with anthers infected by *Microbotryum* sp., and we return to these under ***Microbotryum* species** below.

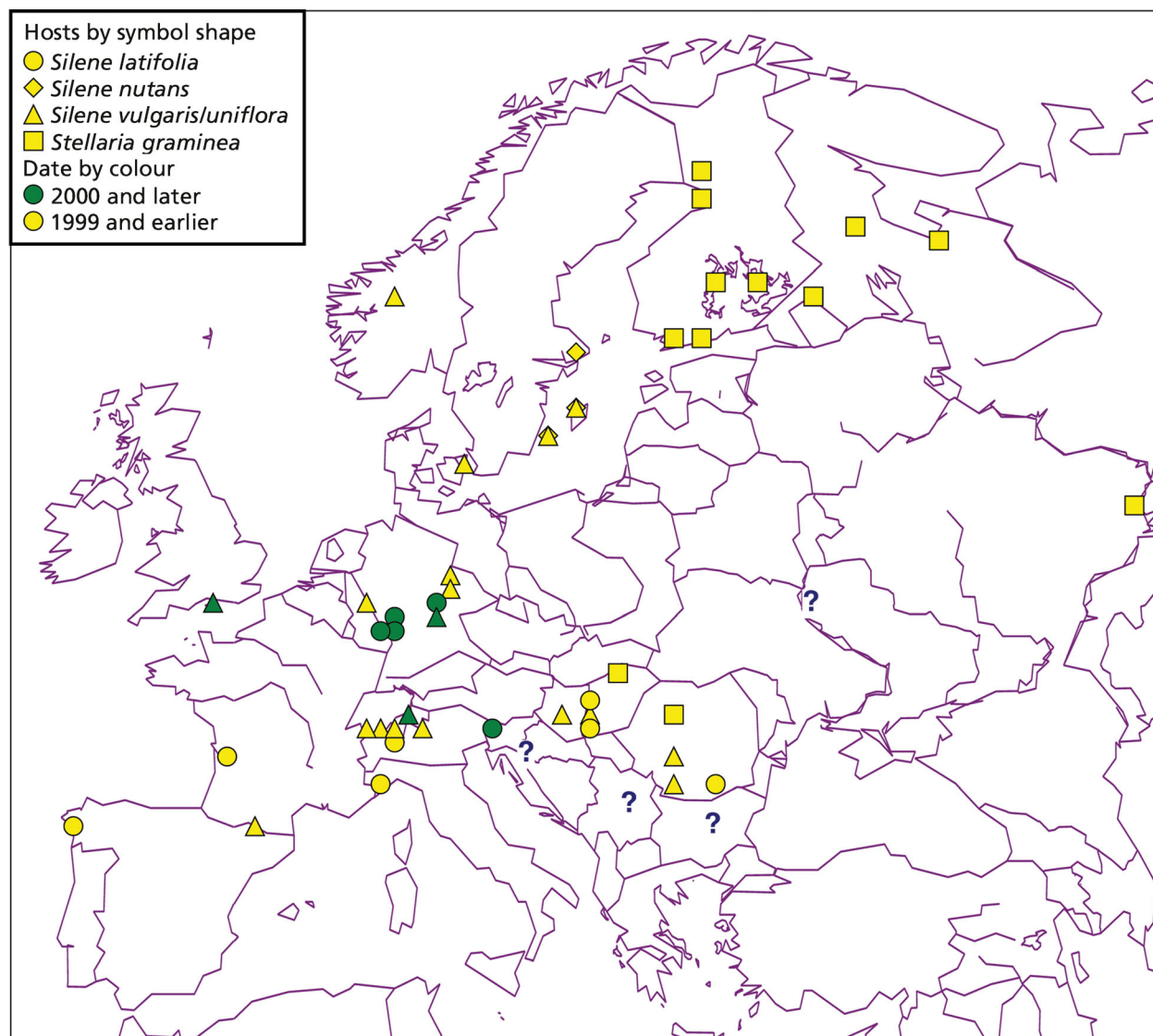
The habitat in both locations (for a habitat example see Fig. 1) consists of stable shingle beaches with sparse vegetation consisting of *Beta vulgaris* L. subsp. *maritima* (L.) Arcang., *Crambe maritima* L., *Glaucium flavum* Crantz, *Plantago lanceolata* L. and *Silene uniflora*; this belongs to the *Rumex crispus*–*Glaucium flavum* shingle community (National Vegetation Classification SD1 (Rodwell *et al.* 2000: 128 – 132)). *Silene uniflora* is frequent in this habitat, which may help *T. melandrii* to persist in relative abundance.

Several observations suggest further details of the life cycle of *Thecaphora melandrii*. In most infected clumps of its host, every flower is infected (Fig. 2A, E, F), which suggests that the infection is systemic. Occasionally there are a few uninfected flowers in a clump, and then it is unclear whether some flowers are able to escape infection and develop normally, or whether the clump contains more than one individual of the host. One host clump at Hook with Warsash was infected with both *T. melandrii* and *Microbotryum silenes-inflatae* (Fig. 2E, ***Microbotryum* species** below); it appeared that this was a single plant, but the possibility of two individuals growing together cannot be ruled out.

Although all the parts of flowers within the calyx are normally infected and swollen (Fig. 2D), occasional flowers on infected plants still produce exerted corollas (Fig. 2F), and the same phenomenon was reported by Kruse *et al.* (2020). So there seems to be some variation in infection intensity even within a host plant.

*Silene uniflora* is regularly robbed for its nectar by insects (presumably short-tongued bees, although this was not observed) which drill holes in the calyx. The same sort of holes were observed in some of the flowers infected by *Thecaphora melandrii* (Fig. 2F), and this suggests a mechanism for infections to spread to new hosts, since infected flowers do not otherwise open. A reviewer noted similar holes on infected specimens of *S. latifolia* subsp. *alba* (Mill.) Greuter & Burdet, possibly made by caterpillars. Spores are also exposed as the flowers senesce, and could also be wind-distributed.

The *ITS* and *28S* sequences extracted from the specimens from southern England were compared with all the available sequences for *Thecaphora melandrii*, the latter included in the analysis of *Thecaphora* species on caryophyllaceous hosts by Vánky & Lutz (2007). Details of the collections and accession



**Map 1.** Known distribution of *Thecaphora melandrii*. Green symbols denote records made since 2000, and yellow symbols records made before 2000. Different symbol shapes denote infections of different hosts (sometimes superimposed). '?' denotes vaguely localised records. Map produced with DMAP.

numbers are given Table 1. No further sequences for *T. melandrii* were available in GenBank.

A Bayesian inference of the phylogenetic relationships within the sampled *Thecaphora* specimens is shown in Fig. 4. The *ITS* and *28S* sequences are remarkably homogenous, with almost no differences. This is surprising, given that it infects several different host species across two genera; of course there may be differences in other areas of the genome, but on the evidence in *ITS* and *28S* it looks as if this is a recently evolved species, so that there has been insufficient time for divergence of the *ITS* and *28S* sequences; this would also suggest that a single pathogen is involved in infecting these host species. It would be worthwhile undertaking artificial infection experiments to confirm that *T. melandrii* does not vary in its infection ability on different hosts.

The lack of differences confirms that the specimens from England are consistent with the species concept for *T. melandrii*, and this also confirms the tentative assignment of *Silene uniflora* as a host by Vánky & Lutz (2007).

### ***Microbotryum* species**

The localities searched for *Thecaphora melandrii* also supported *Microbotryum* specimens, and the morphology as well as the rDNA *ITS* and *28S* sequences for these collections were also examined. The collection details are given in Table 2. According to our molecular phylogenetic analyses, the clump with infections of both *T. melandrii* and *Microbotryum* sp. at Hook with Warsash was infected by *M. silenes-inflatae*,





**Fig. 2.** A *Silene uniflora* plants infected by *Thecaphora melandrii* showing the deformed, unopened flowers. Note that all flowers in a clump are infected. B close-up of infected head (note that *S. uniflora* has forms with and without anthocyanins (Marsden-Jones & Turrill 1957: 289 – 298), which is why there is a difference in the colours). C spore balls, seen by LM, showing the verrucose sculpturing of the spores in contrast to the reticulate pattern on spores of most *Microbotryum* spp.; D section through infected flower showing the swollen inner floral parts; E single clump of *S. uniflora* infected with *T. melandrii* and *Microbotryum silenes-inflatae*; F infected plant with some infected flowers (e.g., upper right) showing corollas, some infected flowers (circled) have holes in their calyces where insects have attempted to rob them for nectar.



and the other site for *T. melandrii* at Gilkicker Point produced *M. lagerheimii*. At Hayling Island where no *Thecaphora* spp. infection was found, the anther smut was *M. silenes-inflatae*. The morphology showed differences between the two species detected by molecular analyses. The sori of *M. lagerheimii* in host anthers were light violaceous, spores were pale violet in transmitted light, globose, subglobose, to broadly ellipsoid,  $5.0 - 7.5 \times 5.0 - 6.5$  ( $-7.0$ )  $\mu\text{m}$  [av.  $\pm$  SD,  $6.3 \pm 0.7 \times 5.9 \pm 0.6 \mu\text{m}$ ,  $n = 30/1$ ]; the wall was reticulate, c.  $0.5 - 1.0 \mu\text{m}$  high, the meshes were more or less polyhedral, usually irregular, and the number of meshes per spore diameter was  $5 - 8$ . The sori of *M. silenes-inflatae* in host anthers were relatively dark violaceous, spores were pale violet or violet in transmitted light, globose, subglobose, to broadly ellipsoid,  $6.0 - 8.5$  ( $-9.5$ )  $\times$  ( $5.5 -$ )  $6.0 - 7.5$  ( $-8.5$ )  $\mu\text{m}$  [av.  $\pm$  SD,  $7.4 \pm 0.8 \times 6.8 \pm 0.6 \mu\text{m}$ ,  $n = 90/3$ ]; the wall was reticulate, c.  $0.8 - 1.3 \mu\text{m}$  high, the meshes were more or less polyhedral, usually irregular, and the number of meshes per spore diameter was  $6 - 9$ . The second specimen from Hayling Island, not investigated by molecular methods, could be identified as *M. silenes-inflatae* based on morphology. *Microbotryum lagerheimii* and *M. silenes-inflatae* are differentiated based on the colour of the sori (pale violaceous vs dark violaceous) and average of spore sizes ( $<7 \mu\text{m}$  vs  $>7 \mu\text{m}$ ) (Fig. 3). This morphology is consistent with data of Denchev (2007a) for both species and Smith *et al.* (2017) for *M. silenes-inflatae* in the Outer Hebrides. Chung *et al.* (2012) have already shown that there are sympatric populations of these two *Microbotryum* species in southern England, so the sites are not necessarily differentiated by these records. By contrast, in the northern part of the UK, in the Outer Hebrides, only *M. silenes-inflatae* has so far been found on *Silene uniflora* (Smith *et al.* 2017). Abbate *et al.* (2018) show that different *Microbotryum* spp. occur widely in low- and high-altitude populations of *S. uniflora* and *S. vulgaris*. Nevertheless, it is clear from our limited records and previous research that populations of any pair of these three species of smut found in this study are able to co-exist in a site, even though they share a host and a similar niche. Further sampling is needed to examine whether all three parasite species can form a stable system.

### Distribution and scarcity of *Thecaphora melandrii*

Table 3 lists all of the records (worldwide) for *Thecaphora melandrii* which we traced in our literature search (excluding those already listed in Table 1 and doubtful records in Table 4).

### Biogeography

In total there are 90 published and herbarium records, and because there are some duplicate collections, even fewer localities. Records based only on the online catalogue of HUV contain at most country-level infor-

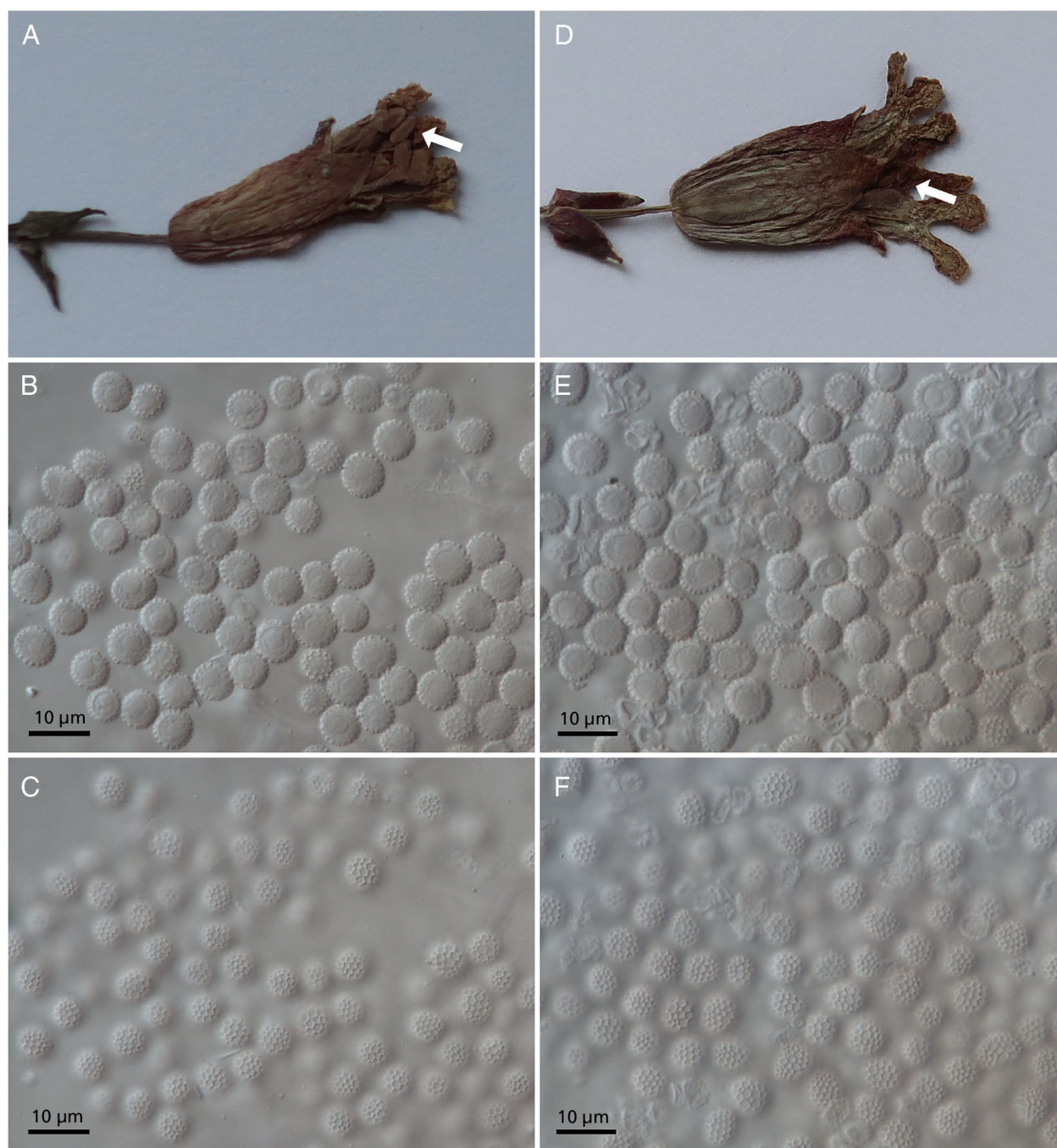
mation. There are undoubtedly collections which have not been published, and some, particularly earlier, collections may be under names which applied to multiple species under current taxonomic concepts, and therefore are not clearly identifiable as *Thecaphora melandrii*. Nevertheless, it seems that this is a scarce species, with few records anywhere; several authors comment specifically on its scarcity (Sydow 1934; Liro 1938; Lindeberg 1959). There has been a surge in recent records, particularly a clutch of records from Germany (Kruse *et al.* 2015, 2017, 2020), probably as result of renewed interest in smuts (but possibly also affected by changes in the publication of records), but the number of recent records is still small by contrast with *Microbotryum* spp. The records of *T. melandrii* are mapped in Map 1. *Thecaphora melandrii* is apparently restricted to Europe, although there are eastern European records from Russia and Ukraine, which suggests that the species may yet be found in Asia, and there is a report from Kazakhstan (Schwartzman 1962, Table 4), although on a host species which requires further evidence to assess whether the smut belongs to this species rather than to another host species-specific taxon. Similarly, reports from America (see Table 4) are not clearly referable to this species without further evidence.

The most recent records from England are notable in being coastal; many of the remaining records (where there is sufficient detail to make an assessment) are inland (although there are also coastal records from Sweden), and largely in continental climates. This is despite the occurrence of its hosts in a wide range of habitats. The English locations are therefore in quite a different habitat type, and show that *Thecaphora melandrii* potentially has a wide biogeographical range and should be sought in further locations.

Since we have well-founded information on the recorded distribution we are able to make a provisional assessment for *Thecaphora melandrii* against the IUCN red list criteria. There is some evidence of decline in the area occupied as shown by recent records (Map 1), but we strongly suspect that this is a result of fluctuation in recording rather than fluctuation in the occurrence of *T. melandrii*. There are many individuals (systemically infecting plants of the hosts) in each locality, so the total population of mature individuals is likely to be large. Finally, no specific threats have been identified. We therefore provisionally suggest that this species should be classified as LC least concern.

### Host range

*Thecaphora melandrii* has been found infecting *Silene vulgaris*, *S. uniflora*, *S. latifolia* and *S. nutans*, and *Stellaria graminea*. The first three *Silene* species are quite closely related (particularly *S. uniflora* and *S. vulgaris*) (Greenberg & Donoghue 2011, Fig. 1), but *S. nutans* is more distantly related within the



**Fig. 3.** *Microbotryum lagerheimii*: A sori in anthers shown by arrow; spores, seen by LM, in B median and C surface views; *M. silenes-inflatae*: D sori in anthers shown by arrow; spores, seen by LM, in E median and F surface views.

many species in the genus *Silene*. The infection of *Stellaria graminea* is perhaps more surprising, as it is considerably more distantly related to *Silene* (Greenberg & Donoghue 2011, Figs 2, 4, 5). Liro (1938) records *T. melandrii* on *Stellaria graminea* from a range of sites scattered across Finland and nearby parts of Russia, and there is a further cluster of records on this host from Romania in HUV. The minimal variation in the DNA from

*T. melandrii* on any of these hosts suggests that it is a single taxon with the ability to infect a range of host species. Infection of further species might therefore also be possible; however, other species of *Silene* are also infected by segregate species (such as *T. italica* M.Lutz & Vánky on *Silene italica* (L.) Pers.).

Table 4 lists infections on a small number of additional hosts which could represent *Thecaphora*



**Table 3.** Literature and web-accessible records of *Thecaphora melandrii* (records from Table 1 are not repeated).

Country	Location	Host	Source	Date
?		<i>Silene vulgaris</i>	HUV1764	July 1920
?		<i>Silene vulgaris</i>	HUV5677	6 Aug. 1972
?		<i>Stellaria graminea</i>	HUV8851	6 July 1961
?		<i>Stellaria graminea</i>	HUV1779	10 July 1968
?		<i>Stellaria graminea</i>	HUV1780	12 July 1968
?		<i>Stellaria graminea</i>	HUV10785	4 July 1982
Bulgaria		<i>Silene latifolia</i>	HUV1744	June 1885
Croatia		<i>Silene vulgaris</i>	Ivić <i>et al.</i> (2013)	1916
Denmark	Lyngby, Seeland	<i>Silene vulgaris</i>	Lind (1913), ?HUV1761	?4 July 1912
Finland	Jyväskylä, Harju, Torikatu	<i>Stellaria graminea</i>	Liro (1938), Vánky & Lutz (2007), HUV1772	7 July 1913
Finland	Ab: Lohja, Lylyis	<i>Stellaria graminea</i>	Liro (1938)	13 July 1904
Finland	N: Pornainen, Laha	<i>Stellaria graminea</i>	Liro (1938)	July 1903
Finland	N: Tuusula, Järvenpää	<i>Stellaria graminea</i>	Liro (1938)	July 1916
Finland	Kl: Impilahti, Hippola	<i>Stellaria graminea</i>	Liro (1938)	23 June 1915
Finland	Sb: Joroinen, Koskenkylä	<i>Stellaria graminea</i>	Liro (1938), HUV16940	20 July 1918
Finland	Kpoc: Sjuigarvi	<i>Stellaria graminea</i>	Liro (1938)	15 July 1896
Finland	Kpor: Vorsogor, nr Onega town	<i>Stellaria graminea</i>	Liro (1938)	28 July 1899
Finland	Ob: Oulu, Merikoski, by the bridge	<i>Stellaria graminea</i>	Liro (1938)	28 June 1928
Finland	Ob: Tervola, Keminjoki, Pallinoja	<i>Stellaria graminea</i>	Liro (1938)	3 Aug. 1933
France	Chateau Eyquem	<i>Silene latifolia</i>	Dauphin (1993)	4 July 1993
Germany	Rheinland, Köln-Zollstock	<i>Silene latifolia</i>	Vánky & Lutz (2007)	29 Sept. 1932
Germany	Rheinland, Köln-Zollstock	<i>Silene latifolia</i>	Ustilagineen Europas #129, Vánky & Lutz (2007), HUV1746, HUV9788, HUV10815	21 June 1934
Germany	Rheinland, Köln-Zollstock	<i>Silene latifolia</i>	Solheim Mycological Herbarium	16 July 1935
Germany	Rheinland, Köln-Zollstock, Sand Pit on the Gottesweg	<i>Silene latifolia</i>		14 June 1937
Germany	Hessen, Hattersheim am Main	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2017)	15 Oct. 2016
Germany	Hessen, Frankfurt am Main, Oberrad, N of Offenbacher Landstraße, fields S of Buchrain, embankment	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2015)	3 Nov. 2013
Germany	Hessen, Main-Taunus-Kreis, Flörsheim/Main, Hochgewann, meadows by railway	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2015)	10 May 2014
Germany	Hessen, Main-Taunus-Kreis, Wiesbaden: Ginsheim-Gustavsburg, main cycle path, dyke	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2015)	17 May 2014
Germany	Hessen, Main-Taunus-Kreis, Flörsheim/Main, main road, meadow at sports club	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2015)	27 July 2014
Germany	Saxony, Eisleben	<i>Silene vulgaris</i>	Örtel (1886), Săvulescu (1957), Vánky & Lutz (2007), ?HUV1760	1875
Germany	Bottendorfer Schachtberg, between Bottendorf and Rossleben	<i>Silene vulgaris</i>	Örtel (1886)	c. 1875
Germany	Ahrtal	<i>Silene vulgaris</i>	Niessen (1937)	≤1937
Germany	Bonn	<i>Silene vulgaris</i>	Niessen (1937)	≤1937
Germany	Rodderberg	<i>Silene vulgaris</i>	Niessen (1937)	≤1937
Germany	Bayern, Oberfranken, Lkr. Haßberge, S of Hassfurt	<i>Silene vulgaris</i>	Kruse <i>et al.</i> (2017)	28 July 2016
Germany	Bayern, Oberfranken, Lkr. Lichtenfels, c. 2.7 km WSW of Bad Staffelstein	<i>Silene vulgaris</i>	Kruse <i>et al.</i> (2017)	10 Aug. 2016
Germany	Bayern, Oberfranken, Lkr. Lichtenfels, c. 2 km N of Zapfendorf	<i>Silene vulgaris</i>	Kruse <i>et al.</i> (2017)	18 Aug. 2016

Germany	Rheinland-Pfalz, Lkr. Mainz-Bingen, Ingelheim: c. 1.3 km E. of Gau-Algesheim	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2020)	14 May 2017
Germany	Thüringen, Lkr. Gotha, c. 2.5 km SSW of Wandersleben	<i>Silene latifolia</i> subsp. <i>alba</i>	Kruse <i>et al.</i> (2020)	many collections 13 June 2017 – 26 Aug. 2019
Hungary		<i>Silene latifolia</i>	HUV1743	26 May 1881
Hungary		<i>Silene latifolia</i>	HUV1745	31 May 1905
Hungary	Nemesnáduvár	<i>Silene latifolia</i>	Sävulescu (1957)	1928
Hungary	Budapest	<i>Silene latifolia</i>	Sävulescu (1957), ?HUV8096	14 June 1934
Hungary		<i>Silene vulgaris</i>	HUV8602	Aug. 1916
Hungary		<i>Silene vulgaris</i>	HUV1765, HUV1767	21 June 1922
Hungary	Foktő, Pest county	<i>Silene vulgaris</i>	Béla (1924)	1924
Italy	Alassio, on the old Roman road S of Croce-Albenga, NE S. Anna	<i>Silene latifolia</i>	Petrak (1970), HUV12868, HUV6086	27 May 1969
Norway	Røysheim, Lom	<i>Silene vulgaris</i>	Sävulescu (1957), Jørstad (1963)	1894
Romania	Bucharest, Cotraceni Botanical Garden	<i>Silene latifolia</i>	Sävulescu (1957), Herbarium Mycologicum Romanicum Fasc XXIX Nr. 1437, HUV1747	26 May 1949
Romania	Bucharest, Herăstrău	<i>Silene latifolia</i>	Sävulescu (1957)	10 May 1926
Romania		<i>Silene latifolia</i>	HUV10646, HUV11254	27 May 1981
Romania	Polovraci	<i>Silene vulgaris</i>	Sävulescu (1957), HUV12767	28 June 1938
Romania	Parcul Poporului, Craiova	<i>Silene vulgaris</i>	Sävulescu (1957)	21 Sept. 1954
Romania	Muntele Baisoara	<i>Stellaria graminea</i>	Sävulescu (1957), HUV1773	10 June 1953
Romania		<i>Stellaria graminea</i>	HUV1774	5 July 1964
Romania		<i>Stellaria graminea</i>	HUV1775, HUV1776, ?HUV8791	2 Aug. 1964
Romania		<i>Stellaria graminea</i>	HUV1777	10 July 1966
Romania		<i>Stellaria graminea</i>	HUV1778	4 July 1968
Romania		<i>Stellaria graminea</i>	HUV1781	13 Aug. 1973
Romania		<i>Stellaria graminea</i>	HUV12869	29 June 1974
Romania		<i>Stellaria graminea</i>	HUV10675	5 July 1981
Romania		<i>Stellaria graminea</i>	HUV11096	12 Aug. 1982
Serbia		<i>Silene vulgaris</i>	HUV1769	14 May 1952
Slovenia	Lake Bohinj, Stara Fužina, meadow close to Studor	<i>Silene latifolia</i> subsp. <i>alba</i>	Lutz & Vánky (2009)	31 July 2006
Spain	Santiago de Compostela and Padrón	<i>Silene latifolia</i>	Losa España (1942); Almaraz (2002)	May 1941
Spain	Hospice de Viella	<i>Silene vulgaris</i>	Durrieu (1962); Almaraz (2002)	12 Sept. 1961
Spain	Hospice de Viella	<i>Silene vulgaris</i>	Durrieu (1966); Almaraz (2002)	
Sweden	Öland, Borgholm	<i>Silene nutans</i>	Lindeberg (1959)	“several collections”
Sweden	Uppland, Norrtälje	<i>Silene nutans</i>	Lindeberg (1959)	
Sweden	Gotland, Visby, below Galgberget	<i>Silene nutans</i>	Lindeberg (1959)	14 June 1920
Sweden	Öland, Högstrum par., St Rör	<i>Silene vulgaris</i>	Lindeberg (1959)	
Sweden	Gotland, Visby	<i>Silene vulgaris</i>	Lindeberg (1959)	24 June 1895
Sweden	Öland, Glömminge	<i>Silene vulgaris</i>	Lindeberg (1959)	13 July 1901
Sweden	Öland, Borgholm	<i>Silene vulgaris</i>	Lindeberg (1959)	16 July 1915
Sweden	Gotland, nr Visby, Bingen mill (“ad molam Bingen pr. Visby”)	<i>Silene vulgaris</i>	Eliasson (1933); Lindeberg (1959)	15 July 1929
Switzerland	Aostatal, Gressen, Crête du Torrent	<i>Silene latifolia</i>	Zogg (1985)	Aug. 1979
Switzerland	Puschlav (Poschiavo), Selva	<i>Silene vulgaris</i>	Zogg (1985)	Sept. 1905
Switzerland	Visperterminen	<i>Silene vulgaris</i>	Zogg (1985)	July 1911
Switzerland	Vergeletto	<i>Silene vulgaris</i>	Bär (1915)	≤1915
Switzerland	Vernayaz (Martigny), Les Marécottes	<i>Silene vulgaris</i>	Mayor & Viennot-Bourgin (1960); Zogg (1985)	Aug. 1954
Ukraine		<i>Silene latifolia</i>	Savchenko & Heluta (2012)	

*melandrii*, but also could be a different species. Further specimens and DNA analysis are needed to assess whether *T. melandrii* is also found in the wild on further species.

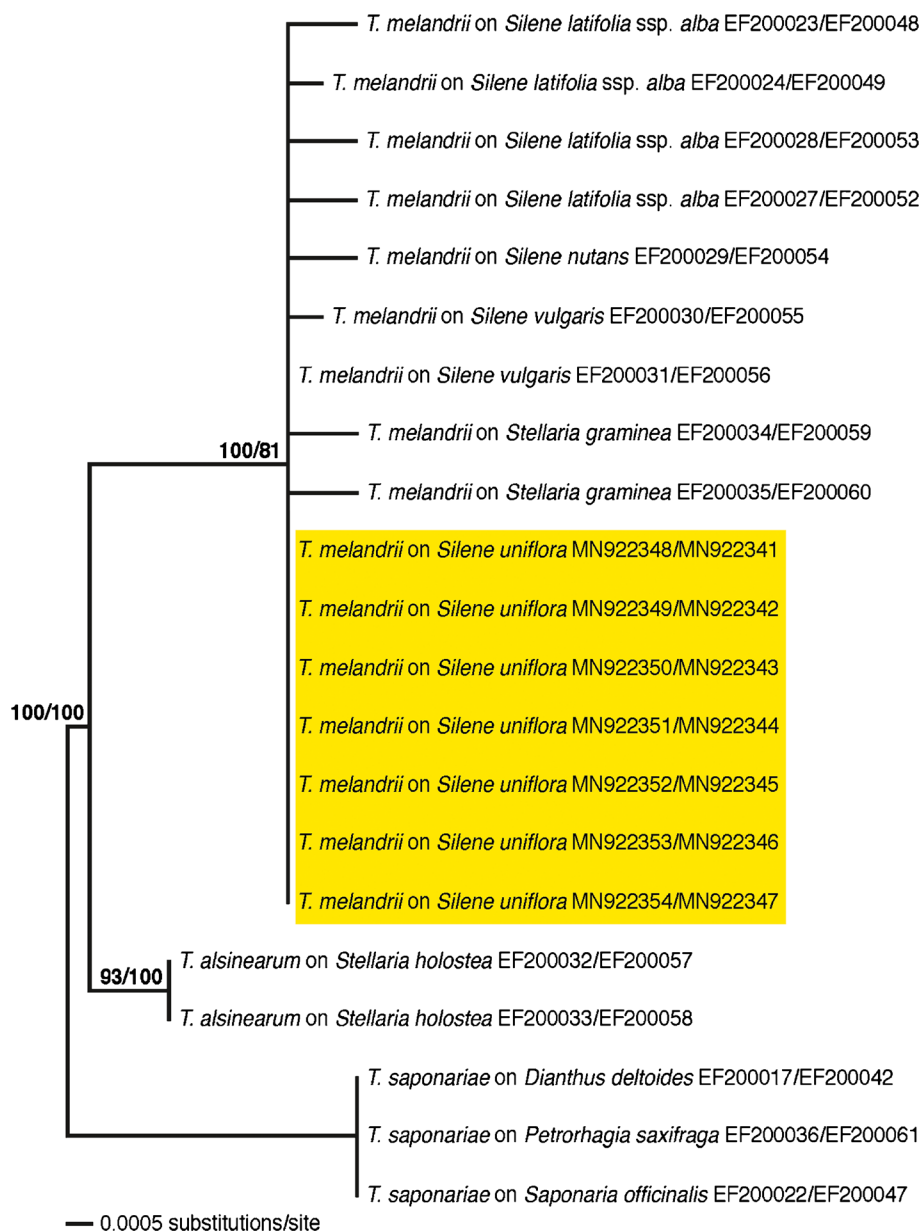
## Discussion

*Thecaphora melandrii* is seen to be a scarce species, with relatively few records, and is apparently restricted to Europe. It does, however, have quite a wide range,



**Table 4.** Literature records which have been excluded from maps and analyses in the main part of the paper. Some are known errors, most were recorded on hosts from which *Thecaphora melandrii* has not been confirmed by DNA analysis. Given the frequency of strict host specificity in smuts, it would be unwise to assume that these are the same species without further evidence.

Country	Location	Host	Source	Date	Notes
Germany	Hetsstedt, Burgörner	<i>Silene latifolia</i>	Scholz & Scholz (2012)		This record is apparently a misidentification of <i>Microbotryum lychmidis-dioicae</i> (Kruise <i>et al.</i> 2015).
Kazakhstan		<i>Silene alexandrae</i> B.Keller	Schwartzman (1962)		This would be a new host; confirmation from DNA required.
Spain	Santiago de Compostela and Padrón	<i>Silene legionensis</i> Lag.	Losa España (1952)		This would be a new host; confirmation from DNA required.
Spain	Valle de Ordesa	<i>Silene saxifraga</i> L., <i>Silene nutans</i>	Losa España (1948)	Aug. 1946	Reported in the anthers with no mention of other parts of the flower, which suggests that this (despite the name) refers to a species of <i>Microbotryum</i> , although <i>S. nutans</i> is an accepted host for <i>Thecaphora melandrii</i> . Piątek <i>et al.</i> (2013) describe <i>M. silenae-saxifragae</i> from the eponymous host. Several similar records from Spain are taken as referring to <i>Microbotryum</i> by Almaraz (2002).
USA	Mt. Majestic, Big Cottonwood Canyon, Utah	<i>Silene menziesii</i> Hook.	Garrett (1910); Jackson (1920)	27 Aug. 1906	All as ' <i>Sorosporium saponariae</i> ', confirmation from DNA required.
USA	nr Mt Rose, Nevada	<i>Silene argenti</i> S. Watson (as <i>S. watsonii</i> )	Jackson (1920)	21 July 1918	
USA	La Sal Mts, nr Gold Basin, Utah	<i>Stellaria curtsii</i> (Rydb.)	Garrett (1914); Jackson (1920)	8 July 1911	
USA	Golden, Colorado	<i>Pseudostellaria jamesiana</i> (Torr.) W.A.Weber & R.Hartm. (as <i>Stellaria jamesiana</i> )	Jackson (1920)	12 June 1905	
USA		<i>Pseudostellaria jamesiana</i> (as <i>Stellaria jamesiana</i> )	HUY2012	6 July 1974	This would be a new host; confirmation from DNA required.



**Fig. 4.** Bayesian inference of phylogenetic relationships within the sampled *Thecaphora* specimens: see *Phylogenetic analyses* under **Materials and Methods** for details. Numbers on branches before slashes are estimates for a posteriori probabilities, numbers on branches after slashes are ML bootstrap support values. Branch lengths were averaged over the sampled trees. They are scaled in terms of expected numbers of nucleotide substitutions per site. The specimens from England are highlighted in orange. *T.* = *Thecaphora*

particularly within central and eastern Europe, and here we demonstrate an extension of the known range to England. The *ITS* and *28S* regions of the genome show little variation, suggesting that *T. melandrii* is homogenous across this range. However, it has a wide host range including species in two genera within the Caryophyllaceae, and on quite distantly related species within the genus *Silene*. These conditions all suggest that it may be distributed more widely, both geographically and across hosts, and that further searching for this species would be valuable.

The coexistence of *Thecaphora melandrii* with species of *Microbotryum* is interesting; the *T. melandrii* infection is systemic and deforms the anthers (and other floral organs) in the host, presumably excluding plants from infection by *Microbotryum* spp. But it would be interesting to examine whether infection by *Microbotryum* spp. has any relation to subsequent infection by *T. melandrii*, and how these relations play out in a population over time. This would be a valuable supplement to the evidence for coexistence of different *Microbotryum* species on the same hosts in Abbate *et al.* (2018).



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