Dipterists Digest



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Cover illustration: *Clytocerus* (*Boreoclytocerus*) *dalii* (Eaton, 1893) (Psychodidae) from North Wales (photo Janet Graham), to celebrate the contribution to knowledge of Psychodidae by Phil Withers (see obituary and bibliography on pages 1–9). This species and 25 others, around a quarter of the presently known British species, were newly described in the 1890s by Rev. Alfred Eaton (1845–1929), vicar of Shepton Montague in Somerset, who distinguished 41 species in his works on this family. The bright patterns of many species in life, which may have attracted him to their study, are lost in slide-mounted specimens necessary for accurate determination.

Further species were recognised in subsequent key works by André Léon Tonnoir (70 species in 1940) and Paul Freeman (71 species in his 1950 Handbook). Scope nevertheless remained for Phil to add 24 species to the British Isles list (three of them as yet only recorded from Ireland), and like Eaton and Tonnoir substantially contributing to the present total of 99 species.

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Dipterists Digest is the journal of the **Dipterists Forum**. It is intended for amateur, semiprofessional and professional field dipterists with interests in British and European flies. All notes and papers submitted to Dipterists Digest are refereed. Articles and notes for publication should be sent to the Editor at the above address, and should be submitted with a current postal and/or e-mail address, which the author agrees will be published with their paper. Articles must not have been accepted for publication elsewhere and should be written in clear and concise English. **Contributions should be supplied either as E-mail attachments or on CD in Word or compatible formats.**

The scope of Dipterists Digest is:

- the behaviour, ecology and natural history of flies;
- new and improved techniques (e.g. collecting, rearing etc.);
- the conservation of flies;
- records and assessments of rare or scarce species and those new to regions, countries etc.;
- local faunal accounts and field meeting results, especially if accompanied by ecological or natural history interpretation;
- descriptions of species new to science;
- notes on identification and deletions or amendments to standard key works and checklists.

Articles should be in A5 format with text in 9-point and Times New Roman font, title 12 point and author's name 10.5 point, with 1.27cm (narrow) side margins. Figures should be drawn in clear black ink, about 1.5 times their printed size and lettered clearly. Colour photographs will also be welcomed. Figures and photographs should be supplied separately as hard copy or as jpegs at 300dpi.

Style and format should follow articles published in recent issues. A short Summary (in the form of an Abstract) should be included at the beginning of each article. References to journals should give the title of the journal in full. **Scientific names should be italicised.** Authors of scientific names should be given in full and nomenclature should follow the most recent checklist, unless reflecting subsequent changes. Descriptions of new species should include a statement of the museum or institution in which type material is being deposited.

Authors will be provided with a pdf of their contribution and, if requested, up to 5 separate copies of papers of two or more pages in length.

Enquiries about subscriptions and information about the **Dipterists Forum** should be addressed to the Membership Secretary, John Showers, 103 Desborough Road, Rothwell, Kettering, Northamptonshire NN14 6JQ, showersjohn@gmail.com

PHIL WITHERS 1954 - 2020

Phil had a long involvement with *Dipterists Digest*. Having been the author of a handbook to the British Psychodidae, published as an issue of the journal in 1989, he was a guest editor in 1993 for issue No. 13 in the First Series, which had preimaginal stages and rearing as a theme. That was while Derek Whiteley, who founded the journal, was still the editor. He then joined the editorial panel in 1994 when Graham Rotheray became editor and remained in that role for the rest of his life. Apart from his Moth Fly handbook, he contributed 25 other articles to this journal on a wide range of subjects. Some informal eulogies appeared in the 2020 Autumn Bulletin. Here an obituary, including an appreciation of his contribution to dipterology, and a bibliography are provided.

Peter Chandler

Phil Withers died suddenly of a heart attack on Sunday 5 July 2020, aged 65, while working with his friend Jocelyn Claude in Eastern France on the identification of French Pipunculidae.

Phil was born in Southend, Essex, on 7 August 1954 and lived all of his childhood in the east of England. His interest in Natural History was an early fixture in his life, at least from adolescence and he graduated in biological sciences in 1975. He took a keen interest in conservation and was very active in the Norfolk Wildlife Trust. At that time Phil lived in Diss, Norfolk and studied a number of Diptera families (See Bibliography). This is where his entomological knowledge and fieldwork really took flight and, more especially, on two wings.

He became a reference point locally in Norfolk, and later nationally, for his chosen fly group, the moth flies (Psychodidae). Phil's introduction to this group of Diptera took place at Malham Tarn Field Centre in the early 1980s, where Henry Disney was his mentor (Disney *et al.* 1982). He was a regular attender at Henry's annual course on Diptera where he learnt to slide-mount these small Diptera. This set Phil off working on a new set of families. He continued to send Henry specimens of Phoridae until recently. Phil made an outstanding contribution to the study of the European and British fauna of moth flies (Psychodidae), adding some 24 species to the British Isles list. In 1989, he published a key to this family as an issue of *Dipterists Digest (First Series)* No. 4 and the draft of a revised edition was released for testing in 2012.

Active fieldwork took Phil all round France and to other parts of Europe and he wrote papers and compiled species lists for a number of families of Diptera in the British, Irish and French fauna. In addition to work published in *Dipterists Digest* he authored some 30 papers in France, jointly and by himself, some of these with *la Société Linnéenne de Lyon* [see Bibliography for details].

Professionally, Phil worked first as a Health and Safety Inspector but later his interest was in Quality Assurance (QA), mostly in relation to preclinical studies performed for the pharmaceutical industry. He worked for a large preclinical laboratory in the UK, then, from 1991 onwards, his work took him to France to take up a QA leadership post in a research organisation based near Lyon. He established his own consultancy company and was active in the French professional society for QA. He was a very well-respected QA expert and a trainer, work which required extensive international travel.

In France he lived first at Le Bourg, Charnay, Lozanne, and then in about 2000 he moved to Sainte Euphémie, where, in June 2006 a small group of Dipterists Forum members visited him to work on his local patch, the Fondation Pierre Vérots Nature Reserve, and some other French sites (*Bulletin of the Dipterists Forum* Autumn 2006 + Spring 2007 No. **62/3**, pp 21-22). A list of the Diptera of this reserve was published in *Dipterists Digest* (Withers 2007).



Phil Withers on fieldwork in the Camargue, France, 9 May 2017, with (above right) Christophe Lauriaut (photos Gabriel Nève).



Phil Withers identifying French Pipunculidae at Bief du Fourg, 4 July 2020 (photos Jocelyn Claude).

Anyone who was in his company for long would realise Phil had a distinctive dry sense of humour, coupled with an energetic and enthusiastic nature. Apart from his professional work, and his work with the Diptera, he had a number of other strong interests. He was a guitarist and singer in a local Blues band "*1-bleu-3*" where he also played the harmonica. The group played many gigs, won local competitions, and produced 3 CDs. He was an ardent cruciverbalist, not only solving crosswords but also sometimes setting them. He was also an avid reader, especially in the fields of ecology and evolutionary biology and also had a penchant for sci-fi and detective novels.

Phil left a family including two daughters and a grandson after whom he named a sciomyzid *Renocera lyami* (Withers 2009).

John Kramer and David Long

Phil arrived in Remoray on the recommendation of Martin C.D. Speight at the end of 2011. A fruitful collaboration was then initiated, Phil taking care of part of the determinations of the families of Diptera he knew and progressively training the staff at the two nature reserves (Ravin de Valbois and Lac de Remoray) on several other families. Between 2012 and 2019 we organised 10 training sessions with him; each staff member specialised in certain families, worked on the fauna of the two Nature Reserves and also received material from other sites in the network, which had set up SyrphtheNet studies, and thus built up a reference collection of species with the support and validation of Phil. Subsequently, each staff member has built up contacts with other relevant specialists of Diptera families. At the same time, the sorting process continued and several families were sent to the vast network of specialists that Phil had built up over the past 40 years. In the end, 2,338 species of Diptera have been inventoried to date in the two national nature reserves of the Doubs, for 88 genera, including 1933 in Remoray and 958 in Valbois. Phil has made a considerable contribution to this consolidation of knowledge and the birth of a strong local dynamic on Diptera!

Jocelyn Claude

Phil's collection will be deposited, according to his will, at the Muséum d'Histoire Naturelle in Geneva (Switzerland). Before that, Jocelyn Claude will record it for publication. Phil's "natural sciences" library has been classified and registered, at the Maison de la Réserve in Labergement-Sainte-Marie (France, 25160). More than 700 books, as well as reprints and photocopies of articles have been integrated, and this collection of national importance, is available and can be consulted on request (http://www.maisondelareserve.fr/accueil.php).

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- Withers, P., Lauriaut, C. and Tissot, B. (in preparation) Mise à jour de la faune de France des Scathophagidae (Diptera)

Species named after Phil Withers

Cratyna (Spathobdella) phili Menzel, 2002 (Sciaridae) Megaselia withersi Disney, 2008 (Phoridae) Thornburghiella withersi Wagner, 1994 (Psychodidae) Triphleba withersi Disney, 1994 (Phoridae) Pseudosmittia withersi Langton, 2012 (Chironomidae) Protearomyia withersi MacGowan, 2014 (Lonchaeidae)

Species described as new to science by Phil Withers

Telmatoscopus vaillanti Withers, 1986 (Psychodidae) (syn. of Seoda morula (Eaton, 1893)) Telmatoscopus ellisi Withers, 1987 (Psychodidae) (also placed in Parajungiella) Suillia dawnae Withers, 1987 (Heleomyzidae) (named for his wife Dawn) Psychoda buxtoni Withers, 1988 (Psychodidae) Psychoda jezeki Withers, 1988 (Psychodidae) (also placed in Chodopsycha) Panimerus goodi Vaillant & Withers, 1992 (Psychodidae) Pericoma barremica Vaillant & Withers, 1993 (Psychodidae) Pericoma calcifera Vaillant & Withers, 1993 (Psychodidae) Pericoma vestita Vaillant & Withers, 1993 (Psychodidae) Tonnoiriella disneyi Withers, 1997 (Psychodidae) (syn. of T. obtusa (Tonnoir, 1919)) Rhexoza lvdiae Withers, 2004 (Scatopsidae) (named for his younger daughter Lydia) Trichomyia minima Withers, 2004 (Psychodidae) Renocera lyami Withers, 2009 (Psychodidae) (named for his grandson Lyam) *Pseudacteon charnavensis* Disney & Withers, 2009 (Phoridae) Periscelis nigra minor Papp & Withers, 2011 (Periscelididae) *Neoalticomerus fabricius* Withers & Papp, 2012 (Odiniidae) Lonchaea bispicata MacGowan & Withers 2014 (Lonchaeidae) Tomosvaryella osito Kehlmaier, Gibbs & Withers, 2019 (Pipunculidae) Cephalops (Semicephalops) brachium Kehlmaier & Withers, 2019 (Pipunculidae) Tonnoiriella aurasica Wagner & Withers, 2020 (Psychodidae) Tonnoiriella italiae Wagner & Withers, 2020 (Psychodidae) Tonnoiriella ikariae Wagner & Withers, 2020 (Psychodidae) Tonnoiriella andradei Wagner & Withers, 2020 (Psychodidae) Tonnoiriella rhodesica Wagner & Withers, 2020 (Psychodidae) Tonnoiriella goncalvesi Wagner & Withers, 2020 (Psychodidae) Forcipomyia pyrenaica Szadziewski, Dominiak & Withers, 2020 (Ceratopogonidae) Monohelea mediterranea Szadziewski, Dominiak & Withers, 2020 (Ceratopogonidae) Tomosvaryella estebani Withers & Claude (submitted) (Pipunculidae)

Two craneflies (Diptera, Tipulidae) at lepidopterist's sugar – Craneflies (Diptera, Tipulidae) have long been known to be attracted to lepidopterist's sugar (Stubbs, A. 1992. Provisional atlas of the long-palped craneflies (Diptera: Tipulinae) of Britain and Ireland. Biological Records Centre, Cambridgeshire. http://nora.nerc.ac.uk/id/eprint/7499/1/Long-palpedCraneflies.pdf); however, observations are relatively few, and unpublished. Those known to the authors are observations from the Netherlands of *Metalimnobia (Metalimnobia) quadrimaculata* (Linnaeus, 1760) collected this way (Pjotr Oosterbroek *pers comm.*), unnamed *Nephrotoma* species collected at sugar in China (Qicheng Yang *pers. comm.*) and on Saturday 28 September 2019 at Ayr in Scotland (as part of the three day National Moth Night 2019), three craneflies were noted at wine ropes but the species were not determined (Eric Rietveld *pers. comm.*).

On the evening of 16 July 2020, the authors were wine-roping and sugaring for moths in a garden near Blewbury, Oxfordshire (SU5385) (V.C. 22, Berkshire). Conditions were still and warm (approximately 19 °C), and observations were made between approximately 10.00pm – 11.30 pm. A lepidopterist's sugar mixture (sugar / cider / treacle) had been applied to a piece of remnant veneered timber approximately 15 cm wide and 1 m tall that was leant up against a hedge. This soon attracted 1 *Pephrotoma flavescens* (Linnaeus, 1758), which stayed around 10 minutes, and then 1 *Pipula (Lunatipula) peliostigma* Schummel, 1833. The latter specimen was captured for identification. Due to the sugaring being carried out at night, there were no direct observations of exactly what the craneflies were doing but presumably they were dabbing their palps on the sugar mixture as cranefly mouthparts allow no more than ingestion of liquids.

It is known that flies respond to the chemicals present in the environment, using olfactory organs located primarily on the antennae and sometimes on the palps, enabling them to find food, mates, or breeding medium (Borror, D.J et al. 1989 Introduction to the Study of Insects. Cengage Learning Inc. Boston, Massachusetts). Fruit fly (Drosophilidae) antennae and palps are covered with a very large number of sensilla which house the olfactory receptor cells (ORC); in particular, the third segment of the antenna and the maxillary palps contain approximately 1200 and 120 olfactory sensory neurons respectively (Boto, M.F. et al. 2013. Elements of olfactory reception in adult Drosophila melanogaster. The Anatomical Record (Hoboken). 2013 Sep; 296(9), 1477-88. doi: 10.1002/ar.22747. Epub 2013 Jul 31. PMID: 23904114.). Though the authors could find no specific papers relating to the sensory biology of Tipulidae antennae or palps, in adults it is known that Nephrotoma suturalis (Loew, 1863) larvae house several sensory sensilla upon their formative antennae and palps, which are porous and enable them to sense their immediate environment within the soil (Baker, G.T. et al. 2000. Cuticular sensory receptors on the antenna and maxillary palps of a fly larva, Nephrotoma suturalis (Diptera: Tipulidae). Invertebrate *Biology* **119**, 342-348. https://doi.org/10.1111/j.1744-7410.2000.tb00020.x). It is therefore likely that adult Tipulidae sensilla enable them to pick up the volatile chemicals within the lepidopterists' sugar mixture, and that craneflies are on occasion attracted to these. More published observations are needed and the authors have engaged the moth trapping community to highlight further examples and to collect specimens - PETE BOARDMAN and VICKY GILSON, Natural England Field Unit, Natural England Mail Hub, Worcester County Hall, Spetchley Road, Worcester, WR5 2NP, England, U.K.: Pete.Boardman@naturalengland.org.uk; Vicky.Gilson@naturalengland.org.uk

Sexual colour dimorphism and wing venation variation in the leafmining fly *Aulagromyza heringii* (Hendel) (Diptera, Agromyzidae)

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Summary

The leaf-mining agromyzid *Aulagromyza heringii* (Hendel, 1920) is reported to show distinct sexual colour dimorphism, a characteristic previously overlooked. The observation is based upon a long series of adults reared over a four-year period and specimens deposited at the Natural History Museum, London. Details and examples are given, along with observations regarding the species' variable wing venation. A provisional key to British *Aulagromyza* and a brief note on the biology of *A. heringii* are also included.

Introduction

Aulagromyza heringii (Hendel, 1920) [frequently misspelt as *heringi*], a widespread and relatively common leaf-miner of ash (*Fraxinus excelsior*) in the United Kingdom, is stated to possess 'yellow third antennal segment, somewhat darkened distally' (Hendel 1931-1936; Papp and Černý 2016; Spencer 1972 and 1976a).

Although this is certainly the case, examination of specimens reared between 2017 and 2020, and material held at the Natural History Museum, London, reveal that darkening of the third antennal segment is specific only to the female, representing a rare example of sexual colour dimorphism in the Agromyzidae. The reared material also highlights variation in the species' wing venation, regarding the presence and position of the second cross-vein.

Discussion

Sexual colour dimorphism

The distinctive larval leaf mines of *A. heringii* were collected in October and November, from various localities across England, between 2016 and 2019. This resulted in 110 adults being successfully reared $[30\beta, 80\varphi]$ in total. Upon examination of every specimen, each year, it became apparent that a distally darkened third antennal segment is only present in the female; all 80 reared females possess a darkened third antennal segment, with all 30 males possessing a pure yellow third antennal segment.

There are 25 pinned specimens of *A. heringii* [incorrectly labelled as *heringi*] held in the British & Irish Agromyzidae collection at the Natural History Museum, London. The collection was recently digitised (Crowther *et al.* 2019), allowing it to be examined remotely; 123 possess an all yellow third antennal segment, 112 possess a darkened third antennal segment [one specimen is too poorly mounted, one specimen is missing the head], confirming the regular presence of sexual dimorphism in colour in this species.

Darkening is present on the inside and the outer face of the third antennal segment and although the amount [from slightly more than ¹/₄ (Fig. 1, right), up to ³/₄ (Fig. 1, left) of the third antennal segment] and strength [from greyish to almost pure black] of darkening is variable (Fig. 1), it is always extremely conspicuous, never resembling the all-yellow third antennal segment of the male (Fig. 2).

Sexual dimorphism is a characteristic infrequently observed in the Agromyzidae; it chiefly affects the size and pubescence of the third antennal segment [as in *Liriomyza commelinae* Frost, 1931], the palps, the stridulatory organ in *Liriomyza* and the amount and positioning of

pubescence of the eye in males of some *Melanagromyza* species (von Tschirnhaus 1991). Also, males of *Ophiomyia pinguis* (Fallén, 1820) lack the lower orbital bristles [*ori*] and all female *Ophiomyia* species lack the vibrissal fasciculus which is present in the males of many of its species.

Sexual colour dimorphism is seemingly even rarer within the Agromyzidae, *Nemorimyza posticata* (Meigen, 1830) [posterior end of abdomen whitish-yellow in male, entirely black in female] and *Phytoliriomyza cyatheae* Spencer, 1976 [male being markedly paler than the female (Spencer, 1976b)] being other rare examples.



Fig. 1. Variation in darkening of third antennal segment in female *A. heringii;* from significantly darkened (left) to least darkened (right).



Fig. 2. Uniform coloration of male A. heringii third antennal segment.

Variation in wing venation

When utilising the keys in the most frequently used literature (Papp and Černý 2016, Spencer 1972 and 1976a), the presence of the second cross-vein (*tp* or M-M or *dm-Cu*) is essential in reaching *A. heringii*. Spencer (1990) also mentioned that the wing venation 'is distinctive, with the outer cross-vein present'. However, the cross-vein can sometimes be absent; 23 [83, 159] of the reared specimens are lacking the second cross-vein (Fig. 3, upper), whilst two female specimens possess the second cross-vein only on one wing.

The aforementioned literature also state that the position of the second cross-vein is 'aligned with the first' (Papp and Černý 2016) or 'normally in continuation of first' (Spencer 1972 and 1976a). Nevertheless, the positioning of this vein can be variable; of the 87 reared specimens possessing the second cross-vein, 51 had the cross-vein in perfect continuation of the first, 21 had the cross-vein situated before the first (Fig. 3, lower), with 15 specimens having the cross-vein positioned distad of the first. Such variation, although infrequent, is well observed in the Agromyzidae (Gibbs and von Tschirnhaus 2019, Nowakowski 1962, Warrington 2018).



Fig. 3. Variation of wing venation in *A. heringü*; upper, second cross-vein absent; lower, second cross-vein present but not in continuation of first.

If the most recent key to *Aulagromyza* (Papp and Černý 2016) is used, specimens lacking the second cross-vein initially run to couplet 16; then, if the male genitalia are examined, couplet 19, where, owing to the rusty-reddish longitudinal bands on the mesonotum, *A. populicola* (Haliday, 1853) would be the determination; however, the male genitalia and dark occiput are different to that of *A. heringii*. Interestingly, if the male genitalia are not examined, the first option at couplet 16 is *Amauromyza fraxini* (Beiger, 1980) [originally described in *Paraphytomyza* (a junior synonym of *Aulagromyza*; von Tschirnhaus (1991) revived the genus

Aulagromyza following the rediscovery of its type species)]. That species shares some similarities with *A. heringii*; the costa extending to, or slightly surpassing, vein R_{4+5} [unusual in *Amauromyza*], second cross-vein absent, is of similar size and is one of only three Palaearctic species [others being *Aulagromyza fraxinivora* (Sasakawa, 1961) and *A. heringii*] known to utilise *Fraxinus* as a host [larval feeding of a *Phytobia* species has also been detected (Spencer 1990)]. However, these three *Fraxinus* miners are readily separated on coloration; *A. fraxini* is an almost entirely dark species; *A. fraxinivora* has the mesonotum brownish-black, densely dusted with grey, with the occiput and dorsal halves of postgenae dark brown; *A. heringii* is mostly yellow.

The larval leaf mines of *A. fraxini* and *A. fraxinivora* can bear some resemblance to those infrequently created by *A. heringii*; however, they do not start with a 'pustule', nor do they possess conspicuous primary and secondary feeding lines, features typical in *A. heringii*.

Provisional key to the British Aulagromyza species

1.	Apex of wing lies between veins R4+5 and M1+22
-	Apex of wing at vein M ₁₊₂ 12
	Orbital setulae totally absent
-	Orbital setulae present [inc. minute or scarce]7
3.	Scutellum yellow centrally [even if extremely faint]4
-	Scutellum uniformly dark [grey or black]5
4.	Third antennal segment and palps yellow; mesonotum with three longitudinal stripes [orbital
	setulae infrequently present but always minute]Aulagromyza trivittata
-	Third antennal segment [may be slightly yellowish at its base] and palps black; mesonotum
	uniformly greyish-blackAulagromyza anteposita
5.	3 +1 <i>dc</i> , jowls angular, proboscis normal
	2 + 0 dc, jowls rounded, proboscis conspicuously lengthenedAulagromyza orphana
6.	Frons light yellow, notopleuron yellowish, all antennal segments black
-	Frons dark, notopleuron at most brownishAulagromyza lucens
7.	2 or 3 pairs of postsutural <i>dc</i>
-	5-7 <i>dc</i> pairs10
8.	Scutellum at least yellow centrally, mesonotum solid, without longitudinal stripes
-	Scutellum bright yellow, frons and orbits yellow, mesonotum with longitudinal stripes
-	Scutellum dark
9.	Frons reddish, mesonotum black, weakly shiningAulagromyza buhri
-	Frons darker, blackish or dark brown, mesonotum matt greyish-black
	Aulagromyza luteoscutellata
10	. Presutural <i>dc</i> pairs strong [twice as long as adjacent <i>acr</i>], all knees bright yellow
	Aulagromyza similis
-	Presutural <i>dc</i> pairs only slightly longer than adjacent <i>acr</i> , at most fore knee yellow11
11	. Fore knee yellowAulagromyza hendeliana
-	Legs all black
12	. Scutellum entirely dark, black or grey
-	Scutellum largely yellow; frons and femora bright yellow
13	. Second cross-vein present [even if present only on one wing]
-	Second cross-vein absent
14	. Mesonotum with 3 rusty-reddish longitudinal bands, otherwise entire imago mostly all yellow

- Mesonotum black or with 3 black bands1
15. Occiput yellow [third antennal segment darkened in female]Aulagromyza heringu
- Occiput darkAulagromyza populicol
16. Mesonotum with dark area solid, shining black, narrowly yellow adjoining scutellum and at
hind corners, all setae yellowAulagromyza tremula
- Mesonotum with dark area divided into bands, setae dark1
17. Scutellum and mesopleura entirely yellow, mesonotum matt grey, with 3 distinct bands
- Scutellum at least narrowly dark outside basal scutellars, mesopleura faintly grey on lowe
margin or more conspicuously blackish-grey, mesonotum matt grey or darker, black bu
distinctly divided into bandsAulagromyza popul

Biology

The biology of *A. heringii* isn't completely known and is somewhat puzzling. Griffiths (1959) stated larvae only in October [in Britain], Hering (1957) cited between September and November, with Spencer (1976a) mentioning 'the autumn'. More recent observations give September to November (Ellis 2017; records held in the National Agromyzidae Recording Scheme database [UK] and *pers. obs.*). No early season or summer generation has been observed.

Spencer (1976a) mentioned 'larvae collected in November produced flies two weeks later'; however, this must be considered an exceptional instance and unrepresentative of its true biology; data obtained from the British & Irish Agromyzidae collection [NHM, London], Skuhravá and Roques (2000) and my extensive collecting, observations and rearings, find adults are present only in the spring [when they can be observed 'in copula' *pers. obs.*]. Therefore, as larval mines do not appear until the autumn, either the egg or early instar larva must enter a diapause until the autumn.

Where pupariation occurs is also interesting. Hering (1957), Robbins (1990), Spencer (1972) and von Tschirnhaus (Ellis 2017) state that pupariation occurs externally, whereas Allen (1958), Ellis (2017), Skuhravá and Roques (2000) and I [based on *pers. obs.* and the many images/notes sent to me by other British naturalists] note that pupariation is always within the mine, with the anterior spiracles penetrating the epidermis, akin to *Chromatomyia* spp. Ellis (2017) discussed the possibility of the internal-pupariating '*heringii*' being an undescribed species; however, dissection and detailed examination of the male genitalia of my reared material confirms that this is not the case – larvae which pupariate within the mine, without doubt, belong to *A. heringii*.

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Comments on the taxonomic status of some British species of Syntormon Loew, 1857 (Diptera, Dolichopodidae)

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Summary

The paper reviews and justifies the inclusion of some species of *Syntormon* on the British list, in relation to recently described Palaearctic species and to old species over which there has been confusion. The genitalia and phallus of the males of all species are illustrated, some for the first time. *Syntormon monile* (Haliday in Walker, 1851) is redescribed from the type specimen and agrees with the usually accepted concept of the species. *Syntormon silvianus* Pârvu, 1989, is a junior synonym of *S. submonilis* Negrobov, 1975. The distinction between *S. submonilis* and *S. monile* is clarified. *S. luteicorne* Parent, 1927 is regarded as not British. Key features of the male of *S. macula* Parent, 1927 are illustrated. Specimens agreeing with *S. setosus* Parent 1938 have been found in Britain but here they are regarded as a colour form of *S. mikii* Strobl, 1899 and this species is not added to the British list. Notes are given on *S. fuscipes* (von Roser, 1840), *S. pumilum* (Meigen, 1824) and *S. sulcipes* (Meigen, 1824) where there is the possibility of confusion with recently described species or synonyms.

Introduction

Species of *Syntormon* are small dark green or yellow-marked flies found in a variety of wetlands. The genus may be recognised in both sexes by a small feature of the antennae, in which the pedicel (second segment) has a 'thumb' (conus) projecting into the inner face of the postpedicel (third segment). Males of most species are easily recognised by their long antennae, resembling those of some *Rhaphium*, but it was not until Robinson (1970) treated the genus as a member of the Sympycninae that the relationship with the Rhaphiinae was severed. Despite their attractive appearance and distinctive male secondary sexual characteristics, the genus has its share of taxonomic issues. Some morphological characters that are constant and useful in characterising other genera are variable in *Syntormon*, for instance, the scape (first antennal segment) may have dorsal hairs or be bare, and the acrostichal setae on the thorax may be uniserial or biserial. This variability extends to colour and is a potential source of taxonomic problems.

In this paper I discuss which species should be recognised in Britain as there have been several additions to the twelve included by d'Assis-Fonseca (1978). Species added since this work are *S. luteicorne* Parent, 1927, *S. pseudospicatum* Strobl, 1899, and *S. silvianum* Pârvu, 1989, while *S. setosum* Parent, 1938, has been recorded from Ireland. Grichanov (2013) reviewed the western Palaearctic species of *Syntormon* and provided the latest key. He identified several groups of species in need of closer examination so his key did not include these unresolved species or those known only from females. All four species recently added to the British list fall into Grichanov's untreated species so there is a need to establish their British status. Some uncontroversial species are also discussed here to clarify their taxonomic status but it is not my intention to resolve issues that do not affect the British fauna. The most important step, that of checking type specimens, has not been done in some cases so some conclusions remain tentative. The male genitalia of dolichopodids are often diagnostic so I have illustrated them for the British species.

Earlier keys by Parent (1938) and Negrobov (1975) that are occasionally consulted may cause confusion as they include erroneous synonyms for *S. pumilum* (Meigen, 1824) and *S. denticulatum* (Zetterstedt, 1843) proposed by Parent (1925) but criticised by Collin (1940). These corrections were not incorporated in the Palaearctic Catalogue (Negrobov 1991) but Chandler

(1998) included them in his checklist of the British Isles, and they are now accepted elsewhere (e.g. Pollet 2011, Grichanov 2013).

Methods

The genitalia of all British species were drawn from British specimens in my collection stored in alcohol, with the exception of a dry-pinned *S. macula* Parent, macerated in dilute potassium hydroxide, and mounted temporarily in a jelly of glycerine and gelatine (Ackland 2015). They were drawn with the aid of a drawing tube (camera lucida) at x200 on a compound microscope. The capsule was drawn in lateral and ventral views, then the phallus was removed and also drawn from these two aspects. In the figures the morphologically ventral surface is uppermost, so the description of the figures appears to be upside down. Antennae and legs were drawn using the same procedure as for the genitalia, with the exception of the femora of a pinned *S. macula* drawn at x80 under a binocular microscope. Terminology follows Sinclair and Cumming (2006) and Cumming and Wood (2017). Information on British distribution and habitat affinity is derived from my own collecting and from data sent to me in my capacity as organiser for dolichopodids in the national recording scheme for empidids and dolichopodids (Dipterists Forum 2019). The data are held privately and are currently not yet publicly available. Distribution maps use data up to 2018.

I treat the gender of the genus *Syntormon* as neuter (Drake and Welter-Schultes, in press) although I use the gender given by the original authors when referring to the name as they gave it (as in the following list). I realise that this will lead to great confusion since the gender has swung between masculine and neuter (Chandler 1998, 2013; Grichanov 2013) but there is no justification, least of all from Loew who proposed the genus, for it being masculine. The treatment of the name *submonilis* is discussed under the account for this species.

Species of *Syntormon* with their authorities mentioned in this paper are: *aulicum* (Meigen, 1824); *bicolorellum* (Zetterstedt, 1843); *bulgariensis* Negrobov & Kechev, 2012; *denticulatum* (Zetterstedt, 1843); *dobrogicus* Pârvu, 1985; *filiger* Verrall, 1912; *francoisi* Meuffels & Grootaert, 1999; *fuscipes* (von Roser, 1840); *giordanii* Negrobov & Matile, 1974; *grootaerti* Maslova, Negrobov & Selivanova, 2017; *iranicus* Negrobov & Matile, 1974; *luteicornis* Parent, 1927; *macula* Parent, 1927; *macula* subsp. *mediterraneus* Grichanov, 2013; *metathesis* (Loew, 1850); *mikii* Strobl, 1899; *monile* (Haliday in Walker, 1851); *pallipes* (Fabricius, 1794); *parvus* Vaillant, 1983; *pennatus* Ringdahl, 1920; *pilitibia* Grichanov, 2013; *spicatum* (Loew, 1857); *submonilis* Negrobov, 1975; *sulcipes* (Meigen, 1824); *tabarkae* Becker, 1918; *tarsatum* (Fallén, 1823); *zelleri* (Loew, 1850).

Results and Discussion

The genitalia of British Syntormon

The genitalia of some western Palaearctic *Syntormon* have already been illustrated; Table 1 lists those that are relevant to the British fauna, although other west Palaearctic species have been illustrated (e.g. *S. pilitibia* in Grichanov 2013, *S. pennatus* in Negrobov *et al.* 2013a). Several of these are potentially or actually relevant to the British fauna. A century ago, Becker (1918) showed the whole genital capsule of many species, often with the tip of the phallus extruded, but these are not adequate to distinguish the species. Several later authors have illustrated or photographed macerated genitalia in lateral and often ventral view, where the phallus is sometimes clearly shown. Among these are some widespread species that were drawn to illustrate the differences with similar species being newly described. Only Pârvu had extracted the phallus and drawn it clearly for the three species listed in Table 1, although Negrobov and Matile (1974)

may be the first authors to have illustrated the extracted phallus of *Syntormon*, in this case for their two newly described species *S. giordanii* and *S. iranicum* from Iran in the eastern Palaearctic.

Table 1. Species of west Palaearctic *Syntormon* whose genitalia have been illustrated and which are relevant to the British fauna. Notes: ¹ Grichanov (2013) suggested that *dobrogicus* is a synonym of *metathesis* (Loew, 1850). ² This synonymy is discussed later.

Species	Reference	Notes
bulgariensis	Negrobov and Kechev 2012	compared with sulcipes
denticulatum	Becker 1918	capsule
¹ dobrogicus	Pârvu 1985	compared with <i>giordanii</i> Negrobov & Matile, 1974 (eastern Palaearctic)
francoisi	Vaillant 1983, as parvum	capsule and surstyli
filiger	Negrobov et al. 2013b	capsule
fuscipes	Becker 1918	capsule
	Grichanov 2001	capsule
macula subsp. mediterraneus	Grichanov 2013	photograph
pumilum	Becker 1918	capsule
-	Maslova et al. 2017	compared with <i>grootaerti</i> Maslova, Negrobov & Selivanova, 2017 (eastern Palaearctic)
spicatum	Vaillant 1983	capsule and surstyli
sulcipes	Negrobov and Kechev	compared with bulgariensis Negrobov &
-	2012	Kechev, 2012
submonilis	Negrobov 1975	capsule and surstyli
	Pârvu 1989	as ² silvianum, compared with monile
tarsatum	Becker 1918	capsule
	Buchmann 1961	capsule
	Pârvu 1984	-
zelleri	Becker 1918	capsule

The structure is consistent in all species (Fig.1a). A transparent hypandrium lies dorsal to the phallus which, at its anterior near-basal part, is supported by an H-shaped postgonite at a section of the phallus that is exceptionally thin-walled and often not possible to discern. The distal half and tip of the phallus is often specific. In most British species, this section is sinuous and helically twisted at the tip, which is easier to appreciate in ventral view, and in a few species the phallus is accompanied by short or long rods that are either clearly part of the phallus or perhaps part of the hypandrium. I use the term 'rod' vaguely to avoid any misconception of homology with appendages found in other Empidoidea. The ventral surstylus is blunt-ended and bears at least one strong ventral seta and several fine hairs; the dorsal surstylus is tapered and bears a long dorsal seta. In lateral view, the surstyli and their setae show small consistent differences between species. The terminology of these lateral appendages follows Sinclair and Cumming (2006), confirmed by Scott Brooks (*pers. comm.*), both being surstyli rather than the dorsal appendage being an epandrial lobe as in Negrobov *et al.* (2017) for *Sympycnus*. The cerci are unremarkable and vary little between species.

Fig. 1. *Syntormon* male genital capsule and extracted phallus in ventral and lateral view, and in ventral view for *S. pumilum*. Species names are given beside each illustration. Scale bar at top of each drawing is 0.1mm.

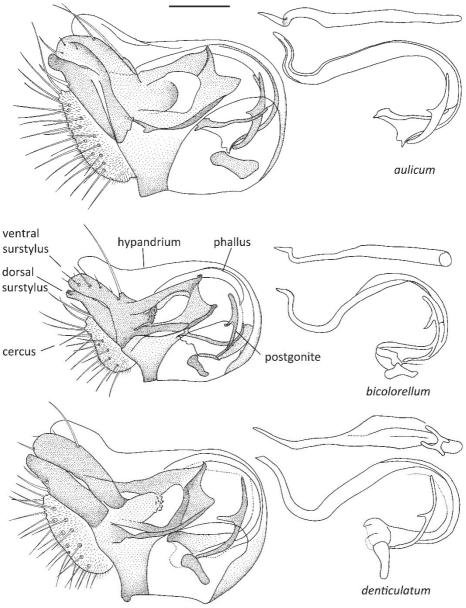


Fig.1a

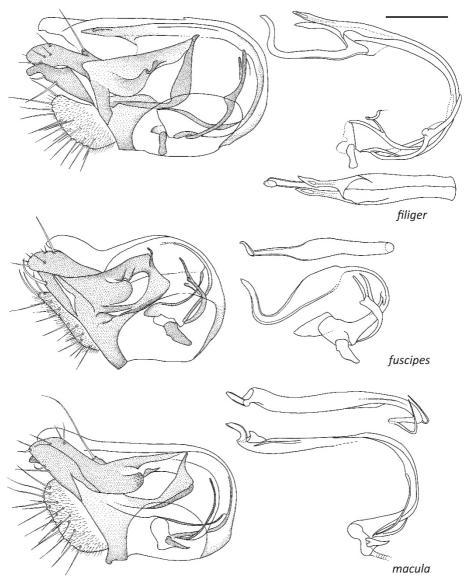
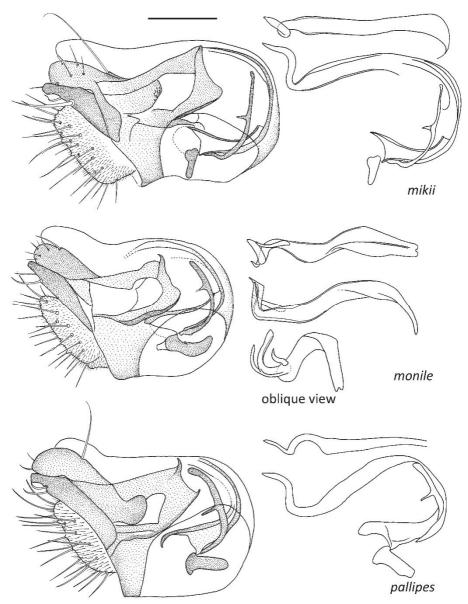
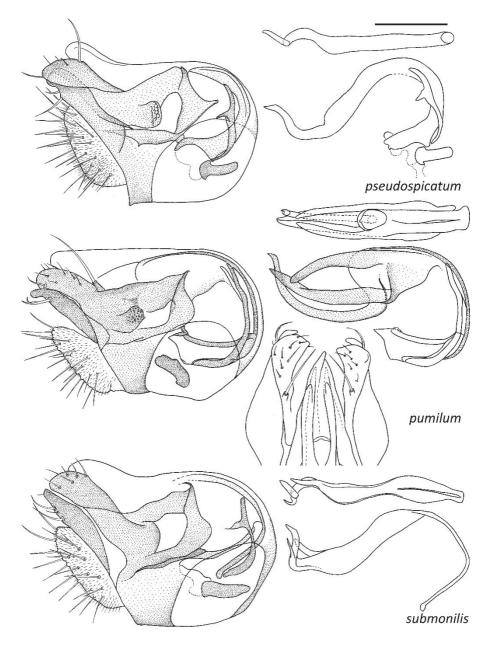


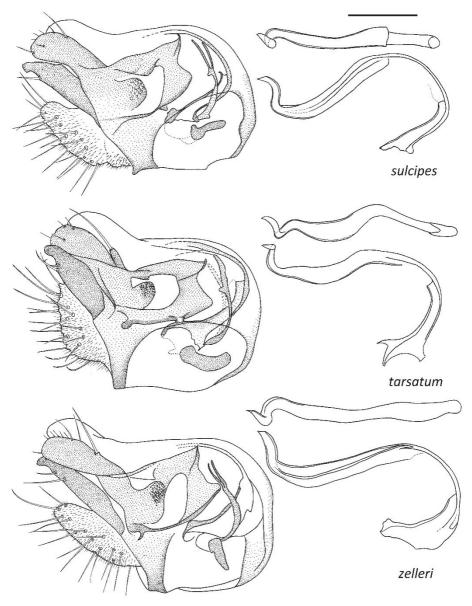
Fig.1b













Externally and at low magnification using a binocular microscope there appear to be rather trivial differences between the species, so the genitalia are of limited use in routine identification. Ventral views of the whole capsules added little to differentiating the species, so only lateral views are shown (Fig. 1). At high power, the species can be grouped on the basis of the shape of the phallus tip, whether the rods are close to the tip or more basal, and variation in the long seta at the base of the ventral surstylus (Table 2). These groups do not correspond to those based on other male secondary sexual characters, such as antennal shape or leg ornamentation, so probably have no phylogenetic significance. As with the external features, these differences are of little practical value in differentiating species as the phallus is tiny and difficult to see clearly without extracting it from the capsule, which cannot be done without some damage to the capsule. Differences between species in the lateral profile of the surstyli are probably more constant as it is usually possible to orientate the capsule at the same angle for viewing. Viewing dorsally, however, is less satisfactory as it is possible to introduce a different shape in the surstyli with a small tilt of the capsule.

The rods of the phallus deserve describing. The trifid tips of *S. monile* and *S. submonilis* consist of two rods slightly shorter than the phallus, to which they clearly belong. These phalli are almost identical so this pair of species is distinguishable on external features (their front tarsi) but not using the genitalia. The arrangement has been illustrated for *S. monile* in an oblique view, looking slightly along the shaft, when the three points of the tip are more apparent (Fig. 1c). The long rods of *S. filiger* and *S. pumilum* may be part of the hypandrium (Fig. 1b, d). They may perhaps act as guides for the phallus, particularly those of *S. pumilum* whose two pairs of rods almost surround the phallus. The rods in *S. filiger* appear to have ducts opening at their tips suggesting that they may not be for support but have another function, whereas no ducts were visible in the rods of *S. pumilum*.

		Phallus shape				
		helical tip	helical tip	helical tip	trifid tip	
			with apical	with long		
			flange	rods		
	long basal seta	aulicum,	macula	filiger,		
	on a distinct	bicolorellum,		pumilum		
	tubercle	mikii, tarsatum				
Ventral	long mid or	denticulatum,				
surstylus	more distal seta,	fuscipes, pallipes,				
chaetotaxy	no tubercle	pseudospicatum,				
		sulcipes, zelleri				
	no seta				monile,	
					submonilis	

Table 2. Species of Syntormon grouped by features of the male genitalia.

Notes on the British species

Syntormon fuscipes (von Roser, 1840)

There is no doubt that the species known in Britain as *S. fuscipes* is the same as von Roser's type specimen, as Denninger (1950) examined this specimen. It fitted Becker's (1918) concept of the same species, although Becker assumed this was Loew's *S. spicatum* owing to von Roser's unhelpfully brief description, which reads "tarsorum posticorum articula primo appendice furcato" (posterior basitarsus with forked appendix). Its brevity apparently also frustrated Becker

(1918) who, after quoting this, remarked "Das ist alles." and put the species aside. Becker gave figures of the hind leg and basitarsus of Loew's S. spicatum, and a key, so Denninger (who was clearly using Becker's work) was unlikely to have confused it with S. monile or S. submonilis which have a very similar forked hind basitarsus (Fig 7j). So Denninger seems correct in making the synonymy of Loew's S. spicatum with S. fuscipes, although his comments are scarcely more expansive than von Roser's (Hier zeigt die Art spicatus Loew die charakteristischen, in 2 bis 3 Spitzen gespaltenen Haken an den etwas gebogenen Hintermetatarsen). However, Grichanov (2013) restored S. spicatum from synonymy, apparently without having examined either type specimen, and stating that it is known only from Loew's type specimen. Becker (1918) thought that Loew had made mistakes in his description of the haired pedicel which is bare in other species in this group, and the ratios of the hind tarsus segments, and these two discrepancies are Grichanov's basis for assuming the species is distinct. Such errors seem more likely than that Loew found the only known specimen of a new species, distinguished only by these two features. If Loew did indeed make a mistake about presence of hairs on the scape of his S. spicatum then this was odd since he incorrectly placed much emphasis on this character in his definition of dolichopodid genera.

Another west Palaearctic species with a forked hind basitarsus is *S. francoisi*, the replacement name for *S. parvum* described by Vaillant (1983). His description is very brief but he illustrated the antennae, hind basitarsus and genitalia. The form of the setae on hind basitarsus is the principal difference between *S. francoisi* and *S. fuscipes*, as the difference he gives for genitalia seem uninterpretable to me. Assuming that Vaillant was using Parent's (1938) well illustrated book, which is almost certain as he quotes Parent's incorrect species name for a *Rhaphium* in the same paper, then it is highly improbable that he mistook his new species for the *monile | submonilis* pair of species, although the setae on hind basitarsus of *S. submonilis* and *S. francoisi* are very similar (but distinctly different from those of *S. fuscipes* or *S. monile*; Fig. 7k, l, m). A possibility remains that Vaillant's species is *S. spicatum sensu* Loew, assuming that Grichanov is correct in retaining this species distinct from *fuscipes*. This cannot be resolved without examining type material.

Two figures of the genitalia of *fuscipes* have been published. Vaillant's (1983) shows the phallus having a simple end, as in British material (Fig. 1b), whereas Grichanov's (2001) clearly shows a trifid tip, resembling those of *S. monile* and *S. submonilis* as shown in my Fig. 1c and d, and the other appendages also more closely resemble these species than *fuscipes*. This is an Afrotropical specimen from Kenya or perhaps Burundi, and the detailed description given by Grichanov suggests that neither of the two phenotypes he describes is the *S. fuscipes* occurring in Britain. Their simple front tarsi preclude them being *S. monile* or *S. submonilis*. I checked several more British specimens of *fuscipes* to ensure that they all have the same genitalia as the example drawn and that they conform to the description in Parent (1938), and I am satisfied that they are the same as the mainland European species and not the same as the Afrotropical specimens. Grichanov (2001) stated that he has not seen specimens of European *S. fuscipes*, so his suggestion that his specimens represent a different species seems to be very likely. None of this affects the British fauna as our *S. fuscipes* remains the species recognised by Becker and later authors.

Syntormon luteicorne Parent 1927

Parent (1927) described *S. luteicorne* from a female; males have not been described. It remains a little-known species recorded only from Romania (Pârvu 1984), Czech Republic, France and Belgium although this last specimen cannot be located (Speight *et al.* 1995). As males are undescribed, there remains doubt about whether it is a valid species. Grichanov (2013) suggested that specimens identified as *S. luteicorne* may be aberrant or immature examples of a related *Syntormon* species in the group whose females have a pair of longish hairs on their face, for

example, *S. tabarkae* Becker or *Ceratops seguyi* Vaillant. It resembles *S. bicolorellum* and this has caused further problems since this species was once considered the only member of the genus *Bathycranium*. Speight *et al.* (1995) synonymised these two genera but, before that happened, Negrobov (1975) included *S. luteicorne* in his key to male *Syntormon*, distinguishing it from all others in the genus in his first couplet on the sole basis of its pale antennae. Negrobov probably assumed that this character was true for the unknown males as, at that time, it was the only species of *Syntormon* with pale antennae. But since *Bathycranium* and *Syntormon* have been synonymised, it is highly likely that the same male specimen with pale antennae would be identified as either *bicolorellum* or *luteicorne*, depending on whether it had been regarded as a *Bathycranium* or a *Syntormon*. As the detailed analysis of Speight *et al.* (1995) shows, there is no justification for treating these two genera as distinct.

Speight *et al.* (1995) re-described the types of *S. luteicorne* and *S. bicolorellum*, designated female lectotypes, and provided a key to distinguish the females, based on the colour of the tergites and calypter hairs, degree of protrusion of the lower half of the face and the length of the facial hairs. Parent (1927) gave the angle of the posterior cross-vein (dm-m, = dm-cu) as the only potentially useful feature to distinguish his new species *S. luteicorne* from other *Syntormon* but he did not compare it with *S. bicolorellum* which he regarded as belonging to *Bathycranium*. Over 30 pinned female specimens of *S. bicolorellum* in my collection agree with the characters given for this species by Speight *et al.* (1995), but the angle of vein dm-m varies from 'upright' to making an oblique angle with M_4 (=CuA₁). Therefore, of all the characters suggested by these authors that may also apply to males, only the colour of the tergites and calypter hairs are applicable (tergites extensively yellow in *S. bicolorellum*, green in *S. luteicorne*; calypter hairs yellow in *S. bicolorellum*, black in *S. luteicorne*); the facial characters are inapplicable to males whose faces have a very different structure. Whether *S. luteicorne* is a good species appears to be unresolvable on current information.

Syntormon luteicorne has a chequered history as a member of the British Isles fauna. It was added to the Irish list by Blackith *et al.* (1990) based on male specimens that they later concluded were *S. bicolorellum* (Speight *et al.* 1995), and this correction appeared in the British Isles checklist (Chandler 1998). In a little-known report, Howe (2002) added *S. luteicorne* to the Welsh fauna, based on two males collected in the same sample on the Gwent Levels (ST243799, 25.v.2000, leg. J.C. Deeming). These were sent by John Deeming to C.E. Dyte who identified them. I have examined one of these specimens, in the Cardiff Museum collection, and it is indistinguishable in all respects from *S. bicolorellum* in my collection. In particular, the calypter hairs are entirely pale, the abdomen is predominantly pale with dark bands almost identical to those illustrated by Blackith *et al.* (1990) for the specimens that they later identified as *S. bicolorellum*, and the wing is identical to that illustrated by Parent (1938) for *S. bicolorellum*. Its antenna is identical to that in Fig. 2 for *S. bicolorellum* from my collection.

The second of these Welsh specimens that was sent to Dyte may be the male that, in 2018, was in the NHM (London) in unincorporated material from his collection, standing under *S. mikii*, and labelled by Dyte "RF4 *Syntormon* near *mikii*" with the only locality data being "Newport Reens [ditches] near Cardiff', without a date. This specimen is also undoubtedly *S. bicolorellum*. I cannot find notes on how Dyte came to his conclusion that this was new, or later that he thought it was *S. luteicorne* and not "near *S. mikii*", or indeed why he did not recognise it as *S. bicolorellum* even though he was aware of the mistake made by Blackith and Speight (in litt. to John Deeming).

I suggest that S. luteicorne remains omitted from the British list.

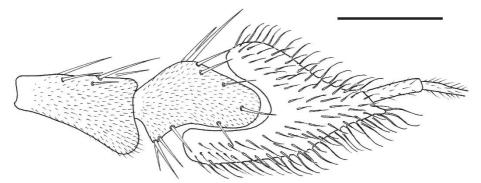


Fig. 2. Syntormon bicolorellum male antenna, inside face. Scale line = 0.1mm.

Syntormon macula Parent, 1927

There is no doubt about the identity of this species or its place on the British list. In Britain, females are uncommon but their localities and number of specimens far outnumber those of males, of which I know only seven specimens from five localities (Fig. 3; d'Assis-Fonseca 1949, Chandler 2003, Denton and Chandler 2004, my own recording). I have examined the male (NHM, London) that d'Assis-Fonseca (1949) used in his description and have compared my own single male with his description from which it differs in small points of colour that are within the variation expected in the genus. These differences are the colour of the thoracic dorsum, pleura and dark parts of the tergites (in my specimens these are green or greenish black on the tergites and show no coppery hue described by d'Assis-Fonseca), the hind coxae are rather dirty yellow although darker basally, and not 'black, yellowish at the extreme apex'; and the tarsi are clearly vellow until the fourth tarsomere (not 'all brownish'). d'Assis-Fonseca (1978) used the coxa and tarsus colours in his key but they are clearly unreliable characters. The ventral chaetotaxy of the mid femur is the same in both my specimen and d'Assis-Fonseca's (Fig. 4). The most striking character is the mainly yellow abdomen resembling that of S. aulicum, S. bicolorellum and S. mikii, but it is not mentioned in the key. The antenna is strongly narrowed in the apical half, resembling those of *filiger* and *pumilum* (Fig. 4).

Grichanov (2013) described the subspecies Syntormon macula mediterraneus from five males collected in Israel and Greece. He did not consider it conspecific with the nominal species as it did not agree entirely with the description by d'Assis-Fonseca (1949). Apart from a few differences in colour which may be within expected variation, the most important differences between the two British males that I have examined and the description of the subspecies are that the metepimeron is yellow (dark in British specimens), the mid femur lacks the short but distinct ventral seta and hairs, there are 4-5 black upper postoculars (10 in my male), the front tibia has a distinct antero-dorsal setal serration (almost indistinguishable in British males, and far from the condition in, for instance, S. pumilum), and the arista (both segments of the stylomere) is 1.3 times the length of the postpedicel (1.0 times in my male, whose style is intact and not broken at the tip; Fig. 4). Grichanov may be correct in concluding that his Mediterranean specimens belong to a different taxon to the nominal S. macula, assuming that Parent's French females have males more like the British ones than the Mediterranean taxon. However, the similarities are considerable, for example, the relative lengths of the leg segments are given here (Table 3). These are remarkably similar to those given by Grichanov for the subspecies, even without adjusting the units to proportions of one leg segment. The phallus can be distinguished in his photograph (his

fig. 13) and it closely resembles my figure, in particular it has the small dorsal flange that precedes the twisted tip, a feature not found in other British species (Fig. 1b). The status of this taxon remains to be tested but, in view of the very few males available for comparison, I think that it is probably identical to Parent's *S. macula*.

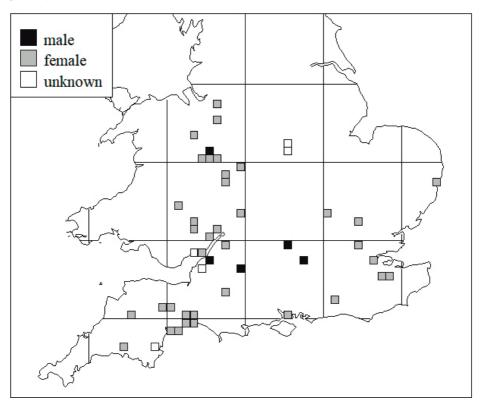


Fig. 3. Distribution of *Syntormon macula* in Britain, showing hectads where only females, or males (with or without females) or those of unknown sex have been recorded between 1947 and 2018.

 Table 3. Relative lengths of leg segments of a male Syntormon macula from Oxfordshire.

 Eye-graticule units at x90 magnification, 1 unit = 0.011mm.

	femur	tibia	tarsus 1	tarsus 2	tarsus 3	tarsus 4	tarsus 5
Front	76	89	50	24	19	12	10
Mid	104	129	59	29	23	14	10
Hind	130	167	34	32	26	17	12

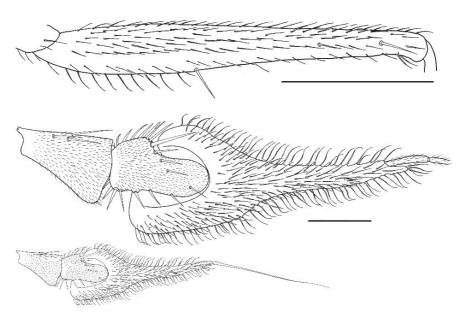


Fig. 4. *Syntormon macula* male mid femur (anterior face) and antenna (inner face) with inset of antennae with the arista. Scale lines = 1mm (femur) and 0.1mm (antenna).

Syntormon monile (Haliday in Walker, 1851)

Grichanov (2013) listed *S. monile, S. submonilis* and *S. silvianum* as one of the groups of species in need of investigation. Their hind basitarsi are forked at the base (Fig. 7j) and the last two tarsomeres of the mid leg are expanded. Confusion among them had not been resolved because Haliday's type specimen could not be found.

When Peter Hodge (1993) found S. silvianum in Britain, he tried to establish the identity of S. silvianum and S. monile by examining Haliday's type of S. monile. He searched for it in the Haliday collection in the National Museum of Ireland, Dublin, but without success. I therefore enquired at three museums that might have held it. Zoë Simmons at Oxford University Museum of Natural History (OUMNH) located a specimen in the J.C. Dale Collection, and this is almost certainly Haliday's type of *Rhaphium monile*. The specimen came to the OUMNH through John Westwood, who was the first Hope Professor responsible for the new entomology collection in the mid-19th century and he greatly enlarged the initial collection donated by Frederick Hope through donations and purchases. Among the donations was the J.C. Dale collection. I scanned the voluminous correspondence of Haliday to Dale held in the museum's library, hoping to find a reference to this and other specimens. Haliday's cursive writing is attractive but very difficult to read so, although his underlining of species and genus names made them stand out, I probably overlooked the relevant information. I did find reference to "monile (n sp.)" in a checklist of dolichopodids and ephydrids that he had prepared for Dale in a letter dated 3 July 1847 (4 years before its formal publication). A later annotation in this checklist made by Dale in red ink refers to "cinereum Hal. Ms W.p. 195-", which suggests that Dale might have had Haliday's manuscript that Walker (1851) used in *Insecta Britannica* (cinereum is Achalcus cinereus). However, even

without confirmation from correspondence, it is almost certain that this is the specimen on which Haliday based his description.



Fig. 5. *Syntormon monile* Haliday type specimen in Oxford University Museum, in lateral (a), dorsal (b) and anterior (c) views; hind tarsus showing the forked basitarsus (d); front right-hand leg showing the tibia with its well-developed pecten, the basitarsus with only very short ventral hairs and cylindrical second tarsomere, obscured by detritus (e). Courtesy of Oxford University Museum of Natural History.

The fly presently stands under "Syntormon monile" although I do not know who arranged and labelled the collection. There are no data labels on the staging pin but the specimen stands above a label in writing that Zoë Simmons says is that of Haliday, '*Rhaphium n. sp. No* 1000'. Loew separated his new genus *Syntormon* from *Rhaphium* in 1857, a few years after Haliday's (1851) description was published under *Rhaphium*. The fly is glued, dorsal side uppermost, to an irregularly shaped card which was characteristic of Haliday (Fig. 5a, b). It is covered in dust, insect frass and residual mould which obscure some features but it retains all its legs, antennae and wings although one wing is bent at right-angles and the other bent near the tip against the pin. The right-hand mid tarsus is glued to the card and clearly shows the expanded fourth and fifth tarsomeres which were regarded as the specific feature of *monile*, and the hind basitarsus has the clear basal projection found in three of the British species (Fig. 5b, d). The front right-hand tibia and tarsus are visible but tarsomeres 3-5 are missing (Fig. 5e); on the left-hand leg, tarsomeres 4 and 5 are missing. The right-hand pleura have a hole with concave sides as if it had been micropinned but there is no matching hole or damage on the left-hand side.

A redescription of the specimen is given below. A few characters were obscured or missing and, while they could have been described from typical British material, I have left out this information as the most important characters were visible, although less so in the photographs. These are: the front femur is entirely yellow and has no dorsal dark streak whose absence cannot be due to fading as the dark apical ring on the hind femur is still clear; the front tibia has only tiny hairs posteriorly; the front basitarsus is gently swollen apically with longer apical dorsal hairs but only tiny ones ventrally and posteriorly, and the second tarsomere is clearly a simple cylinder with no indication of a swollen base (although detritus obscures this in Fig. 5e). The abdomen is apparently entirely green, which is the only obvious discrepancy with Haliday's description, but the extreme lateral edges are not visible so their colour is unknown. I provided a label "LECTOTYPE *Syntormon monilis* (Haliday in Walker, 1851) det. C.M. Drake, 2019". Further discussion and figures of *S. monile* occur later under *S. silvianum* and *S. submonilis*.

Nine more specimens stand under *S. monile* in the Dale collection in the OUMNH but none would have been used by Haliday in his description. Eight of them are Haliday's on his hall-mark irregular staging cards. They include $1 \leq S$. *monile* with a typed label "Feb. 1865" (day number obscured by pin) which is presumably an accession date as Haliday moved to Italy in 1862 and did not collect anything in the British Isles after that. A female *Syntormon* has a small postero-dorsal seta on the front tibia so may not be either *S. monile* or *S. submonilis*. The only specimen that is not Haliday's is a male *S. monile* on a micropin, rather than glued as are all Haliday's. The remaining species belong to four other genera and it is likely that they were allocated to the wrong place by Dale or a later worker.

Syntormon monile Redescription. Male. Body length 2.4mm; wing length 2.4mm measured from base, 2.1 mm measured from vein h. Head. Frons metallic green either side of ocellar triangle; ocellus raised above level of flat upper frons. Face silver-dusted (strongly shrunken); occiput metallic green but dulled by grey dust. Eyes finely hairy; lower and front facets about twice diameter of upper facets. Palps small, elongate oval, black with pale brown dusting and inconspicuous fine short white hairs. Antennae black; scape bare, with apical inwardly directed conical projection; pedicel with coronet of apical short setae, the longest dorsal seta about equal to the width of the pedicel near its base, and long conus twice as long as scape; postpedicel long, almost parallel in basal half, tapered in apical half to pointed tip; entirely covered with short dense slightly curled pale hairs arising from simple insertions; arista inserted dorsally just behind tip of postpedicel, very finely pubescent, appearing almost bare, slightly shorter than postpedicel; ratio of lengths of scape: pedicel to tip of conus: postpedicel: arista 6:13:26:23. Chaetotaxy typical for the genus: 2 long ocellars, 2 long upper orbitals, 2 short postocellars, their length equal to ocellar

triangle length, postoculars black in upper third (7 setae including 2 set back from marginal row at vertex), white in lower two thirds (not all visible), several long white setae on lower occiput behind postocular row. Thorax. Metallic dark green, metepimeron black; dorsum sub-shining, in anterior and posterior view darker along rows of ac and dc setae and at most seta insertion points; pleura ground colour mainly obscured by grey-white dust; scutellum more shiny metallic on smooth central third, granular and coppery green on lateral thirds; dorsum flat in front of scutellum in area bordered by last two dc and end of ac row; ac setae biserial throughout, about 15 in each row, row ending between 4th and 5th dc setae, moderately long, ac at 4th dc about ¹/₃ its length, ac setae at suture about as long as distance between ac and dc rows; dc setae -2 pre- and 4 post-suturals (several missing), 5th inset; intra-alar setae – 1 pre- and 2 post-suturals, middle one placed more dorsally and close to posterior seta; 1 strong posterior supra-alar; 1 strong anterior supra-alar; anterior slope of dorsum with about 8 fine short black setulae in front of dc, 3 longer black setulae outside dc; 2 notopleurals, anterior stronger and almost on lower suture; 1 strong upper and 1 small lower postpronotals; about 5 fine short white lower and about 8 or more fine white upper proepisternals; 3 fine white katepisternal hairs just in front of posterior spiracle; vertical row of several (most lost) white metepimeron hairs on posterior edge; scutellum with 2 long strong lateral setae, 2 very short fine pale apical hairs inside of the strong setae, and a similar hair on side in front of lateral seta. Legs. All pale yellow of similar hue but black or dark in the following parts: on basal ³/₄ of mid and most of hind coxae which are yellow-tipped, outer basal corner of front coxa for ¹/₆ or less of its length but entirely yellow on anterior inner face at base, front leg tarsomere 3 (at least – others are missing), mid leg tarsomeres 4+5, apical third of hind femur, hind leg tarsomeres 4+5, hind tarsomeres 1-3 dusky yellow. Chaetotaxy: all setae and vestiture black except where otherwise stated. Front leg: coxa I – all hairs and apical setae white; femur I – ?1 short pre-apical py, ventral vestiture of tiny vellow hairs: tibia I – no setae: ad pecten of stout setulae in apical half, the apical ones just longer than shaft's width (about 1.3 times), their basal diameter about half the length of the gap separating them, apicals minute or possibly lost, posterior apical comb well developed; tarsus I – basitarsus swollen in apical two-fifths where there are anterior and posterior clusters of longer hairs, hairs on basal ²/₃ of shaft shorter than shaft's width, tarsomere 2 cylindrical, vestiture hairs not longer than shaft's width, tarsomere 3 short cylindrical (only one present). Mid leg: coxa II – anterior hairs and most apical setulae white, a few black apicals; femur II – anterior and posterior preapicals about 1.5 times shaft's width, a shorter pv preapical; ventral vestiture fine and pale to base, on basal $\frac{1}{3}$ with row of about 7 upright pale hairs distinctly longer than black vestiture; tibia II – 4 ad at $\frac{1}{4}$ paired with 1 pd, $\frac{2}{5}$, $\frac{1}{2}$ and $\frac{2}{3}$, all of about 2.5 times width of shaft; apicals ad and d both strong (pd scar only); tarsus II - tarsomeres 1-3 unmodified, 4+5 dorso-ventrally flattened, 2.5 times width of third tarsomere. Hind leg: $\cos x$ III – 1 strong black outer seta at basal $\frac{1}{3}$, a few tiny white hairs on upper and lower parts of outer face; femur III – strong pre-apical anterior, av and pv; pv vestiture pale fine and sparse, depth of femur 1.5 times maximum depth of mid and fore femora; tibia III – 3 ad at $\frac{1}{5}$, $\frac{1}{3}$ and $\frac{1}{2}$, 4 pd more-or-less equally spaced, with shorter setae interspersed; 1 ventral at $\frac{2}{3}$; vestiture of fairly long hair, longest equal to shaft's width (comb not visible); width of tibia shaft distinctly greater than mid tibia (nearly 1.5 times); tarsus III – basitarsus very gently bowed ventrally with large basal ventral branch, terminating in a pointed apical seta, a more or less straight and finely tapered seta ventrally just before the tip and another proximal to this, which is curved and blunttipped, and with a few finer shorter hairs on the branch's shaft; posteriorly at inner curve of tarsomere and branch with row of longer vestiture; remaining tarsomeres unmodified. Claws (missing on front legs) short, pulvilli reaching about ³/₄ claw length, empodium scarcely discernible. Length ratios of femur, tibia, tarsomeres 1-5 in arbitrary units: front leg 57:43:28:10: (3-5 missing), mid leg: 60:62:31:14:10:5.5:7, hind leg 58:75:20:20:12:8:7. Wings. Entirely hyaline, grey-tinged, the same shade all over; veins dark but yellow at extreme base; venation typical of *Syntormon*; microtrichia distributed evenly over all cells except extreme base of cells at root of wing, where microtrichia are minute and sparse; calypter and its hairs yellow; halter yellow with slightly dusky knob. **Abdomen.** Tergites metallic green, with strong coppery tinge dorsally, shining but thinly dusted; T2 entirely green (extreme lateral margin curled under so its colour is not visible); all setae and vestiture black dorsally, 4 long white marginal setae on T1 on lower edge, white hairs on T1 laterally and anterior two ranks dorsally, white vestiture along lower margin of all tergites; dorsal vestiture of T2–T4 in 5-6 ranks; longest marginal setae about ½ tergite's length. Sternites all apparently dark; sternite hairs white. Hypopygial capsule black.

Syntormon pseudospicatum Strobl, 1899

Drake (2020) argued that *S. pseudospicatum* is a good species distinct from *S. pallipes* on the basis of its morphology and habitat, but Chursina and Grichanov (2019) disagree and consider *S. pseudospicatum* to be a junior synonym. I recommended that *S. pseudospicatum* should remain on the British list.

Syntormon pumilum (Meigen, 1824)

Maslova *et al.* (2017) described *S. grootaerti* which closely resembles *S. pumilum*, differing in its arista being only about half the length of the postpedicel (equally long in *S. pumilum*), the shape of the small ventral projection of the second tarsomere of the front tarsus and the form of the genitalia. However, their illustration of the genitalia of *S. pumilum* does not agree with mine for British material (Fig. 1d); in particular, our species has conspicuous rods alongside the phallus, which are not shown for *S. pumilum* by Maslova *et al.* (2017), but are clearly shown for *S. grootaerti* in which the phallus has been extruded in their figure. Perhaps the rods were not visible in their undismembered specimen of *S. pumilum*; I often found it difficult to distinguish the structure of the phallus, even in well macerated specimens, without removing it. I illustrate the genitalia in ventral view as this aspect shows the shape of the ventral lobe of the surstylus, which Maslova *et al.* use as a feature that distinguishes the two species. In my drawing, one side appears square-ended and the other slightly produced as I had not arranged the capsule absolutely 'flat' in the mount. This changes with the angle of viewing so this single specimen encompasses both states used to distinguish *S. pumilum* from *S. grootaerti.* It would be worth checking in greater detail the similarity of the phallus of these two species.

Syntormon setosum Parent, 1938

This species is very similar to *S. mikii* and was described from a female which remains the only known sex. Speight and Meuffels (1989) recorded it in Ireland. They stated that it was known only from the single French specimen described by Parent and from Italy (Rampini 1976); no other countries have since been included in Fauna Europaea (Pollet 2011). The differences between *S. setosum* and *S. mikii* are based almost entirely on the colour of the metepimeron, hind coxa and tergites, all of which are browner in *S. setosum* compared to completely yellow in *S. mikii*. Given the variability of colour in some species of *Syntormon*, these differences may be insufficient basis to separate a species, and indeed Speight and Meuffels (1989) were not satisfied that *S. setosum* was anything other than a dark form of *S. mikii*.

Specimens agreeing with *S. setosum* have been recorded at two British sites (Fig. 6). From a coastal reedbed at South Milton Ley, Devon (SX6741), I collected two females on 21 August 2016 (along with males) and two more females on 13 April 2019, but without males. The females taken in August are typical *S. mikii* and the April pair are *S. setosum*, agreeing in all respects with the distinctions used by Speight and Meuffels (1989). The only difference is that there are no *basal* black setae on the front coxae but only the usual apical setae, and I presume this is merely an error in their account. In detail, the metepimeron is brown, slightly paler on the posterior

margin but, on the anterior margin, no different in tone or colour to the adjacent pleura (decidedly yellow in *S. mikii*), the hind coxa is brownish, marginally paler than the mid coxa but far from the yellow of the front coxa although one specimen's front coxa is brown on the outer and basal faces, and the tergites are completely dull dark brown with no hint of pale marks on the lateral margins (completely yellow laterally on tergites 1-5 in *S. mikii*). I asked David Gibbs to check a female that he had collected on 18 May 2005 at Poole Harbour, Dorset (SY9885) and he reported that it has an entirely dark abdomen, the hind coxae are murky yellow but clearly yellower than the mid coxae, and the metepimeron is brownish, darker than the hind coxae but not as dark as the meron. He concluded that it was closer to the *setosum* form. From the same extensive saltmarsh where Gibbs recorded his female '*setosum*', I had fortuitously taken a male *S. mikii* on 21 June 2005 about 5km distant (SY948897) and about 4 weeks later in the same year.

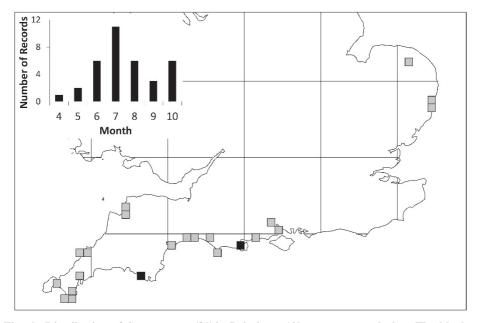


Fig. 6. Distribution of *Syntormon mikii* in Britain at 10km-square resolution. The black square shows where both typical *mikii* and *'setosum'* were found. Histogram shows numbers of records per month (some omitted records have only year but not month).

Other records of *S. setosum* are also for spring-flying individuals. The Irish specimens collected by Speight and Meuffels (1989) were taken on 10 May; the Italian specimens of Rampini (1976) were taken in March and April. Among material in the World Collection at the NHM (London) is a female from Spain taken in April (data label information: Alava Prov., Pantana Sant Engracia, near Villarreal de Alava, 18.iv.1982, leg. C.E. Dyte) which has a dark metepimeron but bright yellow hind coxa, and entirely dark tergites with no trace of yellow patches. Dyte did not add a determination label so perhaps he was unsure of its identity. A second female specimen, from Portugal (Algarve Fuseta, saltmarsh, 12.v.1999. leg. C.E. Dyte), along with a male *S. mikii*, is a typical *S. mikii*, as determined by Dyte. So these Iberian specimens are darker in April and paler in May. Speight and Meuffels (1989) suggested that the dark spring

females had overwintered, and this accounted for their colour, which can be dark in other overwintering dolichopodids such as some *Campsicnemus*, and certainly the late date (11-16 October) of several records in the national recording scheme database indicates that they may well survive into the winter (Dipterists Forum 2019; Fig. 6). Male *S. pallipes* also become progressively paler from spring to autumn (Drake 2020). There is now increasing evidence that spring-flying individuals are dark, so equate with *S. setosum*, and summer to autumn individuals are paler, equating with *S. mikii*. The presence of both taxa at two British sites tends to militate against them being different species, but does not rule out this possibility, although it increases the likelihood that they are a seasonal colour form. I strongly favour this suggestion of Speight and Meuffels (1989) but am left with the dilemma whether to add *S. setosum* as a species new to Britain when I do not believe that the species is real. I have not examined Parent's holotype but I doubt that doing so would resolve the problem as I would probably be faced with a specimen that exactly resembled my own dark individuals. I am therefore taking the unusual step of not adding the species until further evidence is obtained, for instance by recording more frequently in spring and summer at British '*setosum*' sites or undertaking molecular investigation.

Syntormon silvianus Pârvu, 1989 and S. submonilis Negrobov, 1975

Syntormon silvianum has been recognised in Britain for some time (Hodge 1993). Pârvu (1989) described it from Romania and, while mentioning briefly (Pârvu 2000) that it was similar to S. monile, it was not until later (Pârvu 2009) that he provided reasons for attributing the names S. monile and S. silvianum to the two species. His reasoning was based on Haliday's description of two characters: whether the second tergite was entirely green or had yellow lateral marks, and the shape of the front basitarsus. Pârvu confused his account by misreading Haliday's description, thinking that Haliday had described the second tarsomere, when in fact he describes only the basitarsus ("fore metatarsus slightly dilated at the tip"). So either Pârvu's reasoning does not apply to this structural character or, more likely, this is an error in his account as it seems improbable that he would have mistaken these terms. Regarding tergite colour, Haliday says "Abdomen with the second segment usually yellowish beneath and at the sides." When I examined the pinned specimens in my collection, I had 44 S. silvianum of which 43 had entirely green tergites and one had the extreme lateral edge yellow; of 28 S. monile, 11 had obvious yellow patches on the second tergite, in two cases extending dorsally as a complete ring, six had no discernible yellow on the second tergite, and 11 were intermediate and, without close examination, would have been considered entirely green. Specimens in alcohol gave a similar distribution of colours: 21 S. silvianum had dark green tergites and sternites, and of 15 S. monile, five had large unambiguously yellow patches and 10 varied from having small antero-lateral patches to being only vaguely paler than the clearly dark first or fourth tergites, but in all cases the second sternite was pale. The colour of the tergites is therefore only useful for distinguishing clearly pale specimens (= monile) and entirely very dark specimens (= silvianum). As stated under S. monile above. Haliday's type specimen appeared to have entirely green tergites, but his use of the qualification "usually vellowish" suggests that he had several specimens which showed the range of variation as seen in my specimens, or that he had both species.

Negrobov (1975) described *S. submonilis* from the Caucasus. In his key to species, he distinguished it from *S. monile* in having a dark spot at the apex of the hind femora and largely dark hind tibia, in contrast to entirely yellow femora and tibia of *S. monile*, although the description of *S. submonilis* gives only the apices of both the femora and tibia as dark. Using this key, it is not possible to name British *S. monile* as their hind femur is always obviously dark-tipped in the apical quarter to third. Similarly, British *S. silvianum* will not run to *S. submonilis* as their hind tibia is entirely yellow or at most occasionally slightly dusky at the tip but hardly darkened. Pârvu (1989) probably had the same problem as he stated that his new species *S.*

silvianum "is placed after *S. monilis*" in Negrobov's (1975) key. It is unfortunate that, in his otherwise full description, Pârvu omitted the colour of the hind femur, although he did say that the hind tibia was yellow.

However, if the leg colour is disregarded, important elements of the description of S. submonilis closely resemble those of S. silvianum, in particular, the chaetotaxy and shape of the front tibia, basitarsus and second tarsomere when compared against my Fig. 7. Several characters whose lengths are given in the description can be compared with those of S. monile and S. silvianum. I measured the relevant characters in ten individuals each of S. monile and S. silvianum collected from a wide geographic range in Britain. As Negrobov (1975) gives measurements in graticule units, I standardised his and my measurements for each individual to a ratio of the longest leg measurement given (mid basitarsus) as this segment can be measured with reasonable accuracy. Doing so obviates problems of allometry and size differences between individuals. Table 4 gives characters where there was a significant difference in the mean values (Student's ttest) or where S. submonilis falls within the range of values of the other two species. These values also show that S. silvianum is usually closer to S. submonilis than to S. monile in its shorter front tarsomeres 2 and 3, shorter arista, and longer and narrower postpedicel (although the postpedicel length:height ratio in Negrobov's description is way beyond those for British specimens). Negrobov's illustration of the surstylus (his fig. 19) is very similar to those of S. monile and S. silvianum (Fig. 1c, d).

As it seemed likely that *S. submonilis* is the same as *S. silvianum*, I made a request through the Natural History Museum, London, to loan both type specimens. This remained unanswered for several months until the pandemic lockdown in 2020 made it unlikely that they would be seen for some time. I therefore am most grateful to Dr Oleg Negrobov for examining specimens of British *S. monile* and *S. silvianum* that I sent him. He agreed that his *S. submonilis* is the same as Pârvu's *S. silvianum*. Although I have not seen Pârvu's type specimen, his clear and accurate figures and description leave no doubt that this is the species we have in Britain, and which Dr Negrobov regards as *S. submonilis*.

Syntormon submonilis Negrobov, 1975 = silvianus Pârvu, 1989, new synonymy

	monile	silvianum	submonilis
front leg tarsomere 2	0.33 (0.29-0.35)	0.24 (0.21-0.28)	0.26
front leg tarsomere 3	0.24 (0.21-0.28)	0.18 (0.16-0.19)	0.21
postpedicel length	0.86 (0.73-1.00)	0.71 (0.66-0.74)	0.68
postpedicel length / arista length	1.11 (0.96–1.26)	0.86 (0.79-0.95)	0.72
postpedicel length / height	2.46 (2.18-2.78)	2.14 (2.00-2.33)	3.5–4 (as given by
			Negrobov)

Table 4. Comparison of lengths relative to mid basitarsus and ratios of characters that show highly significant differences between *S. monile* and *S. silvianum* (mean with minimum and maximum values, N=10) and the single value for *S. submonilis* given by Negrobov (1975).

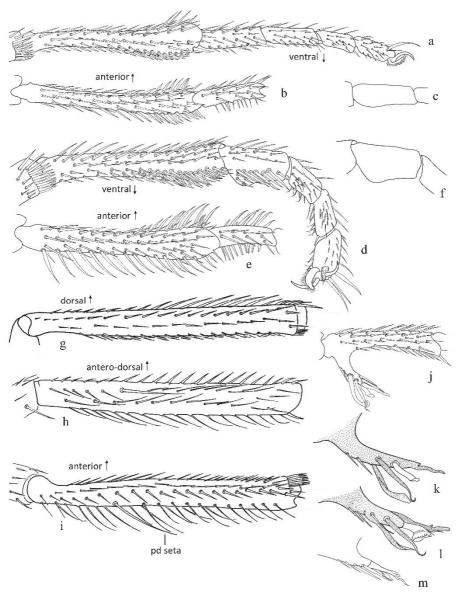


Fig. 7. *Syntormon monile* (a, b, c, g, j, k), *S. submonilis* (d, e, f, h, i, l) and *S. fuscipes* (m) front tarsus, tibia and hind basitarsus. Front tarsus lateral view anterior face (a, d); dorsal view with anterior face towards top of page (b, e); second tarsomere without hairs in lateral view (c, f); front tibia in posterodorsal view (g, h) to show pecten at its widest, and in anterodorsal view (i) to show posterior hairs at their widest; posterior basitarsus, anterior face (j) and with detail of its ventral branch (k, l, m).

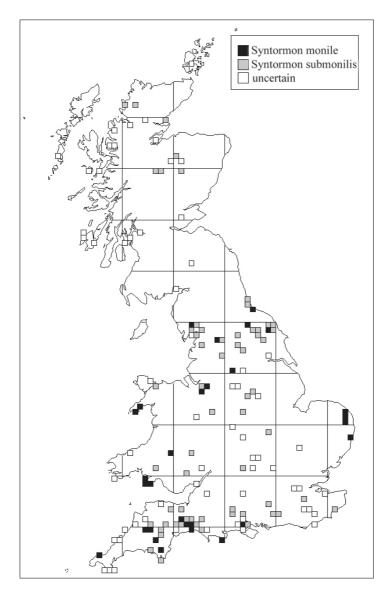


Fig. 8. Distribution of *Syntormon monile* and *S. submonilis* in Britain at 10km-square resolution. Note that 'uncertain' records on the west Scottish coast do not show up well.

I use Negrobov's spelling of *submonilis*, rather than change it to *submonile*. ICZN (1999) appears to allow either spelling, depending which rules are followed. The word 'monile, -is' is a Latin third declension neuter noun meaning a necklace or ornamental neck band, presumably an allusion by Haliday to the yellow marks on the tergites. It is treated as a noun in apposition, that is, acting as an adjective, as in 'cat food'. Such names must be written in either the nominative

or genitive case (ICZN paragraph 11.9.1), and need not nor may be changed to agree with the gender of the genus (31.2.1) but the original spelling must be retained (31.2.1 and 34.2.1). These rules lead to *submonilis*. The historical change from Haliday's *monile* to *monilis* appears to have been an error made on the assumption that *monile* was an adjective and so had to agree with the then-masculine gender of *Syntormon*. But there is no justification for emending Negrobov's spelling, despite the use of the genitive making no sense in the word *submonilis*. An alternative argument is that the code explicitly states that the name may be "a noun in the nominative singular standing in apposition to the generic name" (11.9.1.2), thus giving only *monile*. The code allows changes in the original spelling if there is clear evidence of an inadvertent error but spelling the noun with an inappropriate case does not appear to fall within the scope of paragraph 32.5. For the working entomologist, the confusion of having both *monile* and *submonilis* seems to be unavoidable.

Pârvu and Negrobov should be given credit for recognising that their species was not Haliday's since there was much confusion in the standard literature of the time. Loew (1857) and Parent (1938) made redescriptions of what they considered to be *S. monile*, and Becker (1918) figured the hind basitarsus. When their descriptions and figures are compared with Fig. 7 and the key I provide below, Loew's and Becker's descriptions are a better fit with *S. submonilis / S. silvianum* and Parent's figure and some of his description (not all, particularly the dark dorsal surface of the front femur) fits *S. monile*. Verrall (1875, p.147) briefly described his *Synarthrus monilis* in which he gives the front femur as "dusky above, the front tibia with a row of small spines all the way down" – this is almost certainly *S. submonilis*.

The following couplet distinguishes males and females of these two species. It mentions far more characters than needed for identification but summarises most of the differences.

Males

Females

1 Front tibia pd setae distinct and usually longer than shaft's width; sternites dark; front coxa dark in basal ¹/₅ to ¹/₄; front femur usually with dark shade along dorsal surface visible in side view if faint, sometimes absent; setulae of front tibial pecten stout and as long as shaft's width; postpedicel slightly more conical, on anterior face slightly wider from conus of pedicel to front margin than to ventral and dorsal margins; tergites 2 and 3 always dark

Syntormon submonilis (as silvianum) was recognised in Britain by Hodge (1993), with assistance from C.E. Dyte. Yerbury (1912) may have been the first person to note two forms of *S. monile*. In his list of Diptera from north-west Scotland, he noted under *S. monile* ".... an interesting variety with simpler front tarsi was taken at Loch Assynt [Sutherland], 26th July 1911, 3." This is most likely to be the true *S. monile*, and his other records from Loch Assynt (18.vi.1911), Golspie (9 and 15.vi.1904) and Nethy Bridge (27.vii and 2.viii.1904, 6.vii.1905) are in the NHM (London) under *S. silvianum*, probably identified by C.E. Dyte, but there are no Scottish specimens of *S. monile* collected by him.

In Britain, *S. submonilis* is the more frequent of the two species but, owing to confusion with *S. monile*, it is not possible to give definitive maps of the two species. While all records of *S. submonilis* will have been correctly identified, many older records could be either species. It would be unproductive to trace these specimens as the records were submitted by over 50 recorders. The species aggregate occurs widely in Britain north to Orkney, with perhaps a genuine scarcity of *S. monile* in south-east England and without definite Scottish records although Yerbury's possible Scottish *S. monile*, just mentioned, has been plotted on the map as 'uncertain' since the specimen has not been seen (Fig. 8).

Syntormon sulcipes (Meigen, 1824)

This is a distinctive species with a conspicuously broad and, at least in British material, entirely black hind tibia. It is mentioned here as *S. bulgariensis* Negrobov & Kechev, 2012, is very similar but the genitalia, which they illustrate well for both species, differ from British *S. sulcipes* in the ventral surstylus having a long basal seta on a tubercle, whereas in British material the seta is more distal and not on a tubercle. Like *S. bulgariensis*, British *S. sulcipes* have black hind tibiae but always have yellow femora (black in *S. bulgariensis*). Grichanov (*in litt.*) has suggested that *S. bulgariensis* is Parent's (1938) variety *obscurior* of *S. sulcipes*.

Conclusions

The British list of *Syntormon* remains unchanged at 15 species (Chandler 1998, and most recent update Dipterists Forum website 2019). I have irritatingly changed some species-name endings to neuter, back to those in Chandler (1998) after having been changed to masculine in Chandler (2013). The long-standing issue of the identity of *S. monile, S. submonilis* and *S. silvianum* has been resolved, but there are still two issues that may affect the British list. Firstly *S. setosum* is more likely to be a colour form than a species so, although there are English examples, I suggest that it is not added to the British (as distinct from Irish) list. I realise that this is unsatisfactory – how can it be a full species in Ireland but only a colour form in England? – but resolution of the reality of this taxon may be difficult as it is known only from rare females that do not seem to show any structural differences from *S. mikii*. Secondly, there is still lingering doubt over the identity of Loew's *S. spicatum*, and how or whether it differs from von Roser's *S. fuscipes* although, whatever the outcome of that issue, it is unlikely to affect the British list. While our island may have a small fauna, it does have the advantage that I can safely leave other uncertainties raised in this paper for mainland specialists to resolve.

Acknowledgements

I thank several colleagues for their kind help in preparing this paper. John Deeming, Cardiff Museum, loaned his specimens of *S. luteicorne* and discussed the implications; David Gibbs checked his *S. mikii*; Peter Hodge gave permission to use elements of his draft but unpublished paper on *S. silvianum* for which I had long ago offered but failed to provide illustrations; Zoë Simmons of the Oxford University Museum of Natural History (OUMNH), Duncan Sivell of the Natural History Museum, London, and Ryan Mitchell at Ulster Museum, Belfast, all searched for the elusive Haliday type specimen of *Syntormon monile*, and I am particularly grateful to Zoë for locating it; Duncan and Zoë provided access and valuable help at their museums; Val McAtear of the Royal Entomological Society's library provided obscure literature, and Emily Chen helped with access to the OUMNH's library archives; Robyn Crowther (OUMNH) took the photographs for Fig. 6; Oleg Negrobov most kindly checked my specimens of *S. monile* and *S. submonilis* and confirmed the synonymy given here; Marc Pollet and Igor Grichanov made valuable comments on the first draft; Scott Brooks and Bradley Sinclair clarified some morphological nomenclature; Peter Chandler and Francisco Welter-Schultes confirmed my understanding of the *monile / submonilis* conundrum. Distribution maps were made using DMAP.

I thank Petr Heřman for pointing out my error (in Drake 2020) in ascribing the type specimen of *Syntormon pseudospicatus* to the Naturhistorisches Museum, Vienna - the Strobl collection is at the Naturhistorisches Museum, Admont.

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Mechanisms and patterns of larval feeding in *Tephritis neesii* (Meigen), *Tephritis vespertina* (Loew) and *Xyphosia miliaria* (Schrank) (Diptera, Tephritidae)

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Summary

Morphological analyses, observations and videos were used to resolve the mechanisms and patterns of larval feeding in *Tephritis neesii* (Meigen), *Tephritis vespertina* (Loew) and *Xyphosia miliaria* (Schrank) (Diptera, Tephritidae). All three species share a feeding mechanism comprising a pivoting head skeleton and fixed mandibles. In contrast, feeding patterns distinguish each species and match the characteristics of the particular Asteraceae capitula in which they develop.

Introduction

It is unfortunate that feeding mechanisms in cyclorrhaphan larvae (Diptera) are not better known, i.e. the ways in which morphology and behaviour combine during feeding to transfer food from an external source into the alimentary tract. This is because feeding mechanisms not only help explain how larvae live, they are a source of information for taxonomic, ecological and other interests (Rotheray 2019a).

Moreover, feeding patterns are frequent, i.e. ordered, predictable feeding, and a further source of information for understanding dipteran biology. In certain larval Tephritidae (Diptera) feeding patterns partition species that develop in shared Asteraceae capitula or flowerheads (Headrick and Goeden 1996). For example, Straw (1989) found that in the capitulum of burdock, *Arctium minus* (Asteraceae), the larva of *Tephritis bardanae* (Schrank) (Tephritidae) feeds on developing, pre-fertilised flowers, whereas the larva of *Terellia tussilaginis* (Fabricius) (Tephritidae) feeds on maturing seeds.

Asteraceae are a structurally diverse group of plants (Stace 2010). Such diversity includes their capitula. The capitulum of ox-eye daisy, *Leucanthemum vulgare*, is, for instance, broad with a dense arrangement of short, firm florets. In contrast, the capitulum of cats-ear, *Hypochaeris radicata*, is narrow with longer, softer florets. If such variations influence the feeding mechanisms and patterns of their associated tephritids, *Tephritis neesii* (Meigen) (Diptera, Tephritidae) and *T. vespertina* (Loew) (Diptera, Tephritidae) respectively, this is unclear.

In this two-year investigation, morphological analyses were combined with observations and videos to assess feeding in larval *T. neesii*, *T. vespertina* and also, *Xyphosia miliaria* (Schrank) (Tephritidae), relative to the characteristics of their foodplant capitula. *X. miliaria* was included since the capitulum of its foodplant studied here, *Cirsium palustre* (Asteraceae), has a contrasting set of characteristics to those of *L. vulgare* and *H. radicata* and provides a further point of comparison.

Materials and methods

In June and July 2019, in the Fleet Valley, Dumfriesshire, populations of *T. neesii*, *T. vespertina* and *X. miliaria* were located by collecting capitula of their foodplants, *L. vulgare*, *H. radicata* and *C. palustre* respectively; adults were identified using White (1988). Between 27 May and 18 June 2020, feeding in each larval stage was monitored by visiting populations 4-6 times for each tephritid species and removing about 20 capitula into plastic bags. Within a day of collection

each capitulum was opened and the positions and numbers of tephritid eggs, larvae and puparia were recorded. Samples of capitula were measured across the receptacle and maximum floret height recorded. Larvae of various sizes were fixed in hot water and preserved in 70% alcohol. Live larvae were observed using a Wild M5 stereo microscope and photographed with an Olympus TG-5 camera placed over an objective lens of the microscope. Images and videos were uploaded to a MacBook Pro computer and examined using Adobe Photoshop Elements 2019 and iMovie 10.1.12.

Head skeletons were examined by extracting them from puparia. The antero-ventral section of the puparium, loosened by the emerging adult and containing the head skeleton, was placed in a solution of potassium hydroxide for about 45 minutes and pins were used to free head skeletons. They were washed in acetic acid to prevent further clearing and stored in 70% alcohol. Head skeletons in situ were also examined. The front end of a preserved larva was cut across the metathorax and the cut section cleared in potassium hydroxide for up to an hour and obscuring tissue removed with pins and forceps. Sections were washed in acetic acid and preserved in 70% alcohol. The morphology of head skeletons and preserved larvae was examined using the stereo microscope.

Results

Tephritis neesii

Foodplant *L. vulgare*: compared to foodplants of the two other tephritids assessed here, *L. vulgare* plants were clumped and formed isolated patches of up to $8m^2$, n = 5; mean width of capitula 12.5mm, range 7-18mm, SD 2.9, n = 52; florets up to 5mm long and forming a dense mat over the surface (Fig. 1); disc florets up to 2mm shorter near the centre than the edge; receptacle mushroom-shaped with a tapered margin (Fig. 2a); capitulum open at all times.

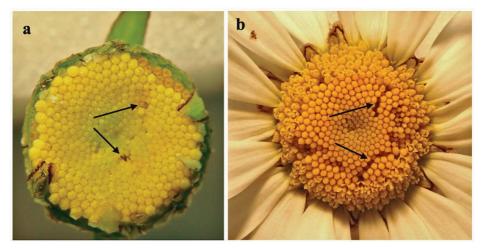


Fig. 1. *Tephritis neesii*, capitula of foodplant, *L. vulgare*, apical view of flower disc: a, recently opened capitulum, arrows indicate oviposition scars; b, older capitulum; arrows indicate larval feeding tracks.

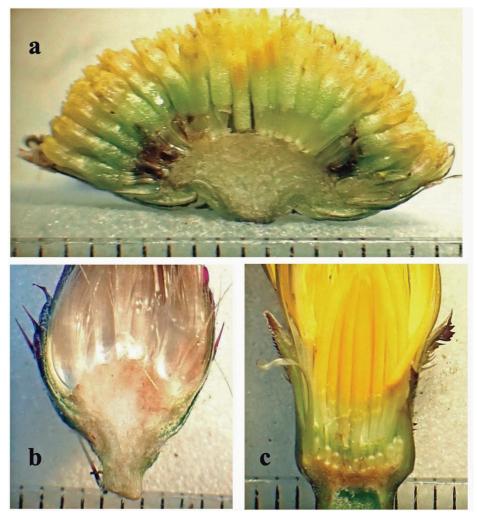


Fig. 2. Sections through foodplant capitula of Asteraceae, mm ruler along lower margin of each image: a, *L. vulgare*; b, *C. palustre*; c, *H. radicata*.

Infestation and larval feeding pattern: mean number of larvae per capitulum 4.1, range 0-12, SD 2.7, number of capitula assessed 70, 91.6% of capitula infested; eggs in the apex of florets or between them, occasionally eggs at the base of florets (Fig. 3a); eggs off-centre in capitula; oviposition in small, closed capitula 4-8mm in diameter with the involucre folded over the disc and larger, open capitula with involucre turned back and white ray florets fully developed; for short distances, first stage larvae either burrow transversely across florets or burrow down an individual floret; larvae descend eventually to the surface of the receptacle and tunnel through the developing ovaries leaving behind a permanent, dark-coloured feeding track (Fig. 3b) and at the capitulum surface, lines of florets at a lower level appear (Fig. 1b); second and third stage larvae

remain at ovary level and tunnel through them and the lower ends of florets. Third stage larvae may include receptacle tissue and leave behind shallow, U-shaped gouges in its surface and sometimes, deeper cavities (Fig. 3c); second and early third stage larvae tunnel round the capitula rim and only towards the centre in heavily infested capitula (5+ larvae); larvae often feed upside down; pupation takes place in tunnels.

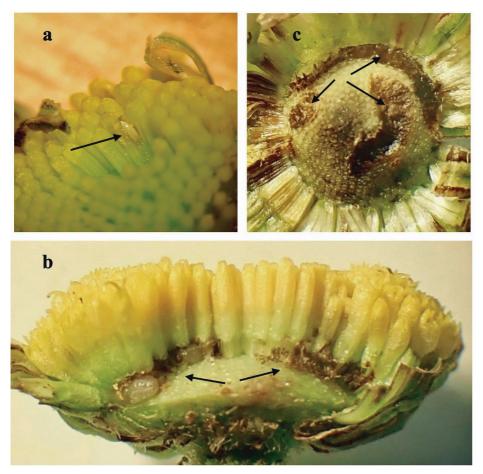


Fig. 3. *Tephritis neesii* infestation of *L. vulgare*: a, arrow points to an egg placed inside the apex of a flower; b, arrows point to larval feeding tracks through the ovaries, second stage larvae visible on the left-hand side; c, flowers removed and arrows point to brown feeding tracks in the receptacle.

Tephritis vespertina

Foodplant *H. radicata*: compared to *L. vulgare*, plants of *H. radicata* were at lower densities, more widely dispersed and not clumped; mean width of capitula 8.0mm, range 5-12, SD 1.7, mean floret length 15.6mm, range 10-23, SD 2.7, n = 62; disc florets soft and above ovary level loosely arranged (Fig. 4a); receptacle a thin plate about 2mm thick (Fig. 2c); capitula open and

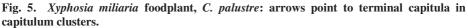
close diurnally and may close partially or completely in overcast or wet conditions (open is the involucre and florets inclined from the centre and closed is florets and involucre upright and approximated); post-fertilised capitulum closed.



Fig. 4. *Tephritis vespertina* infestation of *H. radicata*: a, apex of capitulum with dark centre indicative sign of infestation; b, arrow points to a second stage larva feeding down a flower; c, arrow points to a third stage larva feeding at ovary level; d, puparium in a larval feeding track; e, an individual flower with a dark feeding track.

Infestation and feeding pattern: mean number of larvae per capitulum 1.6, range 1-3, SD 0.7, number of capitula assessed 179; 18.4% of capitula infested; eggs were found in the apical third of individual florets and less frequently between florets and lower down; if both open and closed capitula were used for oviposition this was not confirmed; first and early second instar larvae burrow down a floret towards the surface of the receptacle leaving behind a conspicuous feeding track of torn and fragmented tissue and as larvae develop, adjacent florets are included (Figs 4b, c & e); third stage larvae were found at various heights along feeding tracks, suggesting they move up and down to access additional food rather than moving transversely between florets; tissue from damaged florets often adheres either because of fluids released from it or, more likely, from larval saliva and faeces; prior to pupation most larvae reverse position in feeding tracks and pupate in them (Fig. 4d).





Xyphosia miliaria

Foodplant *C. palustre*: compared to *L. vulgare*, plants of *C. palustre* were at lower densities, more widely dispersed and not clumped; capitulum flask-shaped and occurring in clusters at stem apices; each cluster with a larger, apical or terminal capitulum, about 8-10mm in floret length and diameter that is the first to open and surrounded by 3-5 smaller, auxiliary capitula which develop to the size of terminal capitula and open later (Fig. 5); early growth stage of the main stem comprising 1-4 individual clusters grouped together; these separate as the plant ages and the stem supporting each cluster lengthens; receptable bulb-shaped and about 5-6mm at its widest (Fig. 2b); capitula open and close diurnally and in overcast conditions, but less extensively than *H. radicata* since the involuce does not fold back completely; post-fertilised capitulum closed.

Infestation and feeding pattern: mean number of larvae per capitulum 2.8, range 1-6, SD 1.5, number of capitula assessed 320; 6.8% of capitula infested and twice as many in terminal than

auxiliary capitula; eggs low down among the florets; first and early second stage larvae burrow down a floret towards the ovary (Fig. 6a); subsequent stages burrow into ovaries and lower ends of florets, thereby detaching them from the receptacle; in capitula with 3 or more larvae a majority of ovaries are consumed and loosened florets are a sign of infestation; third stage larvae burrow into the receptacle (Fig. 6b); larvae were occasionally found in stems of foodplants having tunnelled through it; pupation takes place within the excavated space of the capitulum; occasionally capitula with no larvae were encountered although signs of feeding, black material and damage to the lower ends of florets, were present.

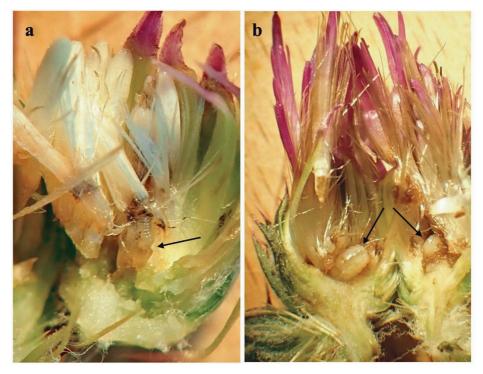


Fig. 6. *Xyphosia miliaria* infestation of *C. palustre*: a, arrow points to a second stage larva feeding at the base of a flower; b, arrows point to third stage larvae feeding on receptacle tissue.

Trophic morphology and feeding mechanism

Apart from differences in size which was not assessed in detail, first and second stage larval head skeletons are distinguished from the third in *T. vespertina* and *X. miliaria* by the red not black mandible hooks. First and second stage head skeletons of *T. neesii* have black hooks and are only sometimes vaguely red at the apex of the main, dorsal hook.

Third stage, larval head skeletons of all three species are similar in form (Fig. 7). The dorsal cornu is not evenly sclerotised and except for *T. vespertina* is divided by a V-shaped gap in sclerotisation. The ventral cornu lacks a dorsal apodeme, is slightly shorter than the dorsal cornu and has a large, prominent window (gap in sclerotisation), about as high as long in *X. miliaria*, and longer than high in *T. neesii* and *T. vespertina*. In a living larva, the dorsal and the

ventral cornu diverge from the vertical plate, the ventral cornu to a slightly greater extent and the apex is slightly inturned. The vertical plate and dorsal and ventral cornu are connected by a translucent membrane. The vertical plate is about twice as high as long with a dorsal bridge, which in *X. miliaria* projects from the dorsal margin (Fig. 7). The anterior margin of the vertical plate is almost at a right angle to the ventral cornu and more or less straight except for the parastomal bar about midway along its height which extends anteriorly and fuses with the intermediate sclerite. Apart from the parastomal bar, the vertical plate and the intermediate sclerite are separated by a narrow gap in sclerotisation and the connecting membrane is apparently flexible and can close.

The intermediate sclerite is heavily sclerotised and near the mid-point, a ventral bridge projects below. Behind the ventral bridge the intermediate sclerite extends in a vertical plane and abuts the vertical plate below the parastomal bar. In front of the ventral bridge the intermediate sclerite extends in a horizontal plane and abuts the rear margin of the mandible and a narrow, flexible gap exists between these two sclerites. From the anterior margin of the ventral bridge a tapering, well-developed labial apparatus is attached, comprising a basal labial plate and sclerites. The labial apparatus inclines up and terminates in a lightly-sclerotised, finger-shaped projection which ends between the mandibles and from its ventral margin, is a translucent, disc-shaped projection (Figs 8 & 9).

In *T. neesii* the main, dorsal mandible hook is relatively short in length and narrow in width with a single secondary hook below and almost directly underneath. The dorsal hooks of *T. vespertina* and *X. miliaria*, being larger, are more conspicuous and the single secondary hook is conspicuously lateral to the main hook. In all three species the mandible base is elongate and fused to the oral cavity, the upside down, cup-shaped section of the pseudocephalon, the sides of which ensheath the mandibles. The open part of the oral cavity that leads to the mouth is confined to just below and between the mandible hooks. At their ends the extended mandible bases are connected by a bridge of light sclerotisation. Posterior to this fusion product a mostly translucent oral plate is attached (Fig. 9). The upper, outer margins of the oral cavity, which are fused on to the mandibles, are coriaceous in the two *Tephritis* species and coated in lines of cirri in *X. miliaria* (Fig. 9). The fleshy labial lobe between and below the mandible hooks is small and insignificant in all three species.

Observations and videos showed that the feeding mechanism of all larval stages of each of the three species was similar. To feed, the head skeleton pivots up and down, which draws the mandibles across plant tissue and fragments it. In third stage larvae, pivots are at a rate of about two per second. Fragments gather in the space between the mandible hooks and are sucked up by the head skeleton pump. During feeding in second and third stage larvae, a peristaltic wave is usually held up between the front of the abdomen and the thorax posterior to the prothorax, with the result that this section of the body is expanded and pressed against the sides of the feeding track. This modified shape is often maintained when the larva is at rest, especially in *T. neesii* (Fig. 10).

The oral plate moves forwards and backwards in time with head skeleton pivots. Due to their fusion to the oral cavity, the mandibles are almost immobile during pivoting and do not independently lower and elevate. Their only movement is a slight divergence or outward movement that takes place at the start of each pivot, but it is less than the distance between the mandibles when at rest. Larvae access plant tissue on all sides by turning the prothorax laterally or turning the entire body, and they also feed upside down. During feeding larvae may incline the head skeleton by a right angle or more relative to the longitudinal axis of the body. Larvae move slowly and, when taken from their capitula and placed on a flat substrate, such as a Petri dish, are poor at locomotion.

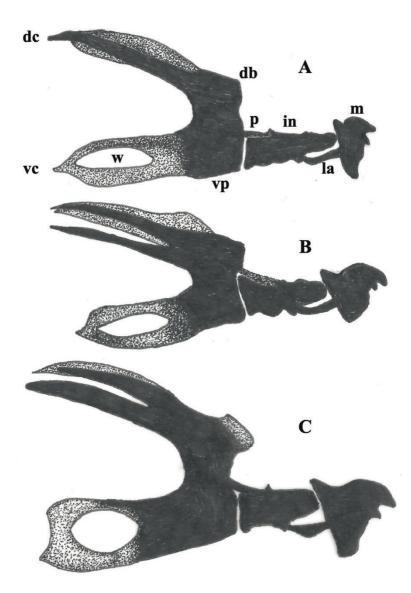


Fig. 7. Third stage larva, whole head skeletons, lateral view, mandible to the right, length about 0.5mm: A, *T. neesii*; B, *T. vespertina*; C, *X. miliaria*; dc = dorsal cornu; db = dorsal bridge; in = intermediate sclerite; la = labial apparatus; m = mandible; p = parastomal bar; vc = ventral cornu; vp = vertical plate; w = window.

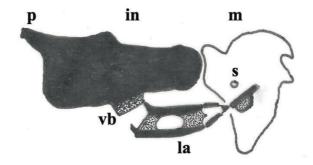


Fig. 8. *Tephritis vespertina*, intermediate sclerite, labial apparatus and mandible, lateral view, one mandible removed and a connection to the ventral bridge cut to show floor of the labial apparatus (la): in = intermediate sclerite; la = labial apparatus; m = mandible; p = parastomal bar; s = mandible sensillum; vb = ventral bridge.

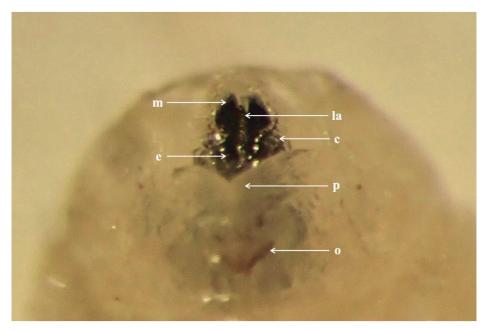
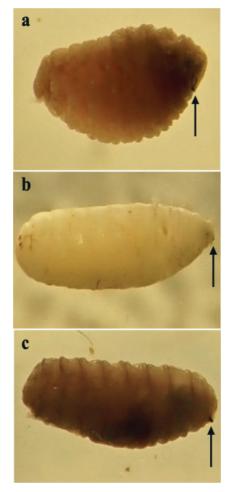
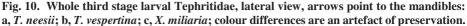


Fig. 9. *Xyphosia miliaria*, third stage larva, ventral view of the head: c = cirri marking the sides of the oral cavity, the apparent fleshy rim round the mandibles is an artefact of preservation; <math>e = elongate mandible base; la = finger-like apex of the labial apparatus; m = mandible hook; o = sclerotised section of oral plate visible through the body wall; p = anteroventral margin of the prothorax which is separated from the pseudocephalon by a deep infold of the body wall within which the mandibles are often concealed.





Discussion

The main aim of this study was to determine the limits of similarity in the feeding mechanisms and patterns of larval *T. neesii*, *T. vespertina* and *X. miliaria* that develop in the capitula of different species of Asteraceae. The larvae of all three species feed on the developing flowers especially the ovaries, and pupate in the capitulum. This is similar to the larva of *T. bardanae* in the capitulum of *A. minus* which as Straw (1989) points out, is advantageous due to high levels of sequestered nutrients.

Foodplant capitula vary in size and shape. The *L. vulgare* capitulum is broad with short florets and around the outer rim at ovary level, *T. neesii* larvae feed transversely through it. In contrast, the *H. radicata* capitulum is narrow with florets about 3x longer and *T. vespertina* larvae feed along their length. Within the flask-shaped capitulum of *C. palustre*, *X. miliaria* larvae feed

in both orientations. Up to the early third stage, larvae feed vertically within and between florets, thereafter they also feed transversely at ovary level. Unlike *T. neesii* and *T. vespertina*, in capitula with three or more *X. miliaria* larvae, all or most flowers are consumed, a pattern similar to that described for this species by Persson (1963). *Tephritis vespertina* is the only species not to feed on the receptacle, which in *H. radicata* is small and thin (Fig. 2c).

Capitula feeding in tephritids can be elaborate. For instance, Romstöck (1987), quoted in Headrick and Goeden (1996), found that the larva of *Tephritis conura* Loew (Tephritidae) augments food levels by inducing callus tissue to grow in the receptacle of its foodplant, *Cirsium heterophyllum* (Asteraceae). Straw (1989) reported a similar phenomenon in *T. bardanae*. The third stage larva of the Nearctic *Paracantha gentilis* Hering (Tephritidae), feeds on sap that fills depressions made in the receptacle of its foodplant, *Cirsium californicum* (Asteraceae) (Headrick and Goeden 1990a). Callus tissue formation and sap feeding were not observed in the tephritid species studied here.

The *L. vulgare* capitulum represents a larger food volume compared to those of *H. radicata* and *C. palustre*. This may in part explain the higher mean number of *T. neesii* larvae recorded per capitulum, 4.1 compared to 1.6 for *T. vespertina* and 2.8 for *X. miliaria*. An additional factor affecting numbers of larvae could be the clumped nature of *L. vulgare* plants which is a growth feature typical of this species (Stace 2010). It is possible that once found, *T. neesii* females reside for long periods in a clump and oviposit a high proportion of their egg loads. This is because the chances of finding another clump are low compared to females of *T. vespertina* and *X. miliaria*, whose foodplants are more widely dispersed. This may explain the high levels of *T. neesii* infestation, more than 90% of capitula infested compared with less than 20% in *T. vespertina* and *X. miliaria*. Even in heavily infested capitula, intact florets remained and aggressive interactions between larvae were not observed, but this possibility was not investigated thoroughly.

Larvae of all three tephritid species use a fragmentation feeding mechanism in which the mandibles are drawn across plant tissue by a pivoting head skeleton. This is the usual mechanism of cyclorrhaphan larvae feeding on firm as opposed to viscous food (Rotheray 2019a). Holding up peristaltic waves during feeding and causing the front of the body to expand and press against the substrate, helps maintain body position during fragmentation. This is also a feature of cyclorrhaphan larvae that excavate firm material (Rotheray 2019a). Fixed mandibles in the three tephritid species studied here may be a specialisation among larvae that feed on firm tissue, but too few taxa have been assessed to be sure. Other larvae feeding on firm food with fixed mandibles include some leaf-mining *Amauromyza* Hendel larvae (Agromyzidae) whose mandibles are fixed in an upright position with the hooks facing forward (Rotheray 2019b). This position suits fragmentation and since the mandibles no longer move, reduces the energy costs of feeding. As with *Amauromyza* and the tephritids studied here, fixed mandibles are unlikely to be confined to these particular species, but a characteristic of a higher taxon to which they belong.

In *Amauromyza* the mandibles are fixed by fusion with the oral cavity and buttressing against the intermediate sclerite (Rotheray 2019b). So it is with *T. neesii, T. vespertina* and *X. miliaria* except that below the hooks, the oral cavity is more extensively fused over the mandibles, and the open part, leading to the mouth, is confined to just below and between the hooks. An elongate mandible base provides for connection with the oral cavity and is a feature of *Amauromyza, T. neesii, T. vespertina* and *X. miliaria*. A sclerotised connection between the mandibles at the elongation apex, helps create a stable structure able to withstand fragmentation forces. The oral plate which attaches to this fusion product has muscles inserted on it and they help draw the mandibles through tissue, but the main power of fragmentation comes from the head skeleton pivot. A movement that is due to large muscles that insert on the basal sclerite and originate on the thoracic body wall (Hartley 1963, Roberts 1970, Rotheray 2019a).

The mandibles, intermediate and basal sclerites are buttressed together which supports pivoting, i.e. the front margin of the intermediate sclerite matches the rear margin of the mandibles and its rear margin matches the front margin of the basal sclerite. The parastomal bar projects from the basal sclerite and fuses with the intermediate sclerite. Nonetheless, slight gaps in sclerotisation exist at either ends of the intermediate sclerite and during pivoting, contraction of various muscles, labial retractors, oral plate retractors and body wall muscles, etc., probably close these gaps, creates a pivot arm across the head skeleton and accounts for the slight outward movement of the mandibles at the start of each pivot.

In cyclorrhaphan larvae, head skeleton performance is optimised via modifications to its size, shape and degree of sclerotisation (Rotheray 2019a). For instance, fixed mandibles in *Amauromyza* correlate to a relatively short ventral cornu that lacks a dorsal apodeme (Rotheray 2019b). These are probably adjustments in response to absence of need to support mandible muscles that originate on the ventral cornu. Supporting a similar optimisation, the ventral cornu of *T. neesii*, *T. vespertina* and *X. miliaria* also lack dorsal apodemes and are shorter than the dorsal cornu. Optimisation in the tephritids is also indicated by the large window in the ventral cornu implying a reduction in sclerotisation, and this extends to reduction of sclerotisation in the dorsal cornu.

Another optimisation is to the labial lobe. In cyclorrhaphan larvae that feed on viscous food the labial lobe lies between the mandibles, covers the mouth and is relatively large and fleshy. It is retracted during feeding to provide access to the mouth, but in larvae that fragment hard food, such as T. neesii, T. vespertina and X. miliaria, it is reduced and insignificant. This is probably because a large, fleshy lobe would interfere with fragmentation. These larvae possess an alternative mechanism for accessing the mouth in the form of the labial apparatus. From the ventral bridge the labial apparatus is plate-like, inclines upwards and tapers to a finger-like projection that reaches forward between the mandibles. In contrast, the labial apparatus of most higher Cyclorrhapha is fused into the floor of the atrium, an extension of the alimentary tract anterior to the salivary duct (Teskey 1981, Rotheray 2019a). Muscles insert on the labial apparatus (Roberts 1970), and in higher cyclorrhaphan larvae their action facilitates the passage of food by dilating the atrium. In certain lower cyclorrhaphan larvae the labial apparatus is free apically and videos show that it depresses or lowers during feeding which helps to guide food into the mouth (Hartley 1963, Rotheray and Lyszkowski 2015). In T. neesii, T. vespertina and X. miliaria the action of the labial muscles is similar to a lower cyclorrhaphan depression of the labial apparatus and hence, provides access to the mouth, natural elasticity closes it. The upwards incline facilitates closure and the labial apparatus may also play roles in controlling and helping food pass through the atrium, for instance, by opening wider to accommodate large fragments. This modified labial apparatus is the median labial lobe of Headrick and Goeden (1990b) and a feature of nonfrugivorous Tephritidae (Headrick and Goeden 1996).

Tephritis neesii, T. vespertina and *X. miliaria* share feeding mechanisms, but the modest differences in the size, shape and arrangement of the mandible hooks may be significant. The most disparate of the three is *T. neesii*, comprising a shorter, thinner main hook and a secondary hook that is almost aligned with it underneath. The main hooks of *T. vespertina* and *X. miliaria* are larger and their secondary hooks are sited more laterally. Narrow, aligned mandible hooks are probably efficient for fragmenting dense food that does not give way when the mandibles are pressed against it, such as the flowers of *L. vulgare*. The flowers of *H. radicata* and *C. palustre* are less dense and, to overcome their tendency to give way when mandibles are pressed against them, longer, less aligned hooks are perhaps more effective since they are better able to catch, pierce and tear tissue.

In summary, the information presented here suggests that capitulum qualities of size, shape and tissue density are important determinants of larval feeding mechanisms and patterns in T.

neesii, *T. vespertina* and *X. miliaria*. Only assessment of a wider range of capitulum developing species will determine if particular points along the continua of capitulum size, shape and density are able to predict feeding mechanisms and patterns. Examination of larval responses to these continua might usefully be extended to frugivorous tephritids, since these qualities are just as variable in fruits. Moreover, since some are agricultural pests, greater attention has been paid to frugivorous than capitulum feeders and much of the data is probably available, albeit scattered across the literature.

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Recent range expansion in British hoverflies (Diptera, Syrphidae)

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Summary

Two forms of range expansion are described: rapid northward shifts by species from southern England, and southward movement by species that were formerly confined to Scotland and north-west England. In both cases there are examples of species that are considered to have been 'native' to the British Isles, as well as recent arrivals. We applied three different analytical methods: distribution mapping: Maxent predictive mapping using relevant environmental variables; and FRESCALO frequency analysis. The most extreme examples are discussed and we postulate why such changes have happened. In addition, there have been accidental imports, most of which have not been possible to follow in detail because they arrived long before there was an active recording scheme; but one, *Cheilosia caerulescens* (Meigen, 1822), arrived at the time that recording has become more effective and is therefore described.

Our analysis suggests two separate drivers of 'natural' range expansion. Firstly, the climate of southern England has changed dramatically since the early 1990s; and, secondly, a suite of specialist species has taken advantage of maturing conifer plantations and the development of a substantial resource of decaying conifer timber (especially in the roots and stump). Range expansion by horticultural imports appears to derive from multiple introductions and gradual expansion, especially in highly urbanised areas.

Introduction

Hoverflies are part of a large assemblage of 'pollinators' that have attracted considerable research interest in the last decade or more (e.g. Biesmeijer *et al.* 2006, Powney *et al.* 2019). Most publications concentrate on the issue of decline using occupancy models but some such as Hallmann *et al.* (2017) quote insect biomass. Yet, amongst the depressing statistics of decline, there are species whose fortunes are improving through range expansion. This account discusses those hoverfly species that have undergone the most dramatic range expansion since the early 1990s and attempts to identify the environmental factors that drive the changes.

Range expansion in insects is well-documented (e.g. Hill *et al.* 2001; Eversham and Cooper, 1998; Sutton *et al.* 2017). It is one of a series of responses to climate change listed by Stange and Ayres (2001), but is not confined to climate influences. In addition to northward range expansion across the British Isles by charismatic hoverflies such as *Volucella zonaria* Poda, 1761, *V. inanis* Linnaeus, 1758 and several others, three hoverfly species that were once thought of as strictly 'Scottish' or confined to the north and west of Britain have spread southwards at a remarkable rate. Furthermore, we consider species that have been accidentally imported and have subsequently become widely established.

This analysis is based on records submitted to the British Hoverfly Recording Scheme (HRS) which, since its inception in 1976 (Ball and Morris 2000), has compiled data from a variety of sources. Data from academic studies, literature records and some museum specimens provide some detail but the main contributions come from a network of voluntary observers. The database currently holds more than 1.3 million records and is amongst the largest invertebrate datasets in Great Britain (after Lepidoptera and Odonata). It is growing at a rate of over 60,000 records per year and has contributions from around 8,000 individuals (precise numbers are not possible because some contributors use different names on different input systems and have been known to use more than one system to input records).

The observer base was comparatively small (and constant) until the advent of digital photography and the growth of social media for natural history recording from around 2009 onwards (Morris and Ball 2019a). Consequently, the pace of change in known hoverfly ranges may partially reflect an increase in recorder effort. Early changes may also have been masked by a relative lack of recorders, whereas current recorder levels are more likely to detect the early signs of range expansion, if the species concerned can be identified from a photograph.

Detecting change

Prior to the mid-1990s, there was little evidence for major changes in the distribution of Britain's hoverflies. The data were comparatively sparse and the numbers of recorders was small: interpretation was complicated by these shortcomings. The arrival and subsequent spread of the readily recognised *Eriozona syrphoides* (Fallén, 1817) (Crow 1968) might have been possible to document had there been enough recorder coverage, but at the time there were relatively few recorders and no system for compiling records.

The first species in which obvious changes could be tracked were two large and charismatic species that were recorded by a wide range of observers: *Volucella zonaria* and *V. inanis*. These species attracted a lot of attention from a wide range of people and published reports provide sufficient information to build a picture of their distribution prior to the establishment of the HRS. By 2004 they were clearly moving northwards (Morris and Ball 2003, 2004). In the following 16 years (to 2020), northward range expansion has become increasingly obvious in several more species, especially: *Cheilosia soror* (Zetterstedt, 1843), *Epistrophe diaphana* (Zetterstedt, 1843) and *Rhingia rostrata* (Linnaeus, 1758).

There have also been several new arrivals that have become firmly established in the past 30 years. *Epistrophe melanostoma* (Zetterstedt, 1843) is typical of a European species that has arrived in southern England, possibly as a result of climate warming. *Sphegina sibirica* Stackelberg, 1953 was first detected in 1991 (Stubbs 1994), but a specimen taken near Inverness in 1976 (Stubbs and Falk 2002) indicates that it may have arrived earlier. It is now distributed over northern and western Britain and its distribution in Europe prior to its arrival in Scotland was primarily Scandinavia, but extending south to Belgium and Germany (Thompson and Torp 1986). *Cheilosia caerulescens* (Meigen, 1822) (Collins and Halstead 2008) completes a trio of species that have arrived and spread recently, and is suspected to have been introduced as larvae in house leeks (*Sempervivum* sp.) imported via the horticultural trade.

Methods

This analysis was confined to a small group of species in which there were strong indications of range expansion. The list was established after initial appraisal of basic maps of all British species, using 'expert judgement' and our detailed knowledge of the species involved. Species showing the most substantial range changes since 1990 were chosen for two reasons: firstly, the levels of recorder effort from 1990 onwards have been enough to detect noteworthy levels of change; and, secondly, all the most dramatic changes that we can follow have occurred after this date. Major changes prior to this date have either been discussed in previous papers (*Volucella inanis* and *V. zonaria*; Morris and Ball 2003, 2004) or the data are too weak to allow detailed interpretation (e.g. *Merodon equestris* (Fabricius, 1794), *Eumerus funeralis* Meigen, 1822 and *Eriozona syrphoides*). Each species is discussed separately because there is no consistent pattern to the changes.

We used three separate analytical processes. Distribution mapping is the traditional way in which changes in species distribution is depicted in atlases. A single map using different symbols to depict particular time-series will show the current situation but any recent symbols will obscure older ones or the absence of any detected presence. Depicting change therefore depends upon several illustrations in a time-series. Our analysis is based on four maps from four periods (henceforth referred to as 'epochs'): 1992 to 1999, 2000 to 2007, 2008 to 2015 and 2015 to 2019 and reflects the availability of the most limiting environmental parameters within our second analysis using Maxent (Phillips *et al.* 2018).

In order to explore possible environmental drivers, species distribution models (SDM) were fitted using Maxent, accessed via the dismo package (Hijmans *et al.* 2017), and mapped using the raster package (Hijmans 2015). Environmental layers at 1km square resolution were derived from European Space Agency (ESA) land cover maps (ESA 2017), a soil classification from the European Soils Database (Panagos *et al.* 2012), gridded weather observations from the Meteorological Office (Met Office *et al.* 2017), and topographical information (Digital Elevation Model - DEM) derived from NASA's Shuttle Radar Topography Mission (NASA JPL 2013).

SDMs were trained using the kilometre squares in which the target species were observed during the period for which all the environmental layers used for modelling were available. The most limiting of these layers were the ESA Land Cover maps, which are currently available from 1992 to 2015.

Maxent models were trained using half of the observed occurrences chosen randomly from those available. A background sample of 5,000 one-kilometre squares was also chosen randomly from those squares from which at least one hoverfly record was received by the HRS during the appropriate period. The potential distribution of the species was then predicted for the complete set of environmental layers and evaluated using the withheld observations.

To explore trends in distribution changes, we used the FRESCALO (FREquency SCAling LOcal) method of Hill (2011) to correct for the confounding effects of spatial and temporal variation in recording effort when attempting to assess changes in the frequency and distribution of species. Hill made available FORTRAN code for the computation of his method along with the example datasets used in his paper. An R package, rFrescalo (see Hill 2011 for link), implementing the method was developed by one of the authors (SGB) and has been verified using Hill's examples. A FRESCALO analysis of unique combinations of species, hectad and year from 1980 to 2018 was generated. This analysis is depicted as a 'trend' using the FRESCALO "TFactor". The TFactor is a measure of the relative frequency of occurrence of the species corrected for recording effort, against year with error bars showing its standard deviation.

Results

After initial review of possible candidates, a total of 11 species were considered suitable for analysis (Table 1).

Species	Status	Range	Main drivers
		expansion	
Cheilosia caerulescens	Recent introduction	North and west	Poor biosecurity – numerous new introductions
Cheilosia soror	Native	North and west	Maximum temperature of warmest month (°C)
Cheilosia vulpina	Native	North and west	Maximum temperature of warmest month (°C)/Soil type
Callicera rufa	Native	South and east	N/A
Epistrophe diaphana	Native	Northwards but less western	Maximum temperature of warmest month (°C)/Soil type

Epistrophe melanostoma	Arrived ~1986	North and east	N/A
Rhingia rostrata	Native	North and west	Soil type/ Maximum
			temperature of warmest
			month (°C)
Sphegina sibirica	Arrived ~1991	South and east	N/A
Volucella inanis	Native	North and west	Maximum temperature
			of warmest month (°C)
Volucella zonaria	Established ~	North and west	Urban & suburban
	1943		cover/ Annual mean
			temperature (°C)
Xylota jakutorum	Native	South and east	Coniferous Woodland
			cover

Table 1. Range change and potential drivers (where detected) for 11 species of British hoverflies believed to be undergoing substantial changes in range.

Distribution mapping provides strong visual evidence of range change over the four epochs, although the results for the period 2016-2019 are weaker than the preceding ones. This weakness is inevitable because the timespan is just four years rather than eight. Frequency analysis using FRESCALO outputs are also shown for most species. It should be borne in mind that these outputs can be negatively influenced by the rise in popularity of photographic recording from around 2010 onwards (Ball and Morris, unpublished). Outputs for *Cheilosia soror* and *C. vulpina* illustrate this problem which is expressed in a strong downward trend from around 2010 onwards.

Results from the Maxent analysis were often inconclusive as in many cases the Receiver Operating Characteristic curve (ROC) was weak and we were unable to achieve a satisfactory Area Under the Curve (AUC) for most species. The AUC provides an indication of the performance of the model and clearly the model in many instances did not achieve the standard (85%) required to be considered a 'good' fit. Nevertheless, the critical environmental parameters for each epoch do usefully indicate the most likely factors responsible for the range change that has been identified from the process. In three species (*Volucella inanis, V. zonaria* and *Xylota jakutorum* Bagachanova, 1980), the results were more reassuring and the AUC for most outputs for these species was 85% or more. Where Maxent outputs provide a useful indication of possible environmental influences, the top 5 parameters for each epoch have been tabulated. In several cases, the numbers of records available for a particular epoch are too low to permit a meaningful Maxent run. In these cases, Maxent outputs have not been presented.

Three separate reasons for changes in range in British hoverflies can be recognised in the species discussed in this analysis: northward range expansion that correlates with climate warming; southward expansion of formerly northern species that can be attributed to changes in land use and woodland development; and the introduction of non-native species that are unlikely to have ever reached Britain without assistance. Each is discussed separately.

Northward range expansion

In this section, we consider species that were once confined largely to southern England but have advanced their range northwards, often quite dramatically. There are several other species where we believe there is limited evidence for northward movement or for a general increase in the frequency with which they are seen. The latter will be addressed in the final discussion.

Cheilosia soror (Figs 1 & 2; Table 2)

In the 1980s and 1990s, this species was believed to be closely associated with calcareous situations and detailed mapping in Surrey seemed to support this position (Morris 1998). Even then, however, outlying records from urban London raised the possibility that calcareous influences might not be critical. Records prior to 2000 were extremely patchy and sporadic, lying primarily south of a line between The Wash and the Severn Estuary. Occasional more northerly records require further investigation and misidentification cannot be discounted.

Since around 2005, the numbers of records have increased markedly, but its north-eastern range barely changed, at least until around 2017 when it was detected further into Lincolnshire than hitherto known. This northward shift had been expected and was detected by regular surveying (by RKAM, who visited suitable sites on a sequence of years until it was located). Meanwhile, in southern England, it has become one of the commonest *Cheilosia* in many places. The most obvious feature of this species' range change is the degree to which it has become a regular part of the hoverfly fauna in areas where it was previously rare or unknown.

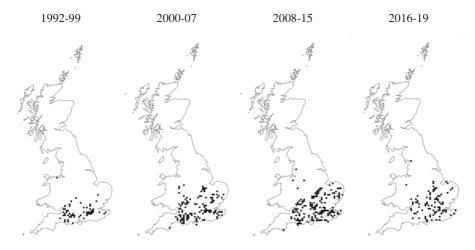


Fig. 1. Recorded distribution of *Cheilosia soror* during four epochs between 1992 and 2019.

Maximum temperature of warmest month (°C) consistently appears to be a dominant factor in the SDMs generated by Maxent for all three epochs. The scale and consistency of this dominance, especially since 2000, suggests that *C. soror* is fitted to hotter climates. The combined values of weather variables in each epoch show an increasing trend for importance, rising from 42.1% in 1992 to 1999 to almost 57.7% in 2008 to 2015; again, indicating that climatic factors are the dominant influence on the distribution of *C. soror*. It is therefore surprising that urban and suburban land cover only feature within the top five variables for the epoch 2000 to 2007. This is at variance with species such as *Volucella inanis* and *V. zonaria*, which clearly benefit from 'urban heat island' effects, and suggests that other variables such as soil type and possibly the biotope are also influential.

Parameter	Feature	% contribution in each epoch		
		1992-99	2000-07	2008-15
Weather	Maximum temperature of warmest month (°C)	26.19	45.82	45.02
Weather	Mean temperature of driest month (°C)	0.31	0.76	11.63
Soil	Dominant FAO soil class of 1km square (categorical)	4.21	19.65	11.28
DEM	Average elevation of pixels in 1km square (m)	17.51	6.48	7.64
Land Cover	Broadleaved Woodland cover (hectares)	3.32	3.11	5.63
Soil	Average soil moisture content for 1km square (categorical)	12.97	6.06	4.98
Land Cover	Urban & suburban cover (hectares)	1.02	4.30	1.58
Weather	Seasonality of rainfall (mm)	9.67	0.61	1.01
Weather	Mean temperature of coolest month (°C)	5.96	0.97	0.06

Table 2. The top five environmental variables governing Maxent SDMs for *Cheilosia soror* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

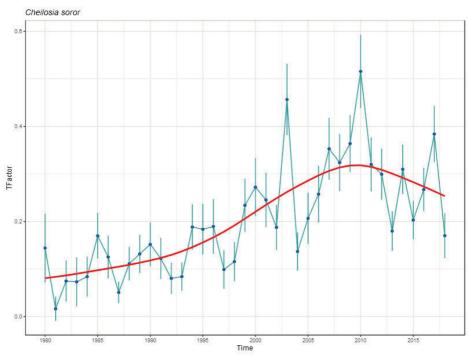


Fig. 2. Frequency of occurrence of *Cheilosia soror* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Cheilosia vulpina (Figs 3 & 4; Table 3)

This is a relatively large and readily identifiable species (in the UK) if examined under the microscope and compared against *C. variabilis* (Panzer, 1798). Confusion is most likely with large individuals of *C. proxima* (Zetterstedt, 1843) if individuals are identified in the field without critical examination under magnification. Older records from northern England and Scotland may not be reliable, as there is growing evidence that this was a southern species whose range and abundance has expanded substantially in the past ten years.

Two environmental variables dominate the Maxent SDMs for *C. vulpina*: maximum temperature of warmest month (°C) and soil type. For *C. vulpina*, climatic factors appear to have a relatively constant influence on the SDMs, ranging from 37.3% in 1992 to 1999, to 42.6% and 37.2% in the subsequent epochs respectively. The influences of land-cover on the epoch from 2008 to 2015 may be important, as the known distribution of *C. vulpina* is seemingly governed by land use and soil type to a much greater extent than *C. soror*.

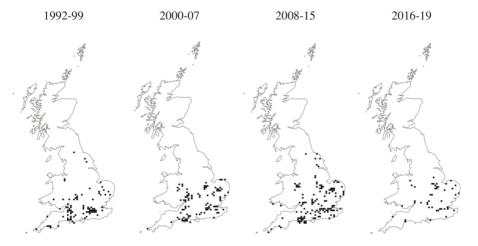


Fig. 3. Recorded distribution of *Cheilosia vulpina* during four epochs between 1992 and 2019.

	Feature	% contribution in each epoch			
Parameter		1992-99	2000- 07	2008- 15	
Weather	Maximum temperature of warmest month (°C)	10.56	37.58	25.71	
Soil	Dominant FAO soil class of 1km square (categorical)	16.31	20.70	16.82	
Land Cover	Urban & suburban cover (hectares)	0.71	2.36	14.25	
Weather	Mean temperature of warmest month (°C)	8.43	0.19	9.17	
Land Cover	Grassland cover (hectares)	3.95	3.83	5.73	
Land Cover	Broadleaved Woodland cover (hectares)	3.01	4.35	4.05	
Weather	Seasonality of temperature (°C)	7.86	0.0541	1.09	

Weather	Mean temperature of coolest month (°C)	8.30	1.76	1.09
Weather	Rainfall during coldest quarter (mm)	2.17	2.99	0.16

Table 3. The top five environmental variables governing Maxent SDMs for *Cheilosia vulpina* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

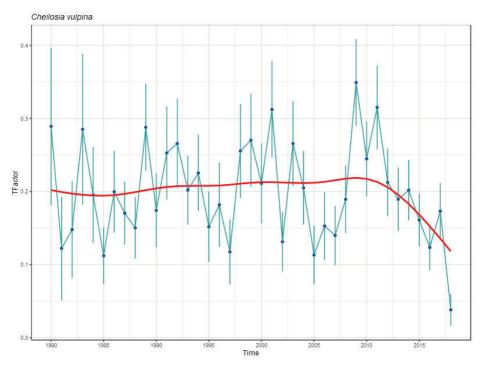


Fig. 4. Frequency of occurrence of *Cheilosia vulpina* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Epistrophe diaphana (Figs 5 & 6; Table 4)

This is a very distinctive animal when the recorder is familiar with it. Our experience of working with photographic recorders has shown, however, that it is frequently confused with the genus *Syrphus*. Older records, especially those from North Wales in the early 1980s, should therefore be treated with caution.

Its expansion started in the early 2000s, especially within Bedfordshire, Northamptonshire and south Lincolnshire where RKAM tracked its progress. It is noteworthy that whilst *E. diaphana* continues to be absent from most of western England, it has spread throughout eastern England, suggesting that it favours the hotter, drier climate. The Maxent outputs also support this interpretation, with Maximum temperature of warmest month (°C) dominating the key environmental parameters from 2000 onwards. It should be noted, however, that rainfall is a further important factor.

The coincidence of the same three environmental parameters, in the same order, dominating both the epochs from 2000 onwards may also be indicative of the dominant influences, especially as urban land cover could suggest urban heat island effects. It should be borne in mind, however, that urban factors may simply reflect the dominant concentration of recording activity.

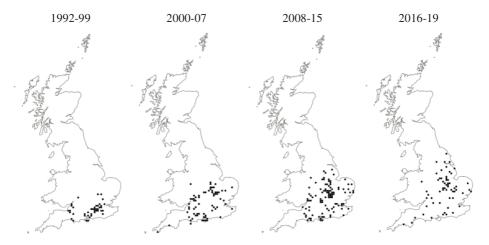


Fig. 5. Recorded distribution of *Epistrophe diaphana* during four epochs between 1992 and 2019.

Parameter	Feature	% contribution in each epoch		
Farameter		1992-99	2000- 07	2008- 15
Weather	Maximum temperature of warmest month (°C)	17.57	36.53	41.15
Soil	Dominant FAO soil class of 1km square (categorical)	10.48	15.55	11.65
Land Cover	Land Cover: Urban & suburban cover (hectares)	2.30	5.55	8.79
Weather	Rainfall during wettest quarter (mm)	0	0.21	5.08
Soil	Average soil moisture content for 1km square (categorical)	0.87	3.26	4.17
Weather	Mean temperature of driest month (°C)	0.26	4.83	2.73
Weather	Annual mean temperature (°C)	17.11	1.72	2.08
Weather	Rainfall during driest month (mm)	30.4575	5.0532	0.2541
Weather	Rainfall during wettest month (mm)	7.2028	0.4948	0

Table 4. The top five environmental variables governing Maxent SDMs for *Epistrophe diaphana* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

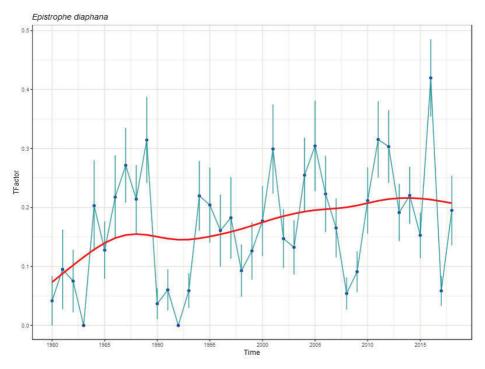


Fig. 6. Frequency of occurrence of *Epistrophe diaphana* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Epistrophe melanostoma (Figs 7, 8 & 9)

When first recognised as a British species (Beuk 1991), the differences between *E. melanostoma* and *E. nitidicollis* (Meigen, 1822) were imperfectly understood by British recorders. It was subsequently found in RKAM's collection from 1986 (Morris 1998). Photographic recording has helped to improve our knowledge, as this is a species that can be initially detected from its bright-orange colouration in the living animal (*E. nitidicollis* is somewhat yellower). Reliance on this 'jizz' character is unwise, however, because there is considerable variation and important differences can be found in the dusting on the frons, colour of scutellar hairs (very variable in *E. nitidicollis*) and in the colour of the mouth edge. Confusion with other European species such as *E. flava* Doczkal & Schmid, 1994 is also possible and care must be taken to make sure that these possibilities have been ruled out. Experience also suggests that *E. melanostoma* emerges a little earlier than *E. nitidicollis* (Fig. 9).

This species' range expansion has been slow, and until the 2000s it was mainly confined south of the Thames. Since 2015, northward and eastern movement has taken it into Bedfordshire and Essex, with records suggesting that its pace of movement is accelerating. Experience from the site from which it was first reported (Mitcham Common) shows that it is well-established and frequently recorded (far more so than *E. nitidicollis*).

Maxent outputs for three epochs were not possible as there were too few records for the period 2000 to 2007. It is difficult to be sure why *E. melanostoma* was so rarely recorded during this time and is possibly a reflection of recorder activity rather than a population change.

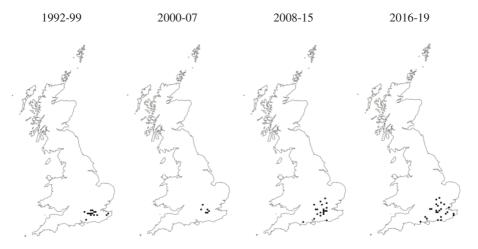


Fig. 7. Recorded distribution of *Epistrophe melanostoma* during four epochs between 1992 and 2019.

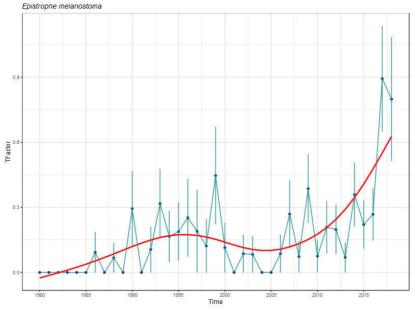


Fig. 8. Frequency of occurrence of *Epistrophe melanostoma* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

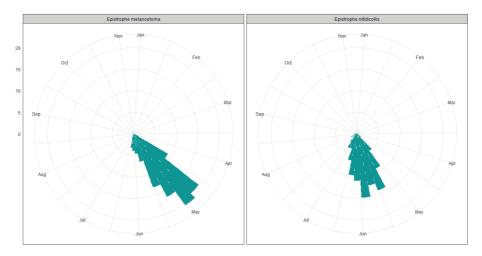


Fig. 9. Phenology of *Epistrophe melanostoma* and *E. nitidicollis* showing the differential in emergence in which *E. melanostoma* appears first.

Rhingia rostrata (Figs 10 & 11; Table 5)

When the first Insect Red Data Book (Shirt 1987) was published, *Rhingia rostrata* was rated as Vulnerable and was a little-known species that was noted for occasional mass-occurrences (Morris 1998; Stubbs and Falk 2002). It was confined to a few sites in southern England, Pembrokeshire and the southern end of the Welsh borders. A few scattered northerly records are probably misidentifications, but we cannot be sure. Range expansion commenced in the late 1990s, especially through the Welsh borders, and by 2004 it had become established in eastern England too (in the vicinity of Peterborough). Thereafter, its spread northwards has been dramatic, reaching Cumbria in 2014 and now being well-established across a substantial part of north-west England. Progress through eastern England has been slower, with few records east and north-east of Leeds and the north-Pennines.

In the past, there has been uncertainty about some northerly records of *R. rostrata* and although we cannot prove it, we believe some to be erroneous. Furthermore, when *R. rostrata* was very rare, it is possible that it was overlooked amongst the plethora of *R. campestris* Meigen, 1822. Today, there are times when *R. rostrata* is by far the commoner of the two, especially in parts of Northamptonshire and Cambridgeshire, and in the Welsh Marches. This species is generally identifiable from photographs and consequently it is now far better recorded.

Maxent analysis of environmental variables gives a range of AUC from 62.67% to 86.17% with considerable variation in between. The top five variables are not consistent and it is difficult to be sure why *R. rostrata* has expanded its range so markedly. If, as the Maxent output suggests, soils are the governing factor, then there is no reason for such a dramatic change.

It would seem that climate variables are highly influential for both the 1992 to 1999 and 2000 to 2007 epochs (44.3% and 47.7% respectively), but these results are confounded by the 2008 to 2015 epoch in which the climate variables make up just 18.6% of the total. These dramatic differences suggest that there is a further factor that is critical but has not been recognised.

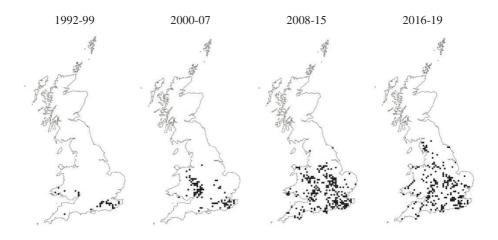


Fig. 10. Recorded distribution of *Rhingia rostrata* during four epochs between 1992 and 2019.

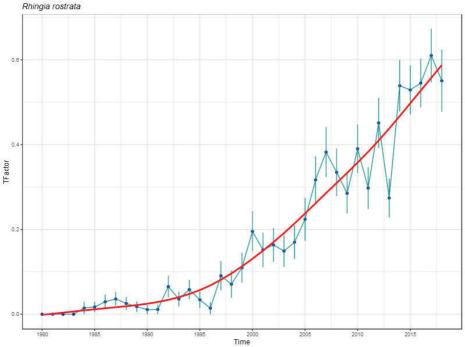


Fig. 11. Frequency of occurrence of *Rhingia rostrata* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Parameter	Feature	% contribution in each epoch		
		1992- 99	2000- 07	2008- 15
Soil	Soil: Dominant FAO soil class of 1km square (categorical)	33.95	18.06	28.38
Weather	Weather: Maximum temperature of warmest month (°C)	3.91	12.71	12.63
Soil	Soil: Average soil moisture content for 1km square (categorical)	0.40	1.94	9.63
DEM	DEM: Average elevation of pixels in 1km square (m)	0.69	6.93	8.45
Land Cover	Land Cover: Broadleaved Woodland cover (hectares)	2.74	7.35	8.30
Weather	Weather: Seasonality of rainfall (mm)	20.40	8.92	3.34
Land Cover	Land Cover: Grassland cover (hectares)	4.77	1.02	2.62
Weather	Weather: Mean temperature of wettest month (°C)	0.13	10.23	1.80
Weather	Weather: Seasonality of temperature (°C)	3.18	12.93	0.41
Weather	Weather: Rainfall during driest month (mm)	12.11	1.34	0.40
Weather	Weather: Minimum temperature of coolest month (°C)	4.58	1.62	0.29

Table 5. The top five environmental variables governing Maxent SDMs for *Rhingia rostrata* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

Volucella inanis (Figs 12, 13 and 14; Table 6)

This is a long-established species that was formerly extensively resident in south-west England. It retreated to a core area in London and south-east England following the extreme winters of the 1960s (Morris and Ball 2003) and started to expand its range in the early 1990s. Unlike other species such as *R. rostrata* and *V. zonaria*, its range change seems to have failed to penetrate Wales or south-west England, and its northward expansion has seemingly halted in the urbanised areas of West Yorkshire and north Cheshire where it might be postulated that urban heat island effects are facilitating its spread and population growth.

Unlike most other Maxent outputs, those for *Volucella inanis* are substantially consistent, even though there is greater variation in the period 1992 to 1999. The AUC for *V. inanis* ranges from 93.54 to 68.64 but the majority are over 80%, suggesting that the fit is more reliable than in many outputs. Importantly, maximum temperature of warmest month (°C) dominates all three epochs. This link correlates well with the hottest part of the year, and suggests that *V. inanis* is more closely dependent upon hot summers than others in this analysis. Such a link would also fit with the apparent absence of *V. inanis* from south-west England and from most of Wales, but does not entirely explain the contraction from south-west England in the 1960s (Morris and Ball 2003) that it has as yet not managed to re-colonise.

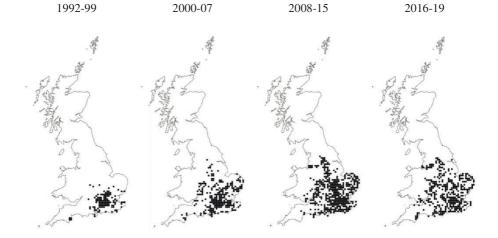


Fig. 12. Recorded distribution of *Volucella inanis* during four epochs between 1992 and 2019.

A correlation with maximum temperatures also seems to fit with this species' phenology (Fig. 13), which is substantially restricted to the likely hottest period (in August). This emergence period is noticeably more restricted than its near relative *V. zonaria* (Fig. 16), which has also undergone a remarkable range expansion but has also extended its range further north (Fig. 14).

Parameter	Feature	% contribution in each epoch		
		1992-99	2000-07	2008-15
Weather	Weather: Maximum temperature of warmest month (°C)	48.0211	52.8942	42.0553
Weather	Weather: Seasonality of temperature (°C)	3.9169	3.163	16.4221
Land Cover	Land Cover: Urban & suburban cover (hectares)	3.9562	8.4522	9.8142
Weather	Weather: Mean temperature of warmest month (°C)	0.688	7.3891	9.3199
Soil	Soil: Dominant FAO soil class of 1km square (categorical)	5.6016	5.8706	7.3377
Weather	Weather: Rainfall during driest month (mm)	0.8142	3.4947	1.5307
Weather	Weather: Seasonality of rainfall (mm)	11.2919	1.4417	1.3902
DEM	DEM: Average elevation of pixels in 1km square (m)	7.263	0.2613	0.6997

Table 6. The top five environmental variables governing Maxent SDMs for *Volucella inanis* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

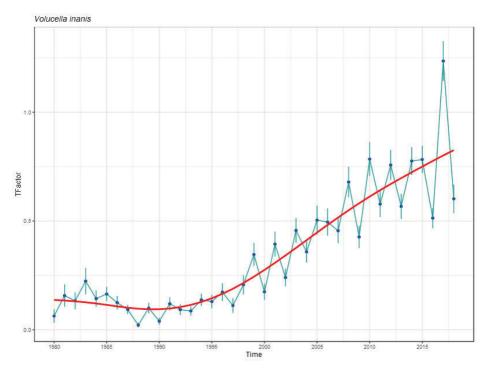


Fig. 13. Frequency of occurrence of *Volucella inanis* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Volucella zonaria (Figs 14, 15 & 16; Table 7)

This is a very large and readily identified species, but confusion with *V. inanis* is possible. We have also investigated and discounted several northerly reports due to confusion with both *Sericomyia silentis* (Harris, 1776) and *Tabanus sudeticus* Zeller, 1842 (Tabanidae). By 2003, *V. zonaria* had expanded its range into the urbanised areas of West Yorkshire, although its presence was extremely sparse. In the following 15 years, it has become firmly established in urbanised Yorkshire, but is more frequently reported from the coast of North Wales, northern Cheshire and south Lancashire. Colonisation in East Yorkshire has been slower, with the earliest records coming from Hull, from where it continues to be intermittently observed. A major acceleration of range was detected from the first record from Lancaster in 2012, followed by reports (supported by photographs) from Silloth in north Cumbria in 2017. Expansion into north-east England has been slower but now extends to County Durham, and with regular reports from the Scarborough area.

In our previous analysis (Morris and Ball 2004) we showed that there was a close match between the occurrence of *V. zonaria* and a combination of high mid-summer and mild midwinter temperatures. These temperatures were once confined to restricted parts of southern England and especially to the suburbs of London and Bristol. The current range of *V. zonaria* appears to continue to be closely linked to urban areas, with relatively few reports from rural locations. This concentration of data may simply be an artefact of recorder activity, but field experience (by RKAM) suggests that this is not so: it is genuinely commoner in urban areas than in more rural locations. Although this observation cannot be considered conclusive, 'urban heat island' effects previously highlighted by us (Morris and Ball 2004) seem to remain an essential part of its range expansion. It remains to be seen whether a recent (2018) record from Glasgow represents an extreme event or if it indicates that the urbanised areas of central Scotland will be colonised in coming years.

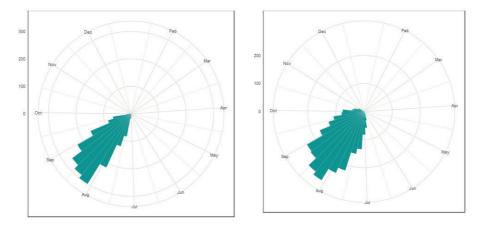


Fig. 14. Phenology of Volucella inanis (left) and V. zonaria (right)

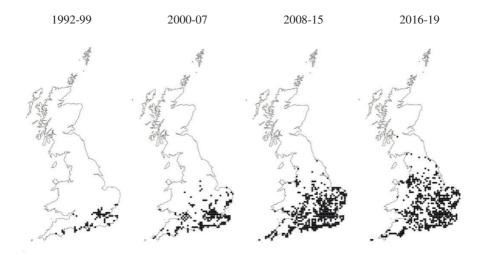


Fig. 15. Recorded distribution of *Volucella zonaria* during four epochs between 1992 and 2019.

Maxent analysis of governing environmental variables presents a remarkably coherent picture even though the rankings do differ in each epoch. Unlike our previous analysis, there is

less evidence for a link to temperatures during the coldest months, but the relationship with urban heat island effects continues to figure strongly. When considered cumulatively, climate variables dominate the analysis almost entirely, although there also appears to be a link to soil type that is most likely to reflect the animal's clear thermophilic preferences: free-draining soils tend to have shorter vegetation and warm up more quickly. Urban influences clearly involve thermal suitability because previous analysis (Morris and Ball 2004) showed how *Volucella zonaria* became established in coastal locations and also in the major conurbations of London and Bristol.

There have been un-documented suggestions that *Volucella zonaria* numbers in recent years have been supplemented by continental invasions. We can find no evidence for this in the data. If this was the case, one might have expected records far from the core strongholds of this species. Such a situation does not seem to have arisen, although it could be argued that records at the edge of the animal's northern range may be representative of such an influx. Such a situation seems unlikely because records prior to the 1940s were in southern England. Most northerly records are coastal, which would be consistent with the species' thermal requirements for warm frost-free winters. Records in subsequent years also suggest that the animal has become established rather than having been a singleton that has travelled beyond its normal range.

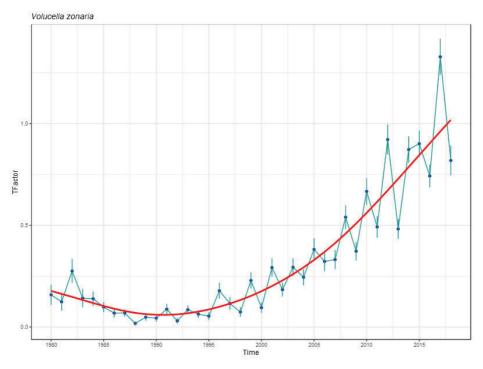


Fig. 16. Frequency of occurrence of *Volucella zonaria* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Parameter	Feature	% contribution in each epoch		
		1992- 99	2000- 07	2008- 15
Weather	Weather: Mean temperature of warmest month (°C)	2.9341	4.7699	38.1648
Land Cover	Land Cover: Urban & suburban cover (hectares)	22.1264	33.7429	29.3921
Weather	Weather: Annual mean temperature (°C)	24.5918	26.1475	7.9986
Soil	Soil: Dominant FAO soil class of 1km square (categorical)	21.3654	6.1242	5.9047
Weather	Weather: Annual temperature range (°C)	0.6559	3.0821	4.4696
Weather	Weather: Seasonality of rainfall (mm)	8.6092	1.3086	1.708
Weather	Weather: Maximum temperature of warmest month (°C)	1.7347	4.2733	1.2
Weather	Weather: Seasonality of temperature (°C)	3.3293	0.6513	0

Table 7. The top five environmental variables governing Maxent SDMs for *Volucella zonaria* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

Southerly movement from Scotland and north-west England

When the HRS was established in 1976, there were seven species that were thought to be strictly 'Scottish'. They were: *Blera fallax* (Linnaeus, 1758), *Callicera rufa* Schummel, 1841, *Cheilosia sahlbergi* Becker, 1894, *Hammerschmidtia ferruginea* (Fallén, 1817), *Helophilus groenlandicus* (Fabricius, 1780), *Pelecocera scaevoides* (Fallén, 1817) and *Pelecocera caledonica* Collin, 1940. In addition, Stubbs and Falk (2003) drew attention to the northern and western distribution of *Xylota jakutorum*, which seemed to be associated with coniferous forest and more recent afforestation. Subsequently, in a GB only context, *Cheilosia ahenea* (von Roser, 1840) has been added (Parker 2001) but is also known from the west coast of Ireland; and *Sphegina sibirica* was first recognised from a specimen taken on Skye in 1991 (Stubbs 1994).

Of these species, it is unclear whether *H. groenlandicus* is genuinely resident, whilst *S. sibirica* may have become established as a result of several arrivals at different locations on the British mainland. In the course of the past three decades, the strong Scottish concentration of records has been diluted by what appears to be migration southwards and eastwards in three species.

Callicera rufa (Figs 18 & 19)

Before the 1980s, when work by the Malloch Society (Rotheray and MacGowan 1990) established its true distribution based on larval records, adult *C. rufa* were rarely seen or reported. It transpired that it was widespread! Furthermore, it was shown that breeding sites were not confined to Scots pine *Pinus sylvestris*. Nevertheless, it also seemed as though *C. rufa* was strictly confined to Scotland, even if it was adapting to rot holes in the stumps of commercially logged conifer plantations.

A record in 2009 from Sherwood Forest was followed by another from Bedfordshire in 2011 and then a flurry of records from sites in Shropshire over the course of the next 8 years. Indeed, one of the Shropshire sites is now so reliable that there is even hoverfly tourism, with

people travelling long distances to see this fly! Records from Norfolk followed, after which there was the remarkable report of artificial rot holes created at the RSPB's Dovestone reserve in the Pennines attracting this species: larvae were found in the first year of the experiment in 2017 (Ken Gartside *pers. comm.*). Remarkably, they were in rot holes in larch *Larix* sp., showing that *C. rufa* was able to take advantage of a range of conifer stumps and not just Scots pine. This record suggests that *C. rufa* is probably far more widely distributed than observational records suggest. Further recent records from Somerset, south Wales and East Yorkshire illustrate the wider impact of its spread.

There is a lot of uncertainty about the origins of the southern population, with two competing theories:

- the Scottish population has spread southwards as the animal took advantage of widespread conifer planting and acceleration in the harvesting of trees in the past decade;
- one or more populations established as a result of individuals arriving from continental Europe.

We think that the evidence provided by Ken Gartside's work indicates that there is a much more widespread population and that this species was present in England and Wales some while before it was detected. It should be borne in mind that records of adults from Scotland are very intermittent, whilst larvae are more frequently found, especially in artificial rot holes. Reports, primarily of adults, from England can be explained by the greater intensity of recording effort; increased awareness of the species and specific efforts made to locate it; and better recording conditions with warm days and sunshine facilitating observations. In addition, observations in England have been primarily males, which have been shown to 'hilltop' and to 'lek' around suitable trees. As a result, some locations have become reliable places to find it, and there is growing evidence from the UK Hoverflies Facebook page (Facebook 2019) of hoverfly observation becoming part of 'wildlife tourism'.

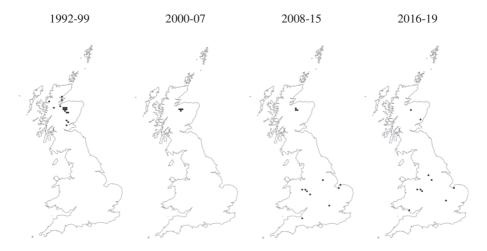


Fig. 18. Recorded distribution of Callicera rufa during four epochs between 1992 and 2019.

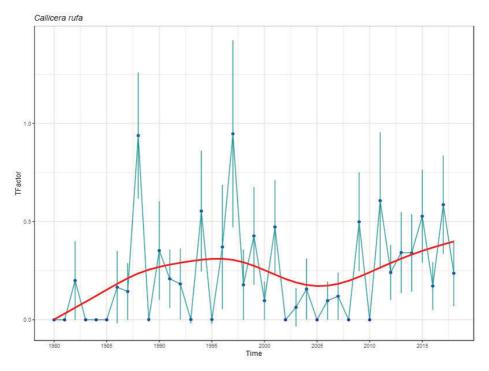


Fig. 19. Frequency of occurrence of *Callicera rufa* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Sphegina sibirica (Figs 20 & 21)

Although first reported from the Isle of Skye in 1991, a specimen taken near Inverness in 1976 was later recognised (Stubbs and Falk 2002) and there is also an early record from Shropshire (16/06/1992). These records suggest that *Sphegina sibirica* may have arrived at several locations. Nevertheless, subsequent events strongly suggest that it first became established in Scotland before moving southwards. Larvae of *S. sibirica* are believed to develop in the decaying cambium of spruce, but the range of locations where it has been found suggest that it may have more catholic requirements. For example, several individuals were recorded in 2010 from a wet flush with hemlock water dropwort *Oenanthe crocata* on Skomer Island. It therefore seems possible that *S. sibirica* develops in a range of situations where there is wet rotting vegetable matter. The strong western bias of its distribution points to a preference for wetter environments and to coniferised locations, although it clearly will exploit situations in the drier south-east. It is probably only a matter of time before *S. sibirica* is found more widely over the whole of Britain.

This species is clearly highly mobile, having been found in mountain passes well away from potential breeding sites and has been taken in some numbers from around the car park at the Cairngorm ski centre (RKAM personal observations). Its rapid dispersal across mainland Britain seems partially to reflect greater breeding opportunities afforded by maturation of conifer plantations, together with its seemingly high propensity for dispersal.

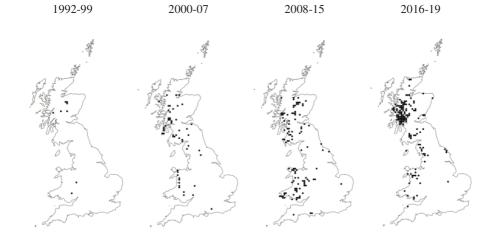


Fig. 20. Recorded distribution of *Sphegina sibirica* during four epochs between 1992 and 2019.

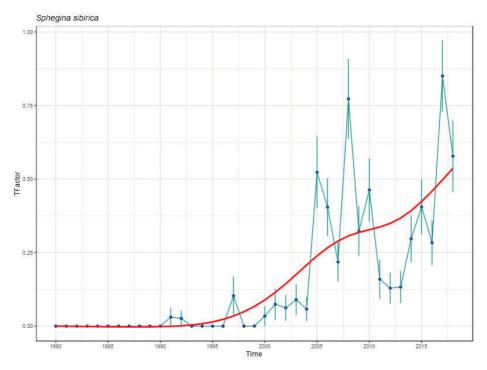


Fig. 21. Frequency of occurrence of *Sphegina sibirica* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Xylota jakutorum (Figs 22 & 23; Table 8)

This species was illustrated in the first edition of Stubbs and Falk (2002) because it seemed to have a northern and western distribution that was entirely separated from the very similar *X*. *florum* (Fabricius, 1805). Confusion between the two species is possible, however, and it is also possible that both distributions included misidentifications. Nevertheless, it is now clear that *X*. *jakutorum* has very substantially expanded its range and occurs sporadically across much of southern and eastern England. As yet, however, the numbers of records are small.

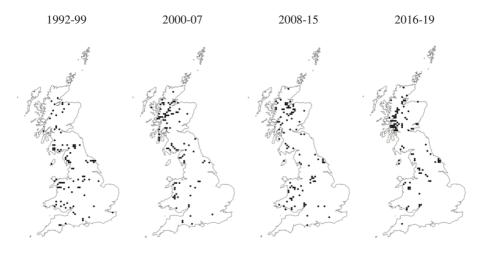


Fig. 22. Recorded distribution of *Xylota jakutorum* during four epochs between 1992 and 2019.

Parameter	Feature	% contribution in each epoch		
		1992- 99	2000- 07	2008- 15
Land Cover	Land Cover: Coniferous Woodland cover (hectares)	41.5585	51.1686	52.2876
Weather	Weather: Maximum temperature of warmest month (°C)	11.6526	8.9072	9.7206
Soil	Soil: Dominant FAO soil class of 1km square (categorical)	4.0078	2.0303	3.8461
Land Cover	Land Cover: Broadleaved Woodland cover (hectares)	4.1789	3.0925	1.8882
Weather	Weather: Temperature isothermality (°C)	1.8596	3.6898	1.1895
Soil	Soil: Average soil moisture content for 1km square (categorical)	9.274	4.1555	0.5211
Weather	Weather: Total annual rainfall (mm)	0.0158	7.6149	0.0296

Table 8. The top five environmental variables governing Maxent SDMs for *Xylota jakutorum* between 1992 and 2015. 1st Dominant – bold, 2nd Dominant – bold italic. Colour code: dark grey dominant factors, pale grey secondary factors in top 5.

As far as we are aware, no effort has been made to systematically record from coniferised woodland in south-east England and it seems likely that such an effort would show that *X. jakutorum* is commoner than records currently suggest. Unlike *X. florum*, *X. jakutorum* is a regular flower visitor (RKAM personal observations) and this habit may provide a first indication of its identity in southern locations.

Unlike examples of northward range change, Maxent shows how closely aligned this species is to coniferous woodland, with this one environmental parameter dominating the analysis. All other parameters make a comparatively small contribution (bearing in mind that the total within the analysis comprises 29 parameters). It would appear that maximum temperature of the warmest month (°C) does have a bearing on the model.

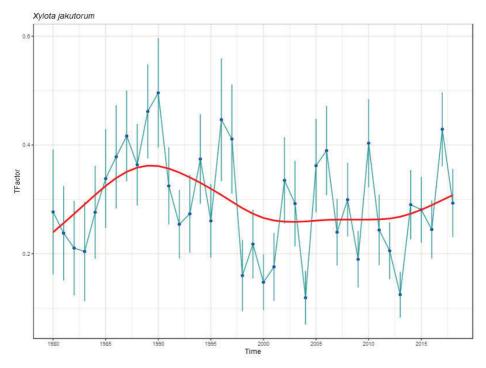


Fig. 23. Frequency of occurrence of *Xylota jakutorum* generated by FRESCALO as a 'TFactor'; corrected for recording effort, against year with error bars showing its standard deviation. The red line is a smoothing spline with 5df.

Accidental imports

The horticulture industry has a long history of importing plant material from overseas sources, a lot of which comes from The Netherlands. Three species probably arrived this way: *Cheilosia caerulescens, Eumerus funeralis* and *Merodon equestris*. In addition, it is possible that imported conifer saplings have led to the arrival of further species such as *Eriozona syrphoides* and perhaps also *Dasysyrphus pauxillus* (Williston, 1887) (although the latter seems less likely as its arrival was at a time when coniferisation had substantially ceased). The only species for which we can map changes with any confidence is *C. caerulescens*.

Cheilosia caerulescens (Fig. 24)

The arrival of *C. caerulescens* was predictable because it had become established in The Netherlands in the 1980s (Reemer 1999), seemingly as a result of the movement of plants by the horticulture industry. By 2005 (when its status was discussed at the International Conference on the Syrphidae in Leiden, The Netherlands), it seemed only a matter of time before it arrived in Britain. Unsurprisingly, it was first detected here in 2006 in South Croydon but went unreported until 2008 (Collins and Halstead 2008), when further evidence of its presence emerged.

The adults are relatively straightforward to identify. They have bare eyes and a slight shade over the r-m cross-vein; the facial profile is also diagnostic, especially when seen in conjunction with hair tufts on the sides of the thorax and abdomen. Larval feeding damage is even more distinctive, involving mines in the leaves of house leeks (*Sempervivum* sp.). This combination of factors, together with its tendency to occur in urban situations, means that is regularly reported by photographic recorders; indeed, almost all records to date have come from photographs posted online rather than by traditional net and pooter methods.

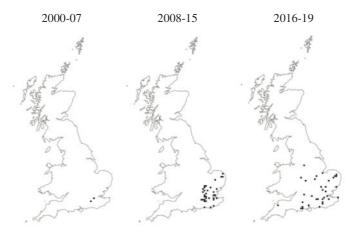


Fig. 24. Recorded distribution of *Cheilosia caerulescens* during three epochs between 2000 and 2019.

Discussion

Range expansion has been demonstrated for a wide range of taxa, including birds (Massimino *et al.* 2015), Lepidoptera (Parmesan *et al.* 1999; Franco *et al.* 2006; Pateman *et al.* 2012; Gillingham *et al.* 2015) and Odonata (Hickling *et al.* 2005). Relatively little has emerged thus far for Diptera, although there has been previous analysis of two species of *Volucella* (Morris and Ball 2003, 2004). This analysis shows that range expansion is more prevalent than hitherto recognised in formal papers.

Although it is possible to detect range change from distribution maps, identification of the controlling environmental variables has proven to be far more challenging. It is possible to highlight the dominant factors for each species, but in several cases the results are not sufficiently robust to be considered reliable. They are therefore indicative at best. There are several possible reasons for weaknesses in the Maxent outputs, but the most likely one is the relative paucity of records for each of the chosen epochs. This problem is compounded because the values used for each environmental variable are averages and, in the case of climate variables, it is possible that peaks or troughs are the most important factors. Analysis of the effects of the 2018 heatwave and

drought shows that there can be a particularly pronounced effect on some species (Morris and Ball 2019b).

In addition to demonstrable range expansion, there are a few species in which overall abundance seems to have increased; a feature best illustrated by *Cheilosia soror*. Not only has its northern boundary extended, it has also become far more extensively recorded within its previous range. A similar situation obtains for *C. vulpina*. In both cases, the ecology of the larval stages is poorly known, but it might be hypothesised that changing climate variables have led to a wider spectrum of potential food resources (believed to be subterranean fungi and plant stems respectively). Bearing in mind that it has been shown that the warming climate envelope has broadened the larval niche of the Brown Argus butterfly *Aricia agestis* (Pateman *et al.* 2012), it seems possible that a similar situation has emerged for some hoverfly species.

These results highlight the problem faced by policy-makers and conservation organisations: positive or negative changes can be detected using opportunistic data, but it is unwise to place too much faith in any predictions of future distribution or abundance. At the moment, the data are too diffuse to be sure that the critical environmental parameters are identified as the reasons for a particular change. Translated into a wider application for understanding the ecological drivers of species' distribution, it is clear that Maxent outputs are unlikely to be sufficiently robust to be sure of the environmental drivers of change (either positive or negative) although they may provide useful clues that can be followed up by field testing.

Precise changes in the distribution of individual species are also extremely difficult to pinpoint using opportunistic data. However, range change in the two most charismatic hoverfly species (*Volucella inanis* and *V. zonaria*) seems to have commenced in the mid-1990s. This point is consistent with a short lag between the global climate regime shift of the 1980s (Reid *et al.* 2016) and expression of individual species' responses. Such a lag is likely to comprise two elements:

- poor data resolution in the early stages that make it difficult to discriminate between real changes and those that arise because of changing recorder activity; and
- delayed responses by the organisms involved, as they approach the critical temperature threshold for expansion.

There seems to have been a longer lag between the 1980s global climate regime shift and responses by species such as *Rhingia rostrata* and *Epistrophe diaphana*. Part of the reason for this difference possibly lies in the degree to which the species are recorded. Unlike the charismatic *Volucella* species, *R. rostrata* and *E. diaphana* would only have been noted by a very few specialist dipterists, whose numbers are very small (Morris and Ball 2019a). A similar problem exists for *Cheilosia soror*, which is within a genus that is difficult to identify, leading to many hoverfly enthusiasts avoiding them (however, females can often be identified from photographs).

Range expansion by *Epistrophe melanostoma* seems to have accelerated in the past 10 years. Part of this apparent expansion potentially lies in the growth of recorder activity since around 2009. Increased awareness of hoverflies and improvements in our ability to identify difficult species from photographs mean that this species is now much more readily detected. Experience from Mitcham Common, which was the location where this species was first detected, suggests that *E. melanostoma* has become increasingly abundant in the past five years; however, this observation should be treated with caution as recorder effort has not been constant.

Bearing in mind that hoverfly diversity is greatest in southern England where the most pronounced impacts of climate change have been felt, it is surprising how few species have responded. There are numerous others that might be expected to expand their range; for example, *Chrysotoxum cautum* (Harris, 1776), *C. verralli* Collin, 1940 and *Volucella inflata* (Fabricius, 1794). In a few species, there are indications of range expansion but, to date, the numbers of

records are too small to be sure what is happening. This is especially true of *Callicera spinolae* Rondani, 1844, which seems to have broken free of its restricted East Anglian range and is now regularly observed in Bedfordshire and has been detected in both London and West Sussex. There also seems to have been an increase in the numbers of records of *C. aurata* (Rossi, 1790) but it is difficult to be sure whether this reflects an increase in abundance or better recording!

Acknowledgements

These analyses are only possible because of the efforts of a small army of recorders. We are indebted to everybody who has contributed records to the HRS dataset. We would also like to thank three unnamed reviewers whose comments have helped to refine this paper.

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Panzeria nemorum (Meigen) (Diptera, Tachinidae) recorded in

Scotland – One female *Panzeria* (formerly *Fausta*) *nemorum* (Meigen) was observed on hogweed (*Heracleum sphondylium*) umbels on a farm track verge (NX58896152) emerging from Castramont Wood SSSI edge (adjacent to Carstramon SWT Reserve) and open grazings, 6.vii.2020, Kirkcudbrightshire, S.W. Scotland. No others were seen during subsequent repeated visits to the site. The specimen was small for this species at around 7mm long, and was slightly aberrant in having fewer bristles on one side of the abdomen (C. Raper *pers. comm.*).

As far as is known, this is the first record in Scotland for a local species more typically associated with downland (Day, C.D. 1948. *British Tachinid Flies*. Buncle, Arbroath) in S. England. The most northerly previous records as shown on the NBN Atlas (https://species.nbnatlas.org/species/NHMSYS0021321535. Accessed 29 October 2020) are for Pembrokeshire and North Essex. The central European habitat is described as woodland, where it is rare, becoming more common in southern Europe (Tschorsnig, H-P. and Herting, B. 1994. Die Raupenfleigen (Diptera: Tachinidae) Mitteleuropas; *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* **506** 1-170).

I would like to thank Chris Raper for drawing my attention to his and R. Rayner's translation of *Die Raupenfleigen Mitteleuropas*, for comments on the specimen and for confirming the identification, the Scottish Wildlife Trust for consent to survey and Ashleigh Whiffin for arranging future deposit of the specimen to the National Museums of Scotland entomological collections – **ROSS H. ANDREW**, 6 Riverbank, Gatehouse of Fleet, Castle Douglas, Dumfries and Galloway, DG7 2JZ

Agathomyia cinerea (Zetterstedt) (Diptera, Platypezidae) feeding on

dead insects - While searching for Platypezidae on 28 September 2020 at East Croft Coppice in in the north of Savernake Forest (SU236683), Wiltshire, I was surprised to see a female of *Agathomyia cinerea* (Zetterstedt, 1852) feeding on a dead common barkfly *Valenzuela flavidus* (Stephen, 1836) (Psocoptera, Caeciliusidae) that was on a hazel leaf under conifers. This barkfly feeds on the microflora on the surface of leaves of a wide range of trees, so has similar habits to adults of Platypezidae, which are well-known to run about rapidly on the surfaces of broad leaves, feeding on surface deposits including honeydew. This feeding behaviour has not apparently been recorded previously in Platypezidae, although often observed in some other flies, e.g. Muscidae, Anthomyiidae and Lauxaniidae (see *A Dipterists Handbook* page 328).



Then, on 9 October 2020, elsewhere in the same woodland (SU235683), 1 observed another female, apparently feeding on an unidentified dead insect, on a hazel leaf in heavy shade under beech.



I am grateful to Keith Alexander for identifying the barkfly and to Peter Chandler for confirming my identification of *A. cinerea* – **PETER ANDREWS**, nomadandrews@hotmail.co.uk

Clarification on the European status of *Phytomyza ilicis* Curtis (Diptera, Agromyzidae)

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Summary

A clarification on the European status of the holly leaf-miner, *Phytomyza ilicis* Curtis, 1846 is discussed, in respect of the comments and findings of Papp and Černý (2020), along with images and notes regarding its similarity to the larval biology of *Phytomyza jucunda* Frost & Sasakawa, 1954.

Introduction

Within Europe, two species of Agromyzidae are known to utilise holly (*Ilex* sp.) as a larval host; *Phytomyza ilicis* Curtis, 1846 and *Phytomyza jucunda* Frost & Sasakawa, 1954. The former is a common species throughout the region, with the latter being a relatively new arrival, its larval mines being discovered on *Ilex aquifolium* and *I. crenata* in Belgium and the Netherlands (Dek and van Steenwinkel 2018).

During their study and description of reared *P. ilicis* material, Papp and Černý (2020) make the following observation; "much to our surprise, after genitalia preparation we found that Kertész's males represent two species (from the same collection). We depicted the form which is corresponding to the former interpretations. Since in the Nearctic there are five other species developing in *Ilex*, only future studies might solve the problem. At present we merely draw attention as to how this species should be treated. We are afraid that all former records of *P. ilicis* from Europe will need to be either confirmed or revised".

In light of the above statement, all *P. ilicis* material in my private collection [including previously undissected reared male specimens] were re-examined; the phallus [in left lateral view] appears slightly different to the illustrations of *P. ilicis* by Spencer (1990) and Papp and Černý (2020) but when viewed from below, the phallus agrees well with Spencer's figure.

In order to ascertain if the 'second' species mentioned by Papp and Černý is a described/undescribed species and if it is conspecific with my reared material, the Kertész specimen and its genitalia preparation were kindly loaned to me, with the results discussed below.

Discussion

Examination of my reared male *P. ilicis* material highlights that the phallus [when viewed laterally] can show some slight natural variation in regards to the shape of mesophallus and hypophallus (Fig. 2); however, these are considered not to be of any taxonomic importance.

When compared to the phallus [in left lateral view] illustrations of Lonsdale and Scheffer (2011) and Spencer (1990), the reared males differ owing to: the clear gap between basiphallus and mesophallus [absent in figures by Lonsdale and Scheffer, and Spencer], the presence of an elongated dot-like paraphallus [not depicted by Lonsdale and Scheffer or Spencer] and the shape of the distiphallus.

Lonsdale and Scheffer (2011) discussed eleven other holly leaf-mining species [*Phytomyza ambigua* Lonsdale & Scheffer, 2011, *Phytomyza ditmani* Kulp, 1968, *Phytomyza glabricola* Kulp, 1968, *Phytomyza ilicicola* Loew, 1872, *Phytomyza leslieae* Lonsdale & Scheffer, 2011, *Phytomyza lineata* Lonsdale & Scheffer, 2011, *Phytomyza nemopanthi* Griffiths & Piercey-Normore, 1995, *Phytomyza opacae* Kulp, 1968, *Phytomyza verticillatae* Kulp, 1968, *Phytomyza*

vomitoriae Kulp, 1968 and *Phytomyza wiggii* Lonsdale & Scheffer, 2011]; although many can be separated on external characters and features of the male genitalia, detailed examination of subtle structures of the male phallus is necessary, with an importance placed on the shape of the hypophallus and relative dimensions of the mesophallus and distiphallus. None of the above species appear to agree exactly with the reared males, whilst the phallus of *P. jucunda* is also dissimilar.

Upon examination of the Kertész 'second' species, when viewed from below (Fig. 1, lower), the phallus agrees well with the reared males and the *ilicis* figures of Lonsdale and Scheffer, and Spencer. In left lateral view (Fig. 1, upper), the phallus again agrees well with the reared males, differing from the *ilicis* figures of Lonsdale and Scheffer, and Spencer, owing to a clear gap between basiphallus and mesophallus, the presence of an elongated dot-like paraphallus and the shape of the distiphallus. Noticeably, in the Kertész male, the hypophallus is absent; however, I believe this has been lost during the dissection process; the interrupted ejaculatory duct is also indicative of artificial damage of the phallus and all other closely related *Phytomyza* spp possess at least short hypophalli.

Based upon my detailed examination of the male genitalia and external morphology, I am of the firm belief that the Kertész material is *Phytomyza ilicis* [with damaged phallus] and not a second species as stated by Papp and Černý. The dissection process and manipulation of the delicate genitalia can frequently cause damaged/missing or artificially orientated parts, often resulting in misidentifications. Unfortunately, Spencer's *P. ilicis* lateral view illustration of the phallus is in a suboptimal position and therefore not a true representation of *P. ilicis*; a more accurate portrayal is shown in Fig. 2. It should be noted that the *ilicis* figures of Lonsdale and Scheffer are of genitalia also in a suboptimal position (Lonsdale *pers. comm.*).

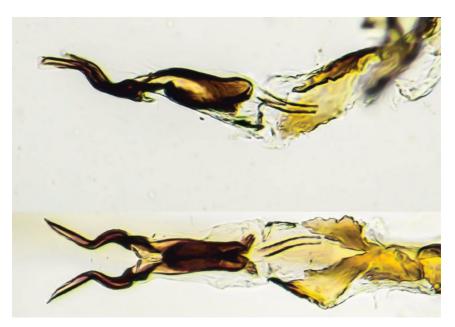


Fig. 1. *Phytomyza ilicis* Curtis: Kertész material; upper, phallus in left lateral view; lower, phallus viewed from below.



Fig. 2. *Phytomyza ilicis* Curtis, phallus; upper three, phallus in left lateral view highlighting variability; lower, phallus viewed from below.

In light of the above findings, the statement of Papp and Černý that '...after genitalia preparation we found that Kertész's males represent two species...' should be disregarded. Nevertheless, the recording of the two *Ilex* mining species currently present in Europe [*P. ilicis* and *P. jucunda*] should be done with caution. The mine of *P. ilicis* is readily recognised, being blotch-like, often with reddish colouration centrally [where the frass is mostly deposited], whereas that of *P. jucunda* consists of a long gallery which strongly widens, often forming a secondary blotch, with frass in an almost continuous, slightly off-centre [not centrally as mentioned by Ellis (2019); agromyzid mines never have frass in the centre of the mine as the larva feeds lying on the left or right side only, singular amongst all world Diptera larvae], dark line. However, *P. ilicis* can form mines (Fig. 3) which are extremely similar, if not identical, to those of *P. jucunda*; adults reared from the larval mines in Fig. 3 all proved to be *P. ilicis*.

To permit a positive determination, examination of the anterior spiracles of the puparium or rearing adult males is necessary; the anterior spiracles of *P. ilicis* are short, closely spaced,

subparallel, slightly bulging medially and constricted before terminal bulb (Lonsdale and Scheffer 2011), whereas in *P. jucunda* the anterior spiracles are relatively long and strikingly bifid.



Fig. 3. *Phytomyza ilicis* Curtis, larval mines agreeing with those of *Phytomyza jucunda* Frost & Sasakawa.

I have observed these very atypical mines, with frass in a slightly off-centre, continuous dark line, in other species of Agromyzidae; *Chromatomyia horticola* (Goureau, 1851) and *C. syngenesiae* Hardy, 1849 both form mines with frass in individual, well-spaced, grains [typical of the genus]; however, I have reared both species from mines which contain frass deposited in a long, continuous, slightly off-centre dark line (Fig. 4).



Fig. 4. Chromatomyia syngenesiae Hardy, atypical larval mine on Centaurea sp.

To conclude, presently, there are only two species of Agromyzidae known to utilise *Ilex* as a host in Europe [*P. ilicis* and *P. jucunda*] and there is no necessity to confirm or revise all former records of *P. ilicis* from Europe [as stated by Papp and Černý], unless these records are based on atypical larval mines or adults reared from atypical mines; any material reared from larval mines resembling those in Fig. 3 should be re-examined to confirm the causer.

Acknowledgements

I would like to thank László Papp (Budapest, Hungary) for kindly sending me the Kertész specimen and his correspondence, Owen Lonsdale (Agriculture and Agri-Food Canada) and Sonja Scheffer (United States Department of Agriculture) for their much-valued discussions and Dr Michael von Tschirnhaus (University of Bielefeld, Germany) for his time and correspondence. Thanks also go to the many naturalists who kindly sent me valuable larval and adult material and Adam Parker for permitting me to use his image (Fig. 3, lower).

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Pachygaster atra (Panzer) (Diptera, Stratiomyidae) in south-east

Scotland – Keith Bland (KPB) and David Horsfield (DH) reported the first Scottish record of *Pachygaster leachii* Stephens *in* Curtis, 1824 (Stratiomyidae) in 2018, the most northerly previous records being Cumberland and North-east Yorkshire (*Dipterists Digest (Second Series*) **25**(2018), 142-143). We can report that the other British species in that genus, *P. atra* (Panzer, 1798), is also to be found in Scotland. KPB took a male and a female *P. atra* at Yellowcraigs Local Nature Reserve, East Lothian (O.S. grid NT5185) on 25.vi.2015, with single females subsequently recorded nearby at Aberlady LNR (O.S. grid NT470803, 1.vii.2017, DH and NT4681, 21.vii.2020, DS). Two additional localities in East Lothian have been discovered in 2020. Large numbers were seen on the leaves of an isolated buckthorn bush (*Rhamnus cathartica*) bordering the estuary at Tyninghame (O.S. grid NT6279, 2.vii.2020, KB & DS), and two females were swept from tree foliage at the inland site of Byres Hill (O.S. grid NT4976, 31.vii. 2020 DS). Note that these localities are in four adjacent tetrads.

George H. Verrall visited Aberlady in July 1873 while returning from a visit to Braemar and he reported *P. ater* (later corrected to *P. atra*) as one of several species of soldierfly encountered there (Verrall, G.H. 1874. Diptera at Braemar, Aberdeen and Aberlady, including six species not hitherto recorded as British. *Scottish Naturalist* **2**(13), 199-202). Verrall (1909. *British Flies* Vol. **5**) mentioned no other Scottish localities and none seem to have been added since (Drake, C.M. 1990. *Provisional atlas of larger British Brachycera* (*Diptera*) of Britain and *Ireland*). It thus appears that *P. atra* has been overlooked in south-east Scotland for almost 150 years.

Elsewhere in Britain, *P. atra* is local in Wales and widespread in England as far north as Yorkshire, with a single outlying record 100 miles further north in Northumberland, recorded by Andy Godfrey from a pitfall trap on Lindisfarne (NU14, 28.viii.2015). East Lothian is about 40 miles north-west of Lindisfarne.

In Scandinavia there are a few records for southern Sweden but none further north according to data via the Global Biodiversity Information Facility (https://www.gbif.org), and it is plausible that *P. atra* has climatic requirements that have restricted its wider occurrence in northern latitudes. Maybe we will see an extension in range as climate changes continue.

We are grateful to John Harrison, the East Lothian Council warden at Aberlady Bay LNR, for permission to collect there, to Andy Godfrey and to Paul Stevens of the Environmental Records Information Centre for the North East of England for details of the Northumberland record. Jeanne Robinson of the Hunterian Museum, Glasgow, and Ashleigh Whiffin of the National Museums of Scotland, Edinburgh kindly confirmed that the collections in their care held no Scottish specimens of *P. atra* – **DONALD SMITH**, Garden Cottage, Clerkington, Haddington EH41 4NJ, **KATTY BAIRD**, 4 Rhodes Holdings, North Berwick, EH39 5PH, **DAVID HORSFIELD**, National Museums Collection Centre, 242 West Granton Road, Edinburgh EH5 1JA, **KEITH P. BLAND**, 35 Charterhall Road, Edinburgh EH9 3HS and **MARTIN HARVEY**, Evermor, Bridge Street, Great Kimble, Aylesbury, HP17 9TN

A Wiltshire record for *Madiza glabra* Fallén (Diptera, Milichiidae)

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Summary

Observations of several Milichiids and Chloropids in a domestic context are reported and discussed.

I have been fascinated in recent months by the sudden appearance in my house of many gravid females of *Madiza glabra* Fallén, 1820 (Milichiidae). This species had not drawn itself to my attention in previous years.

They began to show on 9 August 2020 on the <u>inside</u> of an upstairs bedroom window (Codford, Wiltshire, ST966402) in groups numbering around 30 or more, and they have continued to appear in variable numbers for several weeks. During the night our windows are usually closed or partly closed against the wind; I conclude that, like other species which swarm around our upper floors in late summer (for example, the yellow and black chloropid *Thaumatomyia notata* (Meigen, 1830)) *M. glabra* had entered during the late afternoon or early evening. The observations continue, and both species were present in great numbers this morning, 21 September 2020.



Fig. 1. Madiza glabra - thorax, head indicating proboscis.

The NBN Gateway contains only 34 records of *M. glabra* for the country as a whole; the records closest to my location are two by Martin Drake in South Wales in 1985 and one unattributed and unconfirmed for the New Forest in 1958; there have been no reported Wiltshire observations hitherto. I cannot satisfactorily account for the apparently recent arrival of the species in the county; many common species are under-reported if they are of little interest to recorders, but it is less easy to account for the paucity of records on the Gateway.

It is clear from reported experimental studies (Aldrich and Barros 1995, Kirk-Spriggs *et al.* 2001, and other writers) that milichiid and chloropid flies are attracted preferentially to the scent of E-2-hexenol, as also are the spiders with which they associate. E-2-hexenol is a nearly colourless clear liquid which occurs naturally in tomatoes, banana and black tea, and is used in air care products, cleaning and furnishing products, laundry and dishwashing products. I speculate that *M. glabra* and *T. notata* may have been attracted into the house by residual traces of this chemical in the air. The paper by Kirk-Spriggs *et al.* summarises recent chemical analyses of the residues from aggregation sites of the chloropid *Apotropina gregalis* (Lamb, 1937) and summarises what is known of aggregating Chloropidae and some other Diptera.

I thank Ashley Kirk-Spriggs and Martin Ebejer for helpful comments, and Peter Chandler for a copy of his manuscript key to British Milichiidae.

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CORRECTION:

The pNT cleptoparasite *Leucophora sericea* Robineau-Desvoidy (Diptera, Anthomyiidae) in Norfolk and an update on the aculeate hosts of British *Leucophora* by Nick W. Owens and Mark D. Welch. *Dipterists Digest* 2020 **27**, 231-236. Table 1 p. 234:

Psenulus pallipes should read Diodontus tristis (error in original source).

Leucophora cinerea should be added to the Table and *Diodontus tristis* and *Lasioglossum nitidiusculum* should be listed under that heading.

The entry for Leucophora sericea with Psenulus pallipes in the original table should be removed.

Dilophus bispinosus Lundström (Diptera, Bibionidae) taken in numbers at its only known Welsh locality and new sites in Gloucestershire, Oxfordshire and Middlesex

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Summary

Dilophus bispinosus has now been found in new counties, Gloucestershire and Middlesex, and further observations have become available at its single known locality in Wales. Knowledge of this elusive species has changed dramatically, from the twelve isolated records of single female specimens over a period of more than 100 years, to the first British males being found and then to a mixed catch of specimens at the Welsh site. The implications of the new Welsh find to our understanding of its breeding habitat are explored. The new Oxfordshire locality (actually V.C. 22 Berkshire) is about 5km from an earlier locality (1944).

Introduction

Alexander (2017) reviewed knowledge of this interesting bibionid in Britain and Chandler (2020) has provided an update based on the discovery of the first British male at the first locality found in Wales. The species has now been found on four more occasions and so a further up-date is merited, especially as one of the new occurrences is unique in Britain in being of multiple individuals, of both sexes, and from a site where the species has been found previously – all earlier records, and the other recent records cited here, have been isolated records of single specimens.

Pierce, Alcove and Piercefield Woods SSSI, Monmouthshire

This Site of Special Scientific interest (SSSI) is the southernmost block of woodland on the Welsh side of the Wye Valley Woodlands Special Area of Conservation (SAC). It comprises mixed semi-natural woodland mostly of beech *Fagus sylvatica*, yew *Taxus baccata* and small-leaved lime *Tilia cordata* on steep slopes facing east. The gentler slopes have a relict coppice structure with some standards while the steeper slopes are dominated by old growth beech-yew stands. This woodland, together with neighbouring sites, has been subject to flight interception trapping as part of a Natural Resources Wales (NRW) project to document the saproxylic invertebrate interest of this internationally important wooded landscape – although well-known for its vegetation interest, knowledge of the associated invertebrates has been very limited.

During the 2018 and 2019 field seasons flight interception traps of the four-bottle design (Alexander *et al.* 2016) have been positioned on veteran trees across the southern end of the Welsh side of the SAC. The trapping stations were selected by Rob Bacon (RB) of NRW, in consultation with KNAA, and were emptied by RB periodically across the field season, with the help of Doug Lloyd of the Gwent Wildlife Trust. The samples were then passed to KNAA for sorting and identification, with Diptera being passed to PJC.

A highlight of the 2018 samples was the discovery of the first British male of *Dilophus bispinosus* at the first known site in Wales for the species (Chandler 2020). This discovery is all the more significant for the realisation that the male is distinctive in coloration. The RES Handbook (Freeman and Lane 1985) did not describe the appearance of the male and we have previously assumed it to be very similar to *D. febrilis* (Linnaeus) and perhaps indistinguishable from it without careful examination under the microscope. However, the Pierce Wood male

differs from the dark coloured males of the other species in having yellow legs, and so is unlikely to have been overlooked in the past, as had been suspected.

The male was found in a sample covering the trapping period 26.vi. – 9.viii.2018. It had been suggested (Alexander 2017) that the species develops in soils rich in organic matter but dry and free draining, often alluvial in origin, in areas with a relatively mild microclimate. It appeared to favour sheltered mosaics of flower-rich meadow with trees, woodlands and especially woodland edge. The male was taken by a trap in exactly this type of situation, at the lower edge of Pierce Wood, with open blackthorn scrub and flowery marshy grassland on the river flats beyond (Alexander 2019). The trap was located at the base of a relatively mature blackthorn and rested on the soil surface. The blackthorn was collapsed/broken at stomach height and a small fresh bracket of the fungus *Ganoderma australe* was observed at approx. 10cm above ground height. The grid reference for the trap location was ST536959.



Fig. 1. Trapping situation in Pierce Wood, which produced *D. bispinosus* in numbers in 2019 (the trap is situated mid centre right – arrowed).

The 2019 trapping resulted in a remarkable catch of six males and two females in one of the traps (Alexander 2020). This is the only occasion that more than one individual has been found in Britain, and the first time the species has been detected at a site on a second occasion. This, together with the first British male and the first Welsh record in 2018, makes this site for *D. bispinosus* unique in Britain. The trap this time was located on a recently fallen oak in an area of old growth beech-yew woodland and the trap was suspended about 1m above the soil surface (see Fig. 1). The grid reference was ST538959, relatively close to where the first male was trapped the previous season. The situation is effectively a small woodland glade, only relatively recently

created by the fallen oak tree, and deeper into the main woodland block from the riverbank where one male had been trapped in the previous year.

Crickley Hill & Barrow Wake SSSI, Gloucestershire

In 2019 the National Trust initiated a baseline survey of the saproxylic invertebrates across their Crickley Hill property on the Cotswold escarpment above the city of Gloucester and once again a series of four-bottle design flight interception traps were operated on a selection of veteran trees across the field season. Two distinct areas were trapped: an expanse of old growth beech former wood-pasture (The Scrubbs) and a remnant strip of ancient semi-natural ash, oak, maple, hazel coppice with standards (Crickley Hill Wood). Remarkably, a single male specimen of *D. bispinosus* was found in a sample from a veteran beech in The Scrubbs (SO9216), 21.v - 24.vii.2019. The trap was positioned about 2m height on the tree trunk which is just inside the edge of the veteran beech stand, with flowery limestone grassland a short distance away.

This SSSI has been designated for its range of habitats characteristic of the Cotswold limestone, including species-rich grassland, scrub and semi-natural woodland. The Scrubbs is partly fringed by mixed scrub grading into open grassland and so provides broadly comparable habitat to that found at Pierce Wood in the Wye Gorge.

Cothill NNR, Oxfordshire (Berkshire V.C.)

One female was caught in a Malaise trap operated by Judy Webb, on behalf of Natural England, from 10 May to 1 November 2019, for which the catches of Diptera were identified by PJC. The trap was emptied weekly and this specimen was in the sample collected in the period 14-19.vii.2019. The location of the trap was at SU45959965; it was situated on wet peat, just inside the edge of light woodland fringing the open fen. The trees present were alder, ash, birch, hazel and grey willow. The ground flora was a tall herb mix including hemp agrimony, water mint, tufted hair grass, nettle, wood sedge and dog's mercury on quite wet peat (presumed to be old fen, now wooded). Dry sandy soil woodland is about 20m to the north and here is mostly oak, hazel, ash, holly and birch with dog's mercury and bluebells in spring. This locality, like the 1944 Radley record – about 5km to the east – cited by Alexander (2017), is in the part of Oxfordshire that was formerly included in Berkshire. The proximity of these two records is intriguing and may suggest the presence of a breeding population somewhere in this general area.

Bushy Park, Middlesex

One female was caught by Scotty Dodd on 20.vii.2019, during a survey for the Royal Parks of areas containing hawthorn *Crataegus*. The specimen was identified by him and subsequently confirmed by PJC. It was taken by beating hawthorn in an area (TQ160696) situated NE of the Diana car park and which falls in compartment 23a (see plan in Chandler 2015, fig. 2). The area is bracken-dominated with scattered hawthorns, most of which were in poor health with some heavily colonised by mistletoe (Scotty Dodd *pers. comm.*). The record is of particular interest in that this species was not found during earlier surveys of Bushy Park, to which PJC contributed and in which the two commoner species of *Dilophus* were recorded (Chandler 2015).

Discussion

Three of the most recently discovered sites for *D. bispinosus* are from the south-west of Britain and also share underlying limestone geology and gorge-like landscapes: the Avon Gorge (Leigh Woods), the Wye Gorge (Pierce Wood) and the Cotswold Escarpment (Crickley Hill). Pierce Wood has generated the most change to our knowledge of the species, initially with the first British male and then with the first find of more than one specimen and from a site with a previous record. All earlier and other recent records have been of singletons from sites with no earlier or - so far - subsequent records. Singletons are always difficult to interpret - do they indicate sparse populations or strays beyond the core of the local population(s)? The Pierce Wood experience now suggests the latter as a repositioning of the trapping location has changed the catch from a single male to a remarkable catch of six males and two females.

Now that we appreciate that the single records from English sites may relate to stray individuals a short distance from the actual breeding locations, the significance of the immediate habitat may be diminished. The group of individuals trapped within a recently formed glade in old growth woodland may suggest that relatively warm and sheltered situations within woodland could be the key feature of the habitat for breeding, or at least for males and females to congregate. The data provided here of several males and females together in one trap might indicate a breeding site rather than a behavioural response. Does the capture of males and females together suggest emergence from a close-by larval or pupal habitat or an active attraction of one gender by the presence of the other? This finding of a potential breeding site pushes our knowledge of these flies much further than we had before – it is generally thought that bibionids develop in more open habitats (grasslands, etc), though some bibionids have been found in rotting tree trunks (A. Godfrey pers. comm.). It looks as though bispinosus might develop in decaying wood or alternatively humus-rich woodland soil which has been freshly exposed to sunshine. Both options would require the females to be relatively mobile, exploring the local area for larval habitat opportunities, and this might explain the recording history of individual females found in a wide variety of situations. The 2020 discovery of a female at Cothill, only about 5km from the 1944 Radley record, seems to fit this hypothesis. Mating might occur close to one area of larval habitat, as the adults emerge, and then the females disperse to find new oviposition sites.

Another potentially interesting point is that the four-bottle type of flight interception trap has been generating most of the recent finds rather than Malaise traps which are very popular with dipterists and which have been widely used in woodland situations without finding *bispinosus* (until the Cothill example reported here). Four-bottle traps tend to be suspended at varying heights above the ground surface and so may be more suited to capturing dispersing individuals of this particular species than the ground-based Malaise trap.

This is all speculation, of course, but a hypothesis needs to be formulated before it can be tested against subsequent observations.

Acknowledgements

Rob Bacon initiated the NRW saproxylic invertebrate survey in the Wye Valley Woodlands SAC and has been supported by Mike Howe, who managed the publication process. Laura Lawrance-Owen (National Trust Area Ranger) initiated the Crickley Hill study. We thank Judy Webb and Natural England for enabling us to include the Cothill record, and Scotty Dodd and the Royal Parks for that from Bushy Park. Richard Lane provided a helpful review of an earlier manuscript and suggested expansion of the discussion to explore the implications of the Welsh experience with the species.

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Corrections and changes to the Diptera Checklist (45) – Editor

It is intended to publish here any corrections to the text of the latest Diptera checklist (publication date was 13 November 1998; the final 'cut-off' date for included information was 17 June 1998) and to draw attention to any subsequent changes. All readers are asked to inform me of errors or changes and I thank all those who have already brought these to my attention.

Changes are listed under families; names new to the British Isles list are in bold type. The notes below refer to loss of 3 species due to synonymy and addition of 3 species, resulting in the total remaining at **7216** species (of which 41 are recorded only from Ireland).

An updated version of the checklist, incorporating all corrections and changes that have been reported in *Dipterists Digest*, is available for download from the Dipterists Forum website. It is intended to update this regularly following the appearance of each issue of *Dipterists Digest*.

Psychodidae. The following new synonymies were established by J. JEŽEK, J. OBOŇA, P. GROOTAERT, K. LOCK, P. MANKO and W. DEKONINCK (2020. Review of two Tonnoir moth fly species, overlooked for a century (Diptera: Psychodidae: Psychodinae). *Acta Entomologica Musei Nationalis Pragae* **60**(2), 517-526):

Pneumia vittata (Tonnoir, 1919 – *Pericoma*) (= *Pericoma crispi* Freeman, 1953) *Tonnoiriella obtusa* (Tonnoir, 1919 – *Pericoma*) (= *T. anchoriformis* Salamanna, 1975)

Cecidomyiidae. The following eastern Nearctic species was added to UKSI (= UK species index, maintained at the Natural History Museum) at the request on 7 October 2016 of Steve McWilliam, following a report by Brian Wurzell that it was already widespread in NE London; it is the Silver Maple gall and was recorded on ornamental alien street trees, Silver Maple *Acer saccharinum* and Red Maple, *Acer rubrum*:

Dasineura aceris (Shimer, 1868 - Cecidomyia)

Dolichopodidae. The following new synonymy is established in the present issue: *Syntormon submonilis* Negrobov, 1975 = *S. silvianum* Pârvu, 1989

Agromyzidae. The following species were added by M. ČERNÝ, M. VON TSCHIRNHAUS and K. WINQVIST (2020. First records of Palaearctic Agromyzidae (Diptera) from 40 countries and major islands. *Acta Musei Silesiae, Scientiae naturales* **69**, 193-229): *Chromatomyia* **obscuriceps** (Hendel, 1936 – *Phytomyza*) *Phytomyza* **ranunculella** (Spencer, 1974 – *Napomyza*) The following new synonymy, established by V.V. ZLOBIN (2005. Studies on European species of the genus *Phytoliriomyza* Hendel (Diptera: Agromyzidae). *Russian entomological Journal* **14**(2), 119-123), was overlooked when *P. bornholmensis* was added to the British list by Chandler and Cole (2006):

Phytoliriomyza dorsata (Siebke, 1863) = *P. bornholmensis* Spencer, 1976

The following new synonymy was established by L. PAPP and M. ČERNÝ (2015. Agromyzidae (Diptera) of Hungary. Volume 1. Agromyzinae. 416 pp):

Ophiomyia collini Spencer, 1971 = *O. skanensis* Spencer, 1976

The synonymy of *Phytomyza symphyti* Hendel, 1935 with *P. medicaginis* Hering, 1925 has been recognised in the checklist on the basis of inclusion in *Fauna Europaea*; it was first noted by K.A. SPENCER (1977. Notes on world Agromyzidae, with the description of 16 new species (Diptera: Agromyzidae). *Beiträge zur Entomologie* **27**(2), 233-254), but not immediately accepted by him because of being an inappropriate name based on misidentification of the foodplant by Hering (Barry Warrington *pers. comm.*), so was overlooked in the 1998 checklist.

Muscidae. Following the synonymy of *Mydaea detrita* (Zetterstedt, 1845) = M. *electa* (Zetterstedt, 1860) by A.C. PONT (2011), already included in the checklist, *detrita* should be deleted from the synonymy of M. *orthonevra* (Macquart, 1835).

Sarcophagidae. The following synonymy, attributed in a 2019 update to Whitmore (2011), was first proposed by R. RICHET, R.M. BLACKITH and T. PAPE (2011. *Sarcophaga* of France (Diptera: Sarcophagidae). *Pensoft Series Faunistica* **97**, 327 pp): *Sarcophaga (Heteronychia) compactilobata* (Wyatt, 1991) = *S. (H.) depressifrons* Zetterstedt, 1845

Tachinidae. From the changes resulting from J.E. O'HARA, S.J. HENDERSON and D.M. WOOD (2020. Preliminary checklist of the Tachinidae (Diptera) of the World. Version 2.1. PDF document, 1039 pp), cited in the previous issue, it should also be mentioned that subgenera were not recognised in the genus *Phasia*, so HYALOMYA is now listed as a generic synonym only.

Liriomyza intonsa Spencer, 1976 (Diptera, Agromyzidae) new to

England – On 19.v.2020, I collected a single male *Liriomyza intonsa* Spencer, 1976 from a brownfield site in Hull, East Yorkshire (V.C. 61), representing the first known record for England. This species was added to the British list by D. Gibbs and M. von Tschirnhaus (2016. *Dipterists Digest (Second Series)* **23**, 219-224) on the basis of a single male within a vacuum sample taken in South Wales in 2015.

Gibbs and von Tschirnhaus (*op. cit.*) mentioned that as the specimen was collected within the boundary of a working port, it raises the probability that the species had been imported with plant material or foodstuffs. However, this may not be the case as the collecting site in Hull does not agree with this biotope.

Along with the *L. intonsa* specimen, I also collected two males of *Agromyza macedonica* Černý, 2011 which represents the second known record of this species in Great Britain. This small species was added to the British list by D. Gibbs and M. von Tschirnhaus (2019. *Dipterists Digest (Second Series)* **26**, 67-71), where they mention that *Vicia* seems to be the host plant genus; the collecting site in Hull possesses an abundance of *Vicia cracca*, *V. hirsuta*, *V. tetrasperma* and *V. sativa*; however, until this species is successfully reared, its host plant genus/genera will remain unconfirmed – **BARRY P. WARRINGTON**, 221A Boothferry Road, Hessle, East Yorkshire, HU13 9BB; agromyzidaeRS@gmail.com

A second British site for *Wiedemannia simplex* (Loew) (Diptera, Empididae, Clinocerinae)

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Summary

Further survey work in the Cairngorm National Park has discovered a second British site for the Endangered Empididae *Wiedemannia simplex* (Loew, 1862).

Background

The status of *Wiedemannia simplex* (Loew, 1862) in the British Isles was reviewed by MacGowan (2019). During survey work carried out to inform that review six high level lochs in the Cairngorms were visited during the summer of 2018, with *W. simplex* only being detected at one site. The species was only found at Loch Avon, a locality which has historical records of the species going back to the visits of R.L. Coe in 1936 and 1937. Based on the evidence of this survey it was concluded that this was still the only known British site.

Survey work 2020

As part of a general search for montane Diptera, I made a further visit to Loch Etchachan in the central Cairngorms on 21 July 2020 and somewhat to my surprise discovered a substantial population of *Wiedemannia simplex* occurring along the loch shore. Adults of both sexes were seen in their characteristic situation, just above the waterline on the granite boulders (Fig. 1) along the southern shore of the loch (Fig. 2). Six specimens, 23° and 4° , were retained for the National Museum of Scotland collections. Loch Etchachan lies 1.4km south of Loch Avon, and, at an altitude of 927m, is 200m higher. Loch Etchachan has a surface area of 0.23km² and a maximum depth of 20m (Wikipedia a), compared to Loch Avon which has a surface area of 0.43km² and a maximum depth of 101m (Wikipedia b).



Figs 1-2. Wiedemannia simplex at Loch Etchachan: 1, adult; 2, habitat.

I had previously visited Loch Etchachan (NJ0000) on 26 June 2018, at which time I saw no evidence of this species. That visit was on the same day as I had recorded the species at Loch Avon, which in itself had been the earliest recorded occurrence of *W. simplex*. Previously the species had only been found in July and August with the earliest seasonal date being 13.vii.1936. I can only assume that the emergence of adults at the higher Loch Etchachan had not yet occurred when I visited the site in June 2018. As a result of the 2018 survey, I had concluded that *W. simplex* only occurred in Loch Avon, a deep loch in a narrow glacial trench. I considered that the higher but relatively shallow corrie-lochans were not suitable. However, the occurrence at Loch Etchachan opened up the possibility that there could be further populations in these high corrielochans and as a result further survey work was undertaken.

The first site visited on 29 July 2020 was Loch Coire an Lochain (NH9400) which lies at 995m in a north facing corrie just below Braigh Riabhach, some 6km. west of Loch Avon. This is one of the highest, and due to its aspect, one of the coldest water bodies in the Cairngorms but despite an extensive search of the shoreline no specimens were seen. Subsequently on 7 August 2020 I visited Lochan Uaine (NO0098) just south of the summit of Beinn MacDhuibh. This is another high level lochan situated at 950m in an east facing corrie, less than 2km south of Loch Etchachan, but again despite a shoreline search no specimens of *W. simplex* were observed. On a further visit to Loch Etchachan, on 17 September 2020, no adults were seen in the areas where they had been observed in the previous July, probably indicating the adult flight period was over.

Conclusions

After surveying eight Cairngorm lochs at different altitudes between 2018 and 2020, *W. simplex* has now been found at two sites. This obviously reduces the vulnerability of the species to any possible environmental impacts and with the second site being at an altitude 200m higher than Loch Avon it may act as a buffer against the effects of climatic change. There is, of course, still a possibility that *W. simplex* may yet be found at other localities but with the most obvious sites having been sampled during the flight period, this seems more unlikely. It still remains one of our rarest and most vulnerable British flies and is potentially an important indicator of environmental change.

References

MacGowan, I. 2019. In search of *Wiedemannia simplex* (Loew) (Diptera, Empididae, Clinocerinae). *Dipterists Digest (Second Series)* 25(2018), 179-184.
Wikipedia a https://en.wikipedia.org/wiki/Loch_Etchachan accessed 1st October 2020
Wikipedia b https://en.wikipedia.org/wiki/Loch_A%27an accessed 1st October 2020

Changes to the Irish Diptera List (31) – Editor

This section appears as necessary to keep up to date the initial update of the Irish list in Vol. **10**, 135-146 and the latest checklist of Irish Diptera (Chandler *et al.* 2008). Species are listed under families. The gain of three species cited in the present issue (p. 10) brings the total Irish list to 3461.

Agromyzidae

Aulagromyza tridentata (Loew, 1858) Calycomyza artemisiae (Kaltenbach, 1856) Aulagromyza luteoscutellata (de Meijere, 1924)

Morphological arguments for the retainment of three long time established genera in Agromyzidae (Diptera): *Chromatomyia* Hardy, *Napomyza* Westwood, and *Ptochomyza* Hering

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Summary

Since 2009, the generic breakdown of Agromyzidae has been applied differently in the Old and New World. Back then a first global attempt to use DNA data for the construction of a phylogenetic tree of a subgroup of Phytomyzinae resulted in synonymy of the genus *Chromatomyia* and the transfer of two accepted monophyla (genera) to the status of subgenera. This resulted in 92 new combinations and ten renamings for the economically important family of leaf miner flies with its immense scientific literature. This article provides morphological arguments that *Chromatomyia* is a monophylum, deserving generic justification which is supported by a specific apomorphic pupariation mode. The studied male genitalia of 114 valid *Chromatomyia* species possess one peculiar apomorphic ground pattern, which easily distinguishes them from the remaining 573 valid *Phytomyza* species. As *Phytomyza* may be paraphyletic it is preferable for it not to include a plausibly defined species-rich monophylum. It is hereby proposed to continue with the use of the well-established generic status of *Chromatomyia*, *Ptochomyza* and *Napomyza*. Some important errors in the literature are corrected, including the reinstatement of senior genus group names for monophyla not being protected by the Rules of the ICZN. Seven *Phytomyza* species are formally transferred as new combinations (**comb. nov.**) to *Chromatomyia*.

Introduction

The aim of this article is to discuss for the first time morphological arguments against placing all species treated as *Chromatomyia* within six recognised "monophyletic" species groups of *Phytomyza* Fallén sensu stricto by Winkler *et al.* (2009) and to consider if it was necessary to relegate two accepted and unquestioned genera to the status of subgenera with all the undesirable taxonomic effects. Griffiths (1974) stated: "At present we do not have sufficient historical information on the Agromyzidae to decide such questions of the absolute rank of taxa" – still the case today when we still don't know if *Phytomyza*, the largest genus of Agromyzidae, is paraphyletic (as presumed by several authors).

In December 1849, Hardy (1849) and Walker (1849: 801) simultaneously proposed the name Chromatomyia for genera currently included respectively in the families Agromyzidae and Platystomatidae. On p. 1162 in the same paper, Walker (1849) synonymised his new genus with Lamprogaster Macquart, 1843, which was confirmed by Evenhuis (1989); consequently, it plays no role within this discussion. The exact date of issue of Hardy's article is unknown; that of Walker's article is 8 December (Evenhuis et al. 1989: 879 and 981). Griffiths (1974) decided that Hardy's paper was distributed first and that is accepted until today. Schiner (1864) was the first author who synonymised Chromatomyia Hardy with Phytomyza Fallén, followed by Brazhnikov (1897), the latter of whom was also the first author to treat it as a subgenus of *Phytomyza*. From that date onwards, in 176 publications, different opinions on this generic name were published. After years of thorough studies and rearing Holarctic Agromyzidae from their host plants, Griffiths (1974) resurrected the genus on the basis of detailed morphological and ecological definitions. He only excluded one of the seven species which originally were listed in Chromatomyia by Hardy, namely *Phytomyza ilicis* Curtis, 1846, which Hardy had already included with a question mark. Hardy's definition of the genus was that its species possess a flattened puparium and pupariate in a peculiar mode inside the leaf mines (treated in detail below), which Griffiths also judged to be an apomorphous ground pattern character to define the genus

as a monophylum. As another and more complicated characteristic for all *Chromatomyia* species, Griffiths defined the very specific apomorphous morphology of the phallus (aedeagus) by "the loss of all sclerotization supporting the terminal section of the ejaculatory duct" and "the distal section of the ejaculatory duct is simple (not bifid) and lies below a lobe on the 'dorsal' (in anteriorly directed rest position) side of the aedeagus". As a consequence, Griffiths avoided the terms distiphallus and mesophallus for the definition of the genus. Additional opinions are presented after a new morphological study of the male genitalia, combined with a review of Winkler *et al.* (2009), which presented *Chromatomyia* as a non-monophyletic taxon, thus removing it from the phylogenetic tree of Agromyzidae. Winkler *et al.* (*op. cit.*) also relegated the related genera *Napomyza* Westwood and *Ptochomyza* Hering to the new status of subgenera. This had taxonomic consequences, e.g. the transfer of 94 valid species (46 *Chromatomyia*, 44 *Napomyza*, 4 *Ptochomyza*), and the renaming of ten species because of secondary homonymies and shifting back further species to their original genus. By accepting those decisions, more generic transfers of recently described *Chromatomyia* species would become necessary.

The published approach for a DNA based phylum of *Phytomyza* sensu lato

Winkler *et al.* (2009) did not recognise the monophyly of *Chromatomyia* but accepted the monophyly of the genera *Napomyza* Westwood, 1840 and *Ptochomyza* Hering, 1941. They treated the two latter as subgenera of *Phytomyza* and arranged all *Phytomyza* and *Chromatomyia* species known to them in 27 groups – 24 named ones, one unplaced species group and two species groups unplaced to subgenus *Phytomyza*. Eight new species group names were proposed. Their species groups were mainly based on the similarity of published figures of male genitalia, on which their identifications were based. Host plant relations published by Spencer (1990) and their own DNA results were also used for their new ordering system. Their following seven groups contain 112 species which, since Griffiths' work (1974), undoubtedly were placed in *Chromatomyia*. It is noteworthy that four groups are predominantly or completely composed of *Chromatomyia* spp.:

- 3. ciliata group: 3 Chromatomyia of 14 spp., paraciliata (Godfray) being an accepted transfer to Phytomyza
- 5. syngenesiae group: 26 Chromatomyia of 30 spp.
- 7. loewii group: 2 Chromatomyia of 5 spp.
- 19. agromyzina group: 67 Chromatomyia of 70 spp., incl. the type species periclymeni (de Meijere, 1924) (see below)
- Species unplaced in *Phytomyza* sensu stricto: 5 *Chromatomyia* of 169 spp.
- Species unplaced to subgenus: mimuli group: 5 Chromatomyia of 5 spp.
- Species unplaced to subgenus: scolopendri group: 4 Chromatomyia of 4 spp.

What is the consensus about Chromatomyia within the Agromyzidae?

Agromyzidae contain 3,163 valid species and a further 12 valid names for subspecies. Among them are 575 valid *Phytomyza* species and 114 valid *Chromatomyia* species, one additional valid subspecies in *Chromatomyia* and 9 *Phytomyza* species which are transferred to *Chromatomyia* below. An additional 45 scientific names of the species group are invalid names synonymous with valid *Chromatomyia* species. There are also 1,401 invalid species names globally in the family in December 2020 (statistics after the database of the author).

Since the issue of the article of Winkler *et al.* (2009), in the Old World no expert of Agromyzidae has accepted the synonymisation of the three genus group taxa, *Napomyza* Westwood, 1840, *Chromatomyia* Hardy, 1849 and *Ptochomyza* Hering, 1942 with the genus *Phytomyza* Fallén, 1810. The author collected 2,019 publications on Agromyzidae published from January 2010 until December 2020 (249, 239, 227, 206, 206, 177, 164, 230, 151, 125, 45 publications, respectively). Out of those, only four publications from North America follow Winkler *et al.* and treat *Chromatomyia* and *Ptochomyza* species in the genus *Phytomyza*. Personal discussions with ten Agromyzidae experts in the Old World supported non-acceptance of the synonymisation of *Chromatomyia*, *Napomyza* and *Ptochomyza* with *Phytomyza*. This opinion

was explicitly expressed by Kahanpää in his Finnish checklist (2014: 291-292), Černý and von Tschirnhaus (2014: 160) and Papp and Černý (2020: 19-20, 176, 678). The close relationship of *Ptochomyza* with *Phytomyza* was not supported by Papp and Černý (2017: 390), who considered it more plausibly related to *Aulagromyza* Enderlein, 1936, an unrevised genus of the *Phytomyza* group of Dempewolf (2001). Since Winkler *et al.* (2009), additional described species in *Chromatomyia* are *C. masumiae* Sasakawa, 2010, *C. cepelaki* Černý, 2012 and *C. kerteszi* Černý, 2020. The latest definition of the apomorphous characteristics of *Chromatomyia* by Papp and Černý (2020: 19-20, 103, 107, 176, 179) is supported by the author's observations.

Phallus morphology of Chromatomyia

I exclude the morphological terms dorsal and ventral (ventral always being the side with the rope ladder nerve system of the arthropods) as for those the torsion of the postabdomen of all Cyclorrhapha must also be considered as well as the direction in which the phallus is expanded, caudally as necessary for a morphological orientation (and as in many trap-caught and alcohol preserved specimens) or directed forwards being the rest and active position. A proof of the torsion in all Agromyzidae is the 180° loop of the ejaculatory duct around the basal asymmetric part of the phallus and as well the asymmetry of the two sclerites of the basiphallus. (Fig. 1). Views should be described as "from above" and "from below".

Fundamentally, the distal part of the phallus consists of three peculiar symmetrical terminal lobes, the upper, medial and lower lobe ["ventral lobe" of Spencer (1981: 436-439 and Papp and Černý (2020: 19)] (Fig. 1). The upper lobe is equipped with one or two pairs of symmetrical "supporting sclerites" which can be partly fused but never tube-like or funnel like (in as far they cannot be confused with the distiphalli of *Phytomyza* spp.). I speculate that the sclerites of the upper and medial lobe together may serve as a lever tool to open and to close the sperm flow into the sperm reservoir (Fig. 2); the darkened section in this figure seems to function as a valve. The medial lobe consists of one pair of symmetrical "wedge-shaped sclerites" (Fig. 1B) [as used by Spencer (1981: 450) and Papp and Černý (2020: 19)], which can be atrophied or secondarily lost in certain species. The lower lobe bears one pair of symmetrical sclerites which accompany, stabilise or enclose the base of the ejaculatory duct on its right and left side (Fig. 1C).

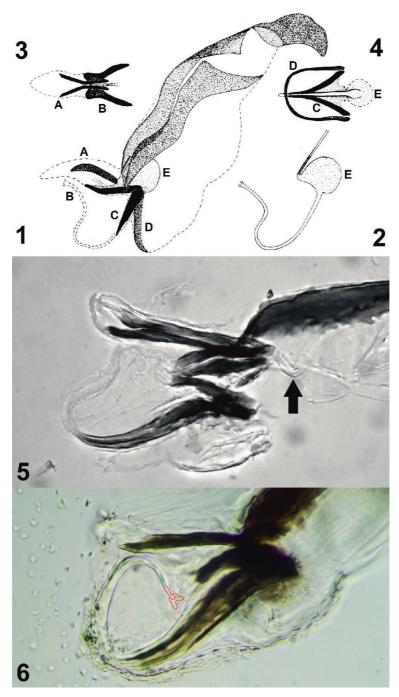
The flagellum-like and simple (not bifid) terminal part of the ejaculatory duct, its hyaline tip in opposed position against the tip of the upper lobe, is singular among all world genera of Agromyzidae. A figure with a split tip for *C. opacella* (Hendel, 1935) in Papp and Černý (2020) does not agree with *opacella* preparations by the author of ten specimens from Iceland and the Austrian Alps. Their figure is likely to have resulted from a terminal coil being twice in microscopical focus. This flagellum-like unsclerotised duct is basally embedded between the sclerites of the lower lobe (Fig. 4) but there are species in which the free terminal tube is shortened and its round distal opening lies on the surface of the end of the sclerotised lower lobe. *Chromatomyia skuratowiczi* (Beiger, 1972) belongs to those species in which a distal hyaline tube cannot be detected in lateral view (description see below).

Finally, for some species (e.g. *opacella*) it must be mentioned that the baggy distal and lower part of the phallus (being mainly hyaline) has a dark distal zone of melanisation appearing like a C-shaped sclerite when viewed from below (Fig. 4D); in lateral view it appears to be an additional sclerite (Fig. 1D). For further detailed explanations of the phallus structure see legend for Figs 1-6. Papp and Černý (2020) introduced as a further generic definition the absence of a hypophallus which, with all its structures, is so typical for most genera of Agromyzidae, including *Phytomyza*. With a few exceptions (such as *Chr. fuscula* (Zetterstedt) and *Chr. castillejae nordica*) the ejaculatory apodeme of *Chromatomyia* spp. is very small or even minute, the latter a term Spencer used in many of his species descriptions. Further arguments for the monophyly of *Chromatomyia* should be studied in Griffiths (1974).

The ductus ejaculatorius in the genus Chromatomyia

Since Griffiths' revision (1980) it remained enigmatic where exactly the tip of the ductus ejaculatorius ends. Griffiths' definition of the genus Chromatomyia is based on the assumption that the upwards curved hyaline flagellum on the upper side of the lower lobe is the end of the ductus. Papp and Černý (2020) expressed the same opinion, though Černý's figures of the phalli of the species beigerae, glacialis, isicae, lonicerae, ochracea, rhaetica, swertiae and tschirnhausi show it correctly ends in the dorsal lobe (as also seen in Fig. 5). Controversially, his figure for ramosa depicts the end going into the flagellum. It is not easy to clarify this morphological situation as the ductus has a diameter of only 6.6µm and is completely unsclerotised. In an unpublished manuscript on the phylogeny of Agromyzidae (in my possession), Griffiths still expressed some doubt about the morphological situation. It can only be detected by a stereomicroscope (x80 or higher magnification), only with transmitted light or phase contrast methods. I was successful with the analysis of my dissection of C. skuratowiczi: the ductus seems to end at the exact base of the sclerites of the upper lobe, as in Fig. 5. There seems to be a valvelike narrowing from which the ductus abruptly proceeds in a right or even slightly acute angle downwards into the lower lobe, not continuing as normal into a long flagellum but ending in a free hyaline round tubule opening. This opening is prolonged in most Chromatomyia species as an upcurved flagellum, which partly touches the tip of the supporting sclerites of the upper lobe. In some species its thin tip is slightly coiled as depicted in the figure of *C. beigerae* of Papp and Černý (2020). As illustrated for C. glacialis and \overline{C} , isicae in Papp and Černý, before or under the base of the supporting sclerites the ejaculatory duct is partially widened to a small or larger hyaline round sperm reservoir, from which the way down to the lower lobe is difficult to detect. In Chromatomyia species a typical sclerotised distiphallus as in *Phytomyza* species is secondarily lost. These facts speak for *Chromatomyia* being a monophyletic group within the "Napomyza group" of Spencer (1990) or the "Phytomvza-Gruppe" of Dempewolf (2001).

Figs 1-6. Terminology of the phalli of *Chromatomyia* spp., all figs show distal parts to left: 1-4, phallus of C. opacella (Hendel), modified after Griffiths (1980); 1, left lateral view with phallophorus at its base [right above], right and left asymmetric sclerites of basiphallus [in centre] and six distal structures (A, B, C, D, E, and [dotted] end of ejaculatory duct); 2, course of distal end of ejaculatory duct in Fig. 1 with sperm reservoir (E) and a dark section presumed to be a valve; 3, upper lobe with pair of supporting sclerites (A) and medial lobe with pair of wedge-shaped sclerites (B) in view from above; 4, distal parts of phallus in view from oblique below and behind: the pair of sclerites of lower lobe (C) stabilise the right and left base of the unsclerotised end of ejaculatory duct; the melanised distal edge (D) of pocketlike lower end of phallus appears like a U-shaped sclerite; 5, C. milii (Kaltenbach) from Spessart mountain, Germany, left view on distal part of phallus with upper, medial and lower lobe, the latter two partly artificially dissected and drawn downwards in order to demonstrate that the ejaculatory duct is fastened to the base of the upper lobe; sperm reservoir and continuation of ejaculatory duct downwards to the lower lobe are hidden. An arrow points to an artificial 90° curvature of the ejaculatory duct (normally being straight, diameter 6.6µm) resulted from the dissection procedure. The curvature is the proof that the duct is fastened to the supporting sclerites of the upper lobe; wedge shaped sclerite of medial lobe artificially split in three longitudinal fragments; 6, C. milii from Hessle, England: the phase contrast image shows the hyaline unsclerotised end of the ejaculatory duct, an apomorphous structure of all Chromatomyia species. Red outline depicts the hyaline funnel-like end of the duct, visible only with difficulties under high magnification. Length of supporting sclerite of upper lobe 83µm.



Pupariation mode

Additional peculiar features support a monophyletic Chromatomyia, namely a very characteristic mode of pupariation inside the mine with the dorsal surface of the puparium attached to the leaf tissue in a so-called "Puppenwiege" (sealed cell with pupa). During pupariation, the thoracic segments of the larva are bent downwards (ventrally) together with the anterior spiracles and those are hooked into and through the plant epidermis, connecting the pupa with the external air. This mode was judged by Dempewolf (2001) to be an apomorphy. The ventral lid of the slippershaped puparium is in contact with the epidermis which itself becomes open, together with the lid, during the emergence procedure. The pupariation behaviour was figured and described by Darvas et al. (2000) for Chromatomyia fuscula (Zetterstedt, 1838) as follows: "The half contracted larva turned toward the epidermis and opened it with its mouthhooks. During the contraction of the anterior part, the anterior spiracles protruded through the epidermis to the outside. The contracted larva secreted a sticky drop of faeces to attach itself on the dorsal surface to the greenish internal side of the leafmine." Such a cement-like droplet is also typical for Calycomyza species like the cosmopolitan C. humeralis (von Roser, 1840). Dempewolf (2001: 36) figured the puparium for Chromatomyia milii (Kaltenbach, 1864), and also described the hatching process of Chromatomyia species.

Winkler *et al.* (2009: p. 277) summarised that a similar "mode of pupariation must have evolved ... six times in *Phytomyza* sensu stricto", related to group or species names in their fig. 2, but this important difference in details of pupariation modes was not described for these suspected parallelisms in *Phytomyza*. This is an important omission in their analysis, which was subsequently continued towards another focus, pupariating inside the leaves, especially those of trees.

Errors in the literature

A confusing error appears in the paper of Winkler *et al.*, in as far as the authors created a new species group (a monophylum), the *agromyzina* group [on page 288 and also treated on pp. 265-268, 270, 271, 273, 275-279, 290, including an "*agromyzina* clade" on p. 291] which includes the type species of *Chromatomyia, Phytomyza periclymeni* de Meijere, 1924 [in the description of *Chromatomyia* Hardy, 1849 it was misidentified as *Phytomyza obscurella* Fallén, 1823]. For a species group with the included type species *P. periclymeni*, Griffiths (1974: 36, 38, 39, 50, 51), in his re-establishment of the genus *Chromatomyia*, erected the *periclymeni*-group, a senior name for the *agromyzina* group, which was overlooked by Winkler *et al.* Furthermore, Winkler *et al.* named the group after a species with typical *Phytomyza* male genitalia, which on first impressions (compare fig. 538 in Spencer, 1990: 144), exclude it from association with *Chromatomyia* species; *P. agromyzina* Meigen, 1830, is a leaf miner of *Cornus* species (Cornaceae), that normally pupariates outside the mine. *Phytomyza agromyzina* has never previously been cited or treated in the genus *Chromatomyia* (218 papers and books refer to this *Cornus* leaf miner).

Puzzle 1: Winkler *et al.* (2009) added an unpublished "Supporting Information" Table S1 (6 sheets) to their article listing the GenBank Accessions combined with the country of origin and the collector for the species used for the phylograms. Their *agromyzina* group is missing in this list; instead 10 *Chromatomyia* species are presented without group correlation on p. 2 and two *Phytomyza* species in the group "unplaced species" on p. 5, *P. agromyzina* and *P. ceanothi.* Contrary to that, *Phytomyza agromyzina* is included on p. 288 in the *agromyzina* group. As it is one of the most important species for the question about *Chromatomyia*, name-giving for a group which includes the type species of *Chromatomyia*, doubt arises about the correct identification. In fig. 1, it is placed closest to *Chromatomyia milii* but considering its pupariation mode and genitalia morphology, it is closely related to *Phytomyza* group. This fact casts doubt over the

accuracy of the interpretation of the molecular results or the reliability of the identification of the material from the State of Washington (Supporting Information, Table S1). In the Nearctic *P. notopleuralis* Spencer, 1969 also develops in the leaves of *Cornus* species, a taxon which the authors and I consider to be a junior synonym of *P. agromyzina*.

Puzzles 2 + 3: Puzzles also occur for other groups, e.g. *P. loewii* Hendel, 1923 in the *P. loewii* group appears as "unplaced species" in the Supporting Information. An enigma is the inclusion of *Phytomyza pusilla* (Förster, 1891) [as Forster, 1891] as a valid species on p. 292, a name for a doubtful fossil (Evenhuis 1994), which no expert has ever studied and which is a primary homonym preoccupied by *Anthomyia pusilla* Meigen, 1826 for an extant species].

It was not stated for which species, represented by "agromyzina grp. s.s." in their fig. 3, the molecular data was used. Was it *P. agromyzina*? Out of the 70 listed species, 29 were listed as new combinations (comb. n.) and for three others (montana, griffithsi, nigrella) new names were created because the generic transfer of *Chromatomyia* produced ten secondary homonyms. Only three *Phytomyza* [sensu stricto] species were included in their agromyzina group, *P. agromyzina*, *P. abeliae*, and *P. ceanothi*. Founded on *P. abeliae* Sasakawa, the *P. abeliae* group had been introduced by Sasakawa (1961: 428); his figure of the phallus may actually represent that of a *Chromatomyia* species. The genitalia figure of *P. ceanothi* Spencer, 1986 (Spencer and Steyskal 1986) undoubtedly belongs to a *Chromatomyia* species pupariating inside the mine. Three further senior group names had been erected earlier, the long-time established *gentianae* group, the *milii* group, and the *periclymeni* group. But together with the name *abeliae* group, they were all neglected or overlooked by Winkler *et al.* They unnecessarily established a new group name on the basis of a typical *Phytomyza* species for all those transferred *Chromatomyia* species, namely "the *agromyzina* group", the right branch of the *agromyzina* clade.

A new species group name is not required, as the generic name *Chromatomyia* was already introduced by Hardy, 1849 being available for the 69 remaining species presented as a monophylum, taking into account the similar male genitalia morphology and the molecular-based phylogram of fig.1. If the molecular data of the four studied species of the *nigra* clade (*C. syngenesiae, C. lactuca, C. fuscula* and *C. nigra*) in their distant position from the *agromyzina* clade are the main reason to reject a monophyly of *Chromatomyia*, why is it not discussed to remove them from this genus in order to retain the generic name for the *agromyzina* group (= *periclymeni* group without *P. agromyzina*), confirmed in the article as being monophyletic together with many more named but not investigated species?

Thirty-one group names (including sg. *Ptochomyza*) have been used or created by Winkler *et al.* for separating the probably paraphyletic genus *Phytomyza* into monophyletic units; some of them were preoccupied by overlooked or neglected senior names [some of those are not discussed here as being outside of the *Chromatomyia* problem]. Confusingly, judged after the peculiar male genitalia, undoubted *Chromatomyia* species were not included together with their close relatives in the "*agromyzina* group" but instead in three further groups (which are presented as monophyla), namely the *syngenesiae* group, *mimuli* group, and *scolopendri* group and in a special section for unplaced species on page 290-291: *C. alysicarpi, C. comta, C. obscuriceps, C. ochracea,* and *C. perangusta.* Probably the three different positions in fig.1 were the reason that *Chromatomyia* was not designated as a subgenus of *Phytomyza* like *Ptochomyza* and *Napomyza.* This article, above and below, explains that the neglect of morphological features of larvae, puparia and male flies is responsible for the overestimation of the molecular positions.

This comment focuses only on one species group which contains the type species of *Chromatomyia* and a selection of 66 former *Chromatomyia* species but 23 other groups created and treated by the authors contain other errors, puzzles and discrepancies in addition to the separated parts of the former monophylum *Chromatomyia*; this makes it impossible to follow the

authors with their grouping of three long time established genera, two of them rich in species since the early 19th century.

Preoccupied group names and a historical correction

Three new group names of Winkler *et al.* (2009) and two group names of Spencer (1990) are used in the course of our subject and are listed below together with their senior synonyms:

P. agromyzina group (new group name), preocc. by *abeliae* group Sasakawa (1961: 428), by *gentianae* group of Sasakawa (1961: 428), by *milii* group of Griffiths (1964: 406, 429-431) and by *periclymeni* group of Griffiths (1974: 36, 38-39, 50, 51), the latter treated again by Spencer (1990: 240) and eponymous after the type species of *Chromatomyia*.

P. anemones group of Spencer (1990) preocc. by paniculatae group of Sasakawa (1961: 428);

P. minuscula group (new group name), preocc. by minuscula group of Sasakawa (1961: 428);

P. notata group of Spencer (1990), preoccupied by ranunculi group of Hendel (1924: 142).

P. scolopendri group (new group name), preocc. by *dryoptericola* group of Sasakawa (1961: 428, 446-448).

Three taxa of the genus group were equipped with the term syn.n. in the Abstract and in Appendix 1: *Napomyza, Chromatomyia* and *Ptochomyza. Napomyza* was introduced already as a subgeneric new taxon by Westwood (1840). Schiner (1864: 313) removed it from subgeneric status, placing it as a normal synonym and was followed by several authors until Hendel (1931-1936) again installed it as subgenus of *Phytomyza*. For the first two genera the lumping was a revised status (stat. rev.) and not a new synonym.

Former Chromatomyia species now scattered in different groups of Phytomyza?

Only 18 former *Chromatomyia* species (out of 114 in the year 2009) were used for the molecularbased construction of the phylograms in figs 1–3, namely *C. mimuli*, nr. *castillejae*, *scolopendri*, *paraciliata*, *syngenesiae*, *lactuca*, *fuscula*, *nigra*, *clematoides*, *ramosa*, *shepherdiana*, *fricki*, *gentianae*, *aprilina*, *milii*, nr. *luzulae*, *tiarellae*, *primulae*. In fig. 1 *Phytomyza ceanothi* and *P. agromyzina* were also treated together with former "*Chromatomyia*" species in the *agromyzina* clade. *Phytomyza ceanothi* is accepted by the author as belonging to *Chromatomyia* but *P. agromyzina* does not belong there (see above).

Chromatomyia paraciliata must be removed from the above list. There was already a debate between H.J.C. Godfray, K.A. Spencer and the author about the generic position of this peculiar species which I possess from Serbia, collected 5.vii.1989, Barno jezero, Durmitor, reared from *Leucanthemum vulgare* and presented to me by Dr Radoslava Spacić, Belgrade. After my experience with many described and still undescribed related species, it belongs to the *P. robustella* group with its typical male genitalia, those figured firstly by Griffiths (1964), with whom I had a long correspondence about that group. In grey font this group name in fig. 1 of Winkler *et al.* was combined "as used in the taxonomic literature" [legend to fig. 1] with the name *paraciliata*. But neither any literature about that exists, nor a former transfer to *Phytomyza*. In as far the new combination by the authors with *Phytomyza* on p. 284 is correct, their shift of *paraciliata* to their new *ciliata* group is surprising and cannot be supported, but transferring to the *ciliata* group removes *paraciliata* from the further discussion about the monophyly of *Chromatomyia*.

On p. 288 in Winkler *et al.*, in addition, *Phytomyza abeliae* is included in the so-called *agromyzina* group. This is accepted by me, based on Sasakawa's figure and the fact that the larva pupariates inside the mine. The species belongs in *Chromatomyia*.

Phylogenetic position of Chromatomyia scolopendri (Robineau-Desvoidy, 1851)

[= *Phytomyza scolopendrii* Goureau, 1851; = *Phytomyza elegans* Goureau, 1851; = *Phytomyza nevadensis* Strobl, 1900; = *Phytomyza flava* auctt. p.p. nec Fallén, 1823 (misidentifications)]. The first species group name proposed by Sasakawa (1961) is the *Phytomyza dryoptericola* group. 163 publications in the author's possession are listing or treating this taxon.

The peculiar fern miner Chromatomyia scolopendri is included in fig. 1 of Winkler et al., closely positioned to Ptochomyza and Napomyza. This is contradictory to all published ecological and morphological details and to my own experience with this species. This result cannot be accepted. It is one of only five Chromatomyia species worldwide oligophagously developing on ferns, the only fern-mining agromyzids of genera in the *Phytomyza* group of Dempewolf (2001). The larvae and puparia possess an extreme heat resistance and drought tolerance, feeding and aestivating for months in their mines. Mines can be found all over Europe and Turkey on dry sun-exposed stone walls in ferns of the genus Asplenium. Molecular adaptations for this physiological stress during dry periods can be predicted. Dempewolf (2001: 15, 23, 24, 201, 208-209, 229, 238) studied C. scolopendri and described some larval peculiarities. He was not doubtful of the correct generic inclusion in Chromatomyia. The male genitalia of this species and another fern-mining species, C. dorsata, are slightly different from other Chromatomyia species. Spencer (1990: 13) mentioned the typical pupariation mode of Chromatomyia species with the slipper-shaped puparia upside down in the leaf with the spiracles penetrating the leaf epidermis but Winkler *et al.* excluded this species from *Phytomyza* s.str. without giving it a generic name. This contradiction to easily observable, complicated morphological and behavioural details (of leaf mine, larva, puparium, male genitalia and behaviour) is one of the most convincing facts against the correct interpretation of the molecular data in fig.1, line 6-8 (C. mimuli, C. nr. *castillejae*, *C. scolopendri*). All three closely related species (based on the molecular results) possess the typical ground pattern of male genitalia like the 69 listed species of the agromyzina group ["C" agromyzina excluded] and all 55 further worldwide Chromatomyia species not mentioned in the article. I collected C. castillejae on its host plant in British Columbia: the species is a typical Chromatomyia. Winkler et al. (2009: 265) removed it from Phytomyza s.str., without giving them a generic name.

Only three former *Chromatomyia* species remain in the molecular part of the study which are enigmatically placed outside the so called *agromyzina* clade (= *periclymeni* group, = *Chromatomyia* s.str.): *C. syngenesiae*, *C. lactuca* and *C. fuscula*. The extremely polyphagous *C. horticola* (Goureau, 1851) as the sibling species of *C. syngenesiae* is one of the most harmful horticultural pests. At least 852 papers and books deal with this pest species, 532 of them in the genus *Chromatomyia*. It is undesirable to exclude the use in applied entomology of this name in favour of *Phytomyza*. Also *C. fuscula*, *C. nigra* and other *Chromatomyia* species are well-known agricultural and horticultural pests, treated in many publications. Their inclusion in a *P. nigra* clade together with the *Phytomyza robustella* group (as in fig. 1) contradicts all previous morphological and biological studies. Inclusion in the possibly paraphyletic genus *Phytomyza* being paraphyletic. We have to await further molecular studies based on more genes and enhanced molecular methods.

Where is the *Phytomyza agromyzina* **group of Winkler** *et al.* **nested in the phylogram?** (Senior name *Chromatomyia periclymeni* group of Griffiths, = *Chromatomyia* Hardy)

Owen Lonsdale (2015) wrote: "Results of the ... study [of Winkler et al. 2009] strongly supported a polyphyletic *Chromatomyia*, and found the lineage containing the type species to be deeply nested within *Phytomyza* providing good support for its synonymy in the same paper". The question arises where is the position of *Phytomyza* sensu stricto in the genus *Phytomyza*,

considered to be paraphyletic in the opinion of several Agromyzidae experts? Of course, the "deepest" group has to include the name-giving type species of the genus and its relatives, Phytomyza ranunculi (Schrank, 1803), eponymous for the Phytomyza ranunculi group. This was introduced by Hendel (1924: 142), later used by Hendel (1931-1936: 525, 527), Rydén (1953: 15), Sasakawa (1961: 428), Spencer (1977: 368) and von Tschirnhaus (1969: 154, with genitalia figures including the hyaline parts) for which Winkler *et al.* used Spencer's name *P. notata* group ascribing to it on p. 275 a "highly apomorphic male aedeagus" (though notata has an extraordinarily short distiphallus with one apical opening. Worldwide, all species of this group, except one from New Zealand (P. anthocercidis Spencer [misspelled by the authors as anthoceridis], host plant genus Anthocercis, Solanaceae) only attack plants of one of the most plesiomorphic dicotyledonous families, the Ranunculaceae, order Ranunculales. Except for the fact that certain species possess an extremely elongated flexible distiphallus tube, bifurcate or not at its end (in the case of P. vibeana from Greenland six times the length of the fly] other apomorphic characters were not noted by the authors for the very simply structured phallus. I would judge that the phalli of members of the P. ranunculi group, in accordance with their plesiomorphic host plant family, present us with a simple and very plesiomorphic morphology. The notata group, in the phylogram of Phytomyza (fig. 1), is positioned as the left branch of the albipennis clade, so well far away from the scolopendri group or a group which contains some former *Chromatomyia* species, the *syngenesiae* group, or the authors' "*agromyzina* group". In as far I would not judge it as "deeply embedded" in *Phytomyza* s.str. but denote it as the crown group of the phylogram at the right end of their fig.1.

Conclusions

The morphological analysis of the complex apomorphous phallus of 114 *Chromatomyia* spp. together with the apomorphous ground pattern of pupariation inside the leaf mine, with the dorsal surface glued to the leaf tissue, anterior spiracles bent down against the leaf epidermis and penetrating it, slipper-shaped slightly flattened puparium in a "sealed cell with pupa" speaks for a monophylum deserving recognition as a separate genus in the *Phytomyza* group of Dempewolf (2001: 237), which contains four further equivalent genera: *Aulagromyza* Enderlein, *Gymnophytomyza* Hendel, *Napomyza* Westwood and *Ptochomyza* Hering. Following Papp and Černý (2020), the new combinations of Winkler *et al.* for 45 *Chromatomyia* spp., 44 *Napomyza* spp., 2 *Ptochomyza* spp. and further species returned into their original genus are rejected. The transfer of *C. paraciliata* to *Phytomyza* is accepted. Also rejected are all 10 nomina nova for species which automatically became secondary homonyms by relegating genera to the status of subgenera (1 *Phytomyza*, 3 *Chromatomyia*, 6 *Napomyza* spp.).

In order to place all world species confirmed to belong to *Chromatomyia* in one uniform generic system, seven *Phytomyza* species are here formally transferred as **comb.** Nov. to *Chromatomyia*: *C. ceanothi* (Spencer, 1986), *C. nemophilae* Eiseman & Lonsdale, 2019, *C. palmeri* (Eiseman & Lonsdale, 2018), *C. palustris* (Eiseman & Lonsdale, 2018), *C. salviarum* Eiseman & Lonsdale, 2019, *C. sempervirentis* (Eiseman & Lonsdale, 2018), *C. tigris* (Eiseman & Lonsdale, 2018), *and C. verbenae* (Eiseman & Lonsdale, 2018). *Napomyza* and *Ptochomyza* deserve no special discussion as they came out as two monophyla in the study of Winkler *et al.* in agreement with the author. Genera and subgenera are theoretical terms, depending on personal opinions about their hierarchy. Griffiths' words cited above should be considered to prevent such a bulk of taxonomical alterations. I propose to follow the breakdown of genera in Dempewolf (2001) and Papp and Černý (2020).

After forty years, K.A. Spencer's statement (1981: 433) is still valid: "Any worker with some familiarity with the male genitalia of the Agromyzidae should be able to recognize the characteristic form of the aedeagus of *Chromatomyia* species without difficulty". Papp and Černý

(2020: 30) agreed with the sentence: "We are convinced that the genus *Chromatomyia* ... is a monophyletic unit". This paper has clarified the exact course of the unsclerotised end of the ductus ejaculatorius, which was partly doubted by myself since Griffiths' reintroduction of the genus *Chromatomyia*.

Outlook

As long as the branches of a symbolic phylogenetic tree of the probably paraphyletic genus *Phytomyza* is not defined on the basis of a multitude of larval and adult morphological features and DNA data, a separation into genera or subgenera with their belonging species groups should not aim in splitting or lumping taxa of the genus group. Such a procedure is nothing else than a horizontal cut through the canopy of the symbolic tree with its main branches, a cut a bit below or slightly above bifurcations in their different heights. The decision in which height you cut the canopy and if a certain branch is the equivalent of a genus or a subgenus depends on personal opinions. Such opinions lead to the situation, that Agromyzidae with 3,163 valid species were divided into 27 (by O. Lonsdale only 21) valid extant taxa of the genus group and Chloropidae with 3,077 species into 215 taxa of the genus group. Both families are of the same geological age appearing as fossils in the early Tertiary (Agromyzidae hitherto only known as larval tracks in cross sections of fossil wood). The different scale for accepting generic names for monophyla let us doubt the justification for such a disequilibrium in creating those theoretical cupboards, namely the genera.

Larval morphology was not used at all in the paper of Winkler *et al.* for a phylogenetic study of a holometabolous insect group with two different life stages, like the long living polyp and the jellyfish. Agromyzidae taxonomy is based mainly on the highly complex genital structures documented for 60 years as a result of the hard work of many authors, but these details are completely neglected in the argumentation in favour of DNA data. DNA studies are helpful but not convincing without parallel evaluated morphological insights.

A symbiosis of molecular and morphological facts is a difficult task for understanding the phylogeny of a group of organisms but it should not be combined with fundamental taxonomic decisions changing the names of well-known agricultural pests, at least not in the first stage of the investigation based mainly on molecular data and without the subsequent discussion of other experts. Just this is the situation in which applied entomologists become upset about taxonomists changing long time established scientific names for global agricultural pests. After more than 12 years advance in DNA techniques, we await with interest future developments combining molecular with morphological data in refining agromyzid phylogeny.

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Three species of Agromyzidae (Diptera) added to the Irish checklist

- Three species of leaf-mining flies are added to the Irish checklist based on their distinctive leaf mines and reared adults. Rodney Monteith came across the mines of *Aulagromyza tridentata* (Loew, 1858) at Greenmount Campus, Co. Antrim, on *Salix cinerea*, 23.viii.2019 and also recorded *Calycomyza artemisiae* (Kaltenbach, 1856) at Hazelbank Park, Whiteabbey, Co. Antrim; mines on *Artemisia vulgaris* were collected 15.vii.2019, with an adult emerging 27.vii.2019.

Aideen O'Doherty discovered the characteristic mines of *Aulagromyza luteoscutellata* (de Meijere, 1924) on *Symphoricarpos*, Gallows Hill, Downpatrick, 28.ix.2019. All records were submitted, with supporting images, via iRecord – **BARRY P. WARRINGTON**, 221A Boothferry Road, Hessle, East Yorkshire, HU13 9BB; agromyzidaeRS@gmail.com

Unexpected discovery of *Sarcophaga* (*Helicophagella*) inopinata (Rohdendorf) (Diptera, Sarcophagidae) from Finland

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Summary

Sarcophaga (Helicophagella) inopinata (Rohdendorf, 1937) is recorded as new to Finland and Northern Europe.

During a field trip to Koivusuo strict nature reserve in Ilomantsi, Finland, on 7 July 2020, I collected a large male flesh fly (Fig. 1A) from flowers of the hogweed *Heracleum sphondylium* ssp. *sibiricum* (Apiaceae). Males of Finnish Sarcophaginae species are usually fairly easy to identify and I was surprised when I was unable to key the specimen using the book on the Fennoscandian species (Pape 1987). However, when leafing through the figures in the book on Central European flesh flies (Povolný and Verves 1997), I noticed that the aedeagus of my specimen matched the illustration of *Sarcophaga (Helicophagella) inopinata* (Rohdendorf, 1937) given as an additional figure belonging to Appendix I of the book. The species is also included in the keys and figures in Blackith *et al.* (1998), which provided more confidence in the determination of the specimen. Eventually, Dr Thomas Pape kindly confirmed the identification from photographs of the male terminalia, which are quite characteristic compared to other species in the group (Fig. 1B).

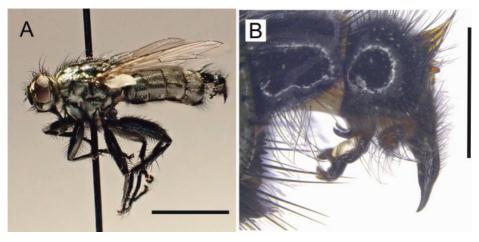


Fig. 1. The first *Sarcophaga inopinata* record from Finland: (A) habitus of the specimen, scale bar 5 mm; (B) terminalia of the same specimen. Compare with fig. 245 in Povolný and Verves (1997) and fig. 4 in Blackith *et al.* (1998). Scale bar 1mm.

Finding of this species in Eastern Finland can be considered surprising, as *S. inopinata* was not known from adjacent countries but only from Hungary, Kazakhstan (type location) and the

Russian Far East (Pape 1996). Overall, the literature on the species' distribution is scarce and for example the Hungarian record is based on *Sarcophaga hortobagyensis* (Mihályi, 1979), which has been interpreted as a junior synonym of *S. inopinata* (Verves 1993, Pape 1996). The biology of *S. inopinata* remains unknown, but some of the known species of *Sarcophaga* sg. *Helicophagella* are obligate parasitoids of snails, while others develop in faeces and small carrion (Blackith *et al.* 1998).

The Finnish specimen was collected in the yard of an old forest ranger's log house in Pirhunvaara, surrounded by a lush grass meadow with a rich flora of flowering plants such as hogweed, field scabious (*Knautia arvensis*, Caprifoliaceae) and oxeye daisy (*Leucanthemum vulgare*, Asteraceae) (Fig. 2). The location has also yielded interesting records of Tachinidae, including *Linnaemya rossica* Zimin, *Onychogonia flaviceps* (Zetterstedt), *Exorista fasciata* (Fallén) and a characteristically southern European species, *Ceromasia rubrifrons* (Macquart). With its meadow, Pirhunvaara differs markedly from its surroundings, as Koivusuo strict nature reserve is mainly known for its large, eccentric raised bogs (Seppä 2002) and old growth pine forests (Metsähallitus 2006). Koivusuo is located in the most eastern part of Finland and has a relatively continental climate with cold, snowy winters and warm summers.

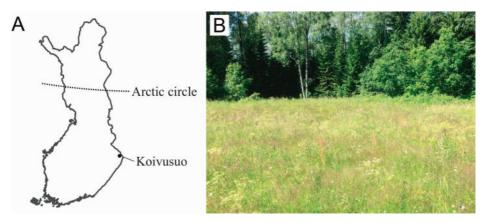


Fig. 2. Collection location of the first Finnish *Sarcophaga inopinata* specimen: (A) Koivusuo strict nature reserve (N62.9729, E31.4010) is located in Ilomantsi, North Karelia, close to the Russian border; (B) meadow in Pirhunvaara, around an old forest ranger's log house.

Although the *Sarcophaga* sensu lato fauna of Finland is dominated by a few abundant species, the finding reported here emphasises the importance of regular collecting of this group too. The Finnish *Sarcophaga inopinata* specimen will be DNA barcoded as a part of the Finnish Barcode of Life initiative (https://en.finbol.org) and submitted to the Barcode of Life Database (https://www.boldsystems.org) to facilitate its identification in the future, especially of female specimens.

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Zodion cinereum (Fabricius) (Diptera, Conopidae) new to Carlow, and a second Irish record – On 13.vi.20, a mating pair and a single individual of this species were photographed by BP on cat's-ear, *Hypochaeris radicata*, flowers at Cranemore in the John's Hill provisional Natural Heritage Area at S869560 in Co. Carlow, Ireland (52.648528 -6.7166090). The site comprises an area of upland mosaic habitat, and the specimens were seen on a forestry firebreak between two plantations, which has regenerated to a dry heath structure with bordering areas of wet heath, dry heath and dry/humid acid grassland in close proximity. Two further individuals were photographed on cat's-ear in a firebreak between a conifer plantation and a wet/dry heath mosaic at S871573 (52.660176 -6.7133115) on 24.vi.2020, and another taken as a voucher at S871567 on 30.vi.2020 (52.654786 -6.7134698). These locations all lie within 1.3km of each other. The species identifications were verified by DKC.

There is a single previous Irish record of this species on a spear thistle, *Cirsium vulgare*, flower in a country lane near the town of Monaghan in August 1958 (Fraser, J. 1958. *Zodion cinereum* (F.) in Ireland. *Entomologist's Monthly Magazine* **94**, 280) and these records appear to be only the second known occurrence in Ireland. This scarce species has previously been recorded on numerous occasions in various locations on the Isle of Man and is otherwise fairly widespread in England and Wales (Conopid Recording Scheme of Britain & Ireland, unpublished). Potential aculeate hosts listed by J.-H. Stuke (2017. *Diptera, Conopidae: World Catalogue of Insects* **15**. Koninklijke Brill, Leiden) include species of *Halictus* and *Megachile*. Large colonies of *Halictus rubicundus* (Christ) are reported at John's Hill, and other species of both *Halictus* and *Megachile* are also likely to be present – **BRIAN POWER**, Ballypierce, Kildavin, Co. Carlow, Ireland and **DAVID K. CLEMENTS**, Conopid Recording Scheme Organiser, 7 Vista Rise, Llandaff, Cardiff, CF5 2SD

New records of Scuttle Flies (Diptera, Phoridae) from Malta

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Summary

The scuttle fly (Diptera, Phoridae) fauna of the Mediterranean islands of Malta is very poorly known, with hitherto only three species reported in the literature. This article adds 13 previously unrecorded species, bringing the total number of named species to 16. Two unnamed species in the genera *Pseudacteon* and *Triphleba* are also recorded. Reference is made to old literature records, and collection data is given for each species. An abbreviated geographical distribution, and a short note on the biology, where known, is given for each species.

Introduction

The Phoridae is a large family of Diptera Cyclorrhapha with at least 240 genera and 3000 species known worldwide, and with 600 species in 34 genera in Europe (Disney 1998). In Europe, two thirds of the species belong to the giant genus *Megaselia* Rondani. Very many species remain unidentified in collections or await discovery. The biology of the family is the most diverse of any family of insects and has been reviewed by Ferrar (1987) and Disney (1994). According to Disney (1998) probably the majority of phorid larvae are predators, parasitoids or parasites.

The phorid fauna of the Maltese islands is very poorly known, with currently only three species recorded in the literature. In 1848, Zetterstedt recorded *Phora atra* (Meigen, 1804) as *Trineura aterrima* (Fabricius, 1794) and also described *Spiniphora punctipennis* (as *Trineura punctipennem*) from Malta. Bezzi and de Stefani-Perez (1897) repeated Zetterstedt's record of *P. atra* (again as *T. aterrima*). Disney (1991) recorded *S. punctipennis* as the only species of the family known from Malta in the Catalogue of Palaearctic Diptera and Gori (1999) mentioned a specimen of *P. atra* in the collection of Camillo Rondani in Florence. Disney (2002) recorded *Chonocephalus depressus* Meijere, 1912, for the first time in the Western Palaearctic, from material collected by the author.

The 13 new records listed in this article are the result of a modest attempt by the author to increase the number of species known from the islands by examining specimens collected by him between 1993 and 2003. The identification of Phoridae is very difficult and the relevant literature is scattered in numerous publications. For this reason, only species which could be identified with certainty or near certainty using the keys by Disney (1983, 1989, 1999) are included. Voucher specimens were mounted on slides as described in Disney (1983) and their collection data is given below for these voucher specimens. A short geographical distribution based mainly on Disney (1991), but updated from various sources if necessary is given for each species, together with notes on its biology where known, drawn from Ferrar (1987) and Disney (1994). As there is currently no accepted subfamily division of the family, species are listed in alphabetical order.

List of species

Chonocephalus depressus Meijere, 1912

Literature records: Disney (2002).

A tramp species transported across the world by man, but as yet unrecorded from the Australasian and Nearctic regions. Details of its known distribution and biology were given by Disney (2002).

Conicera tibialis Schmitz 1925

Malta: Rabat, suburban garden, yellow pan trap, 1 3, 2.ii.1995.

A European species, widely transported to temperate climates across the world by man. Known as "the Coffin Fly", the larvae are necrophagous, especially in buried human corpses and the species is of forensic importance. It has also been reported as a scavenger in wasp and birds' nests.

Diplonevra funebris (Meigen, 1830)

Malta: Rabat, suburban garden, yellow pan trap, 1 ♂, 22.ii.1995.

A Holarctic species, the larvae of which feed on dead invertebrates and have also been reared from wasps' nests. The species is a frequent flower visitor.

Dohrniphora cornuta (Bigot in De La Sagra, 1857)

Malta: Rabat, house, at window, 1 3, 28.xi.1994.

This polysaprophagous originally warm climate synanthropic tramp species has been carried around the world by man and is now cosmopolitan, even occurring in countries with frosty winters. This species has been recorded as breeding on dead bodies and is therefore of some forensic importance. It has also been implicated in causing myiasis in humans.

Hypocerides nearcticus Borgmeier, 1966

Malta: Rabat, house, to light, 1 3, 1.ix.1994.

A tramp species that has been transported around the world by man. Known from the Australasian, Nearctic, Neotropical, Afrotropical (Yemen) and Palaearctic regions. First recorded in Europe from Sweden (Ulefors *et al.* 2001) and subsequently from Spain (Disney and Blasco Zumeta 2004). It is the only species in the family that exhibits pyrophilous behaviour (Klocke *et al.* 2001).

Megaselia angusta (Wood, 1909)

A European species that has been reared from spider eggs. Malta: Wied Qannotta, steppic assemblages, $1 \triangleleft$, 26.ii.1995.

Megaselia diversa (Wood, 1909)

Malta: Rabat, suburban garden, yellow pan trap, $1 \leq i.1995$. A Palaearctic species widely distributed in Europe and European Russia, also known from Israel and the Canary Islands.

Megaselia nigra (Meigen, 1830)

Malta: Buskett, semi-natural woodland, $1 \overset{\circ}{\triangleleft}$, 9.vii.1993; Wied Ghajn Rihana, dry river valley bed, $1 \overset{\circ}{\triangleleft}$, 1.iv.1994; Mistra Valley, karstland, $1 \overset{\circ}{\triangleleft}$, 19.iii.1994.

A Holarctic species, the larvae of which feed on the sporophores of a range of fungi but mainly Agaricaceae.

Megaselia plurispinulosa (Zetterstedt, 1860)

Malta: Rabat, suburban garden, yellow pan trap, 1 3, i.1995.

A Palaearctic species that has been reared from the fungus *Pleurotus cornucopiae*.

Megaselia rufipes (Meigen, 1804)

Malta: Wied Ghajn Rihana, dry river valley bed, $1 \overset{?}{\lhd}$, 22.iv.1994; Rabat, suburban garden, yellow pan trap, $1 \overset{?}{\lhd}$, i.1995.

A Holarctic polysaprophagous species that has been carried around the world by man and is now subcosmopolitan. It is known to develop in human corpses and is therefore of some secondary forensic importance.

Megaselia scalaris (Loew, 1866)

Gozo: Xaghra, farmyard, on chicken meal, 1 Å, 18.xii.1994.

A cosmopolitan polysaprophagous tramp species that has been carried around the world by man and has become established in all temperate regions where frosts can be avoided (such as indoors). It is another species that is known to develop in human corpses and is therefore of some secondary forensic importance. It is known as a producer of myiasis in vertebrates including man.

Megaselia ? verralli (Wood 1910)

Gozo: Ramla, coastal dunes, 1 Å, 11.vi.1994.

A Palaearctic species widely distributed in Europe and European Russia, also known from Israel and the Canary Islands.

Metopina crassinervis Schmitz 1920 Malta: Rabat, suburban garden, yellow pan trap, 1 ♂, ii.1995. A European species.

Metopina heselhausi Schmitz 1914

Malta: Rabat, suburban garden, yellow pan trap, 1 $ardred{C}$, 1.ii.1995; Salina, saltmarsh, 1 $ardred{C}$ and 1 $argred{C}$, 1.viii.2003.

A European species, commoner in Southern Europe, that has been introduced by man to the Canary Islands, Yemen and Iran. Also known from the Afrotropical region. A frequent flower visitor (e.g. *Taraxacum officinale, Reseda lutea* and *Potentilla anserina*). Adults have been collected from buried carrion.

Phora atra (Meigen, 1804)

Literature records: Zetterstedt (1848); Bezzi and de Stefani-Perez (1897); Gori (1999).

Malta: Buskett, semi-natural woodland, 11.iv.1994.

A Holarctic species, which has been reported in association with ants' nests. The males form aerial mating swarms. Adults are frequent flower visitors.

Pseudacteon Coquillett, 1907

One unidentified \circ was collected from Malta, Fiddien, dry river valley system, on 21.ix.1994. Larvae of *Pseudacteon* are parasitoids of adult worker ants. Six species are known from Europe.

Spiniphora punctipennis (Zetterstedt, 1848)

Literature records: Zetterstedt (1848); Disney (1991).

Malta: Rabat, suburban garden, yellow pan trap, 1 ♂, i.1995.

Known from Malta and the Canary Islands. Disney (1994) mentioned it as developing in dead molluscs.

Triphleba Rondani, 1856

One unidentified \eth was collected in a yellow pan trap in Rabat, suburban garden, ii.1995.

About 55 species, with diverse biologies, are known to occur in Europe.

Conclusions

13 new species records of Phoridae are here listed from Malta, but the family remains poorly known. Two species remain identified to genus level. Of the 16 species currently known, 5 are cosmopolitan or tramp species, 4 Holarctic in distribution, 4 Palaearctic and 3 European. More material is preserved in alcohol in the author's collection which when identified, is expected to reveal many more species, as will further collecting and rearing.

Acknowledgements

I am very grateful to Dr. R.H.L. Disney (Cambridge) for identifying *C. depressus* and *H. nearcticus*; Dr. Mauro Gori (Florence) for bringing his record of *P. atra* to my attention; and to my friend and colleague Dr Martin Ebejer (Cowbridge, UK) for reading a draft of the manuscript and suggesting improvements.

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Atylotus fulvus (Meigen) (Diptera, Tabanidae) in southern Scotland

- a female of this species was found in the morning of 8 July 2019 on a stone patio outside my house in the Boreland Hills, Gatehouse of Fleet, Dumfriesshire, Scotland (NX5856) (Fig. 1). It was easily caught due to it being torpid: on being prodded with a pin it was unresponsive, moved slowly and did not fly. Using the keys and species accounts in A.E. Stubbs and M. Drake (2001. *British Soldierflies and their allies*. BENHS) its golden hair colour, yellow femora, clear wings, abdominal markings and golden-yellow antennae and halteres identified it as the golden horsefly, *A. fulvus*.



Fig. 1. Female Atylotus fulvus, Gatehouse of Fleet, Dumfriesshire, Scotland, 8.vii.2019.

Although recorded from Wales, Cumbria, Ireland and Scotland, *A. fulvus* is a species known chiefly from the heathland valley mires of southern England (Stubbs and Drake *op. cit.*). In Scotland old records exist for Aberfoyle, Perthshire (1901) and Banchory, Aberdeenshire (1909) (Verrall, G.H. 1909. *British flies V. Stratiomyidae and succeeding families of the Diptera Brachycera of Great Britain.* London: Gurney and Jackson). Slightly later records exist for Dunkeld (1917) and Rannoch (1923) in Perthshire (Stubbs and Drake *op. cit.*). In addition, a specimen exists in the collections of the National Museum of Scotland collected in 1930 by H.A. Latham from Morven, Argyll and Bute. The most recent published Scottish records appear to be from Glenmoriston, Inverness-shire during the period 2005-2009 (MacDonald, M. 2010. *Thereva handlirschi* Kröber, 1912 (Diptera, Therevidae) and other notable Diptera in N Scotland. *Dipterists Digest (Second Series*) **17**, 47-49). There are a further 12 captures shown on the NBN Atlas for the period 2011 to 2019, between Mull and Inverness; these have not been further investigated (M. Harvey *pers comm.*).

The torpid state of the specimen captured by me is curious. After a couple of hours at room temperature it had not recovered. Attempts to find additional specimens in suitable habitat in the Fleet Valley and surrounding area have not, as yet, proved successful and raises the possibility that the specimen reported here was a stray blown in from further afield and exhausted by a long period of flight. Nonetheless, a specimen from Dumfriesshire extends the range of this

species south in Scotland and with records from Wales and Cumbria, adds to the possibility of a western preference for this species. I am grateful to Ashleigh Whiffin for kindly sending me *A*. *fulvus* data held by the National Museum of Scotland and to Martin Harvey for helpful comments on a previous version of this note – **GRAHAM E. ROTHERAY**, 16 Bracken Wood, Gatehouse of Fleet, Dumfriesshire, DG7 2FA; grahamrotheray@googlemail.com

The winter phorid Triphleba trinervis (Becker, 1901) (Diptera, Phoridae) at Old Hunstanton strandline, West Norfolk (V.C. 28) – A female Triphleba trinervis (Becker, 1901) was collected from strandline deposits at Old Hunstanton, West Norfolk (V.C. 28; TF67984252) on 26.xi.2020. After preliminary inspection under alcohol, it was dissected, slide-mounted in Berlese fluid and examined at magnifications up to ×400. Identification was made using the handbook by R.H.L. Disney (1983. Scuttle Flies, Diptera, Phoridae except Megaselia. Handbooks for the Identification of British Insects Vol. 10, Part 6). Triphleba trinervis is recognised as a cold-adapted species that can be active at temperatures as low as -4 °C (Soszyńska, A. and Durska, E. 2002. Cold-adapted Scuttle-flies species of Triphleba Rondani, Diptera: Phoridae. Annales Zoologici 52, 279-283). It has been reported from beaches in Denmark, where it is a common member of the winter fly fauna of grey dunes, but not noted as occurring in the strandline (Nielsen, B.O., Nielsen, L.B. and Toft, S. 2019. Epigaeic Diptera Brachycera from the coastal sand dunes of National Park Thy, Denmark. Entomologiske Meddelelser 87, 19-40). It is widely distributed in Europe and also occurs in the Nearctic Region (Disney, R.H.L. 1991, Family Phoridae, pp. 143-204. In Soós, A. and Papp, L. (Eds). Catalogue of Palaearctic Diptera. Volume 7 (Dolichopodidae-Platypezidae). 291 pp. Akadémiai Kiadó, Budapest).

There is only a single British record of this fly in the NBN database, from SE022943 in Apedale north of Castle Bolton, North-West Yorkshire (V.C. 65). Disney (1983. *ibid.*) noted that it had been recorded from "Cheshire, Hereford., Lancs., Suffolk and N. Yorks." in January and November. S.J. Falk and P.J. Chandler (2005. A review of the scarce and threatened flies of Great Britain. Part 2: Nematocera and Aschiza not dealt with by Falk (1991). *Species Status* **2**: 1-189. Joint Nature Conservation Committee, Peterborough.) gave it Data Deficient status, and noted that all of the six available records were from inland localities and that, with the exception of the Apedale record (pitfall traps run from November 1976 to February 1977), all were pre-1960. Falk and Chandler (2005. *ibid.*) also stated that the habitat for this species is "unclear"; records were associated with moorland or broad-leaved woodland. Adults occurred in October-February. The present record is the first from the coast of Britain. Inspection of strandlines in winter may prove this large phorid to be more common in Britain than is suggested by current records. I thank Henry Disney for confirming my identification – **MARK WELCH**, 32 Tennyson Place, Ely, Cambridgeshire, United Kingdom CB6 3WE

A Wiltshire record for <i>Madiza glabra</i> Fallén (Diptera, Milichiidae) ANTHONY F. BAINBRIDGE
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