## Dipterists Digest



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Cover illustration: *Pseudolynchia canariensis* (Macquart in Webb & Berthelot, 1839) (Hippoboscidae), first British record from Isleworth, London (see article by Matthew Harrow, p. 166). An addition for the Hippoboscidae and Nycteribiidae Recording Scheme, recently launched by Denise Wawman.

# Dipterists Digest



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#### **Dipterists Digest**

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### The puparium and development site of *Rhingia rostrata* (Linnaeus) and comparison with *R. campestris* Meigen (Diptera, Syrphidae)

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#### Summary

The puparium of *Rhingia rostrata* (Linnaeus) is described and compared with that of *Rhingia campestris* Meigen (Diptera, Syrphidae). Distinguishing characters for each species are recognised. A set of shared early stage characters that define the genus are proposed. *Rhingia rostrata* was reared from a hoverfly lagoon, an artificial development site, from which key features of natural development sites are suggested.

#### Introduction

In Great Britain the genus *Rhingia* Scopoli (Diptera Syrphidae) is represented by two species, *campestris* Meigen and *rostrata* (Linnaeus) (Coe 1953, Stubbs and Falk 2002). The former is common and widespread, the latter less frequent, but since the 1990s it has spread across the southern half of Great Britain (Ball and Morris 2021). The early stages and development site of *R. rostrata* are previously unknown, but those of *R. campestris* have been described by Coe (1942) and Hartley (1961, 1963). The *R. campestris* larva develops in dung and based on its mouthparts, it is a saprophage (Hartley 1963).

In this paper we describe the puparium of *R. rostrata*, which was reared by the first author from a so-called 'hoverfly lagoon'. Hoverfly lagoons are artificial development sites designed to attract naturally occurring saprophagous Syrphidae (*hoverflylagoons.co.uk*). To find characters that, relative to other Syrphidae, enable the third stage larva and puparium of each species to be recognised and distinguished, we compare the puparium of *R. rostrata* with that of *R. campestris*. To help define the genus we propose a set of shared early-stage characters and based on the lagoon, we discuss possible key features of natural development sites.

#### Methods

On 4.iv.2020, a hoverfly lagoon was placed in shady conditions in a garden near Lewes, Brighton, Sussex. The lagoon was made from a plastic milk bottle container with the top cut off and four overflow holes pierced 3cm from the cut rim. The container was filled with cut grass, water, three sticks slightly longer than the lagoon which provide a substrate for larvae to climb out on when ready to pupate, and a layer of dry leaf-litter at the water surface. The container was placed in a plant pot saucer with several drainage holes pierced in the bottom, and filled with dry leaf litter within which larvae pupate (*hoverflylagoons.co.uk/rhingia-rostrata*).

On 23.vi.2020, three puparia were found among dry leaves in the pupation tray. Male *Rhingia* emerged on 27 and 29.vi.2020 and a female on 1.vii.2020. They were readily identified as *R. rostrata* which is known from Sussex (Ball and Morris 2021), by their orange abdomens lacking black side stripes, hind tibiae without black rings and relative to *R. campestris*, by their smaller size and shorter facial snouts. These puparia are described and compared with those of *R. campestris* from the J.C. Hartley collection of Syrphidae (NMSZ.1991.128) at the National Museum of Scotland. The external surface of the puparia of both species was obscured by dried-on detritus. Although this material complicated assessment, no attempts were made to remove it due to the probability of damaging or dislodging body wall features, such as vestiture and lappets

(projections on the anal segment, Hartley 1961). Head skeletons were examined by clearing a puparium of each species in a solution of potassium hydroxide for about 20 minutes and extracting them with pins. To prevent further clearing they were placed in acetic acid for 15 minutes and stored in 70% alcohol. Morphological assessments were made using binocular microscopy. Dimensions were obtained with a measuring eyepiece. Material of *R. rostrata* is deposited in the National Museum of Scotland, Edinburgh.



Fig. 1. *Rhingia rostrata*, puparium, anterior end to the right, length 6mm; a, ventro-lateral view; b, dorsal view.

#### Results

#### R. rostrata puparium (Fig. 1)

**Length**: mean 6.1mm, range 6.0-6.5, n = 3; width: mean 3.1mm, range 3.0-3.5, n = 3; body shape: truncate at anterior and posterior ends with the apex of the anal segment compressed into an inclined plate from which lower margin the posterior respiratory process protrudes to a distance of about 0.8mm; individual segments recognisable from rings of body wall impressions, transverse ridges and patterns of vestiture; vestiture: all thoracic and abdominal segments coated in dark brown, hair-like pubescence that tapers from the base and becomes longer towards the anal segment, up to about 0.1mm long; vestiture increasingly curved backwards towards the anal segment, less so on the ventrum; except for the prothorax, which has a more uniform covering, vestiture on dorsum of each segment with two transverse rows of long pubescence with shorter pubescence in between; dorsal and lateral segmental sensilla borne on stout, cylindrical, dark brown to black papillae that become longer towards the anal segment, up to a length of about

0.4mm; papillae on the 7th segment and the lappets on the anal segment, which have the same form, extending well above the vestiture and each tipped with a crown of radiating setae that are up to about a third as long as the supporting papilla, but setae often broken or tangled with adhering detritus (Figs 1 & 5).



Fig. 2. *Rhingia*, head skeletons extracted from puparia, anterior end to the right, length 1.2mm; a, *R. campestris*; b, *R. rostrata*; dc = dorsal cornu of basal sclerite; dl = remnant of the dorsal lip; is = intermediate sclerite; m = mandible; ml = mandibular lobes; vc = ventral cornu, longitudinal lines are the cibarial ridges; vp = vertical plate, connecting the two sides is the dorsal bridge visible at its apex; NB. the two halves of each head skeleton are out of symmetry with each other because during pupariation one side collapses on to the other.

**Head skeleton** (Fig. 2b): length about 1.2mm; of the saprophagous type, with expanded mandibular lobes forming an oval-shaped filter anteriorly and a ventral cornu bearing cibarial ridges (Hartley 1963); dorsal and ventral bridges present; intermediate sclerite, vertical plate and base of dorsal cornu heavily sclerotised; ventral cornu about 2x as long as dorsal cornu; **locomotor organs**: not developed; **anterior spiracles**: length 0.2mm; inconspicuous; sclerotised

base pale brown and cylindrical; apex an inclined plate with two pairs of openings either side of the ecdysial scar; **posterior spiracles**: elevated on a pale brown base with a mid-point constriction (Fig. 3a); shiny and coated in transverse micro-ridges; spiracular plate slightly sloping towards the mid-line and with large, central ecdysial scars, round the margin of which are sinuous and variably-shaped openings and four groups of short, interspiracular setae, these often missing or broken; **pupal spiracles**: about 0.8mm long; curved slightly backwards; dark brown; upper two thirds with 5-6 raised rings of openings on the lateral and posterior margins; openings surrounded by fine, inconspicuous setae; base and anterior face shiny and coriaceous (Fig. 4a).



Fig. 3. *Rhingia*, posterior respiratory process, dorsal view, length about 0.8mm; a, *R. rostrata*; b, *R. campestris*.



Fig. 4. *Rhingia rostrata*, pupal spiracles, anterior view, length about 0.8mm; a, *R. rostrata*; b, *R. campestris*.

#### Diagnosis of Rhingia based on puparia of R. rostrata and R. campestris

Puparium truncate anteriorly and anal segment forming an inclined plate from which the posterior respiratory process protrudes (Fig. 1); individual segments recognisable from rings of body wall impressions, raised transverse ridges and patterns of vestiture: vestiture: thoracic and abdominal segments coated in conspicuous hair-like pubescence becoming longer towards the anal segment; from the mesothorax to the 7th abdominal segment, dorsum of each segment with two transverse rows of long vestiture with shorter vestiture in between; dorsal and lateral thoracic and abdominal sensilla borne on cylindrical papillae that become longer towards the anal segment, up to 0.6mm long; papillae most conspicuous on the 7th abdominal segment and the 8th or anal segment, standing well above the vestiture and each tipped with a crown of radiating setae (Figs 1 & 5); head skeleton: length about 1.2mm; of the saprophagous type with expanded mandibular lobes forming an oval-shaped filter anteriorly and a ventral cornu with cibarial ridges and 2x as long as the dorsal cornu; dorsal bridge present; intermediate sclerite and vertical plate heavily sclerotised (Fig. 2); locomotor organs: not developed; anterior spiracles: inconspicuous, elevated on a pale brown sclerotised base and with an inclined apex bearing 2-4 openings straddling the rim; posterior spiracles: borne on a shiny, basal projection up to 0.8mm long and with surface sculpturing and a mid-point constriction; colour variable (Fig. 3); sinuous and variably shaped openings on an apical spiracular plate with four groups of short, interspiracular setae on its rim; **pupal spiracles**: up to 0.8mm long; slightly curved backwards; upper two thirds with 5-6 rings of openings on the lateral and posterior margins; colour variable; shiny, coriaceous with fine setae between the openings (Fig. 4).



Fig. 5. *Rhingia campestris*, lappet on the anal segment, length about 0.6mm; cr = crown of radiating setae; det = detritus; lap = lappet; prp = posterior respiratory process; seg 7 = abdominal segment 7; seg 8 = abdominal segment 8, the anal segment.

#### **Recognition and identification**

The early stages of *Rhingia* are similar to those of *Eumerus* Meigen, *Cheilosia* Meigen, *Ferdinandea* Rondani, *Merodon* Meigen and *Portevinia* Goffe (Rotheray 1993). Early stages of *Rhingia* and *Ferdinandea* differ from the others in that their mandibles do not project from the

mouth opening. They are reduced, inconspicuous and support a lightly sclerotised, oval-shaped filter at the front of the head skeleton (Fig. 2). This feature is a development of the mandibular lobes that attach to the lateral margins of the mandibles in the other genera and is characteristic of almost all other Eristalinae (Syrphidae) (Hartley 1963, Rotheray and Gilbert 1999).

*Rhingia* early stages can be distinguished from those of *Ferdinandea* by the stout, cylindrical papillae that support segmental sensilla, especially elongate and conspicuous on the 7th abdominal and anal segments (Figs 1 & 5). In *Ferdinandea* these sensilla are supported by short, inconspicuous, fleshy papillae (Rotheray 1993). The puparia of both *Rhingia* species share many characteristics, but are readily separated. The most conspicuous difference is the colour of the posterior respiratory process, pale brown in *R. rostrata* and dark brown in *R. campestris* (Fig. 3). The colour of the pupal spiracles also differs between the species, dark brown in *R. rostrata* and pale brown in *R. campestris* (Fig. 4). The vestiture is dark brown and short, up to about 0.1mm, in *R. rostrata* and in *R. campestris*, except for a darkened base, it is pale brown and half as long again, up to 0.16mm. The papillae supporting sensilla on abdominal segments 7 and 8 are shorter (up to 0.4mm) with longer setae at the crown (a third or more as long as papillae) in *R. rostrata* than in *R. campestris* (papillae up to 0.6mm long and setae less than a third as long as papillae (Fig. 5). Minor differences apparently exist in the extent of sclerotisation of the vertical plate of the head skeleton (Fig. 2).

Biologically *Rhingia* and *Ferdinandea* differ from most *Eumerus*, *Cheilosia*, *Merodon* and *Portevinia* in developing as saprophages in decaying vegetable matter rather than as phytophages or mixed phytophages/saprophages in live plants and fungi. *Ferdinandea* differs from *Rhingia* in developing in exuding tree sap (Rotheray 1993).

#### Discussion

The descriptions and comparisons we make here are based on puparia and with the exception of the pupal spiracles which appear after pupariation, the morphological characters referred to apply to the third stage larva and probably to the second stage. Certain larval structures are, however, collapsed and indecipherable in puparia, such as the pseudocephalon and the front of the prothorax (Rotheray 2019). It is possible that distinguishing characters are present in these structures which include the antennomaxillary organs and the dorsal and lateral lips. For instance, although differences are apparent between the dorsal lips in the extracted head skeletons of the two species, dl in Fig. 2, they are probably an artefact of the extraction process. Examination of dorsal lips in larvae would confirm this.

In *Rhingia* and *Ferdinandea*, mandibles that support a filter at the front of the head skeleton rather than being involved directly in food gathering are probably a development associated with a switch to a strictly saprophagous way of life (Rotheray and Gilbert 1999). A functional advantage may be more rapid processing of food through the head skeleton.

Gravid *R. campestris* oviposit on vegetation overhanging dung and first stage larvae drop into it (Coe 1942). If *R. rostrata* shares the same oviposition strategy, this was possible since vegetation overhung the hoverfly lagoon. The hoverfly lagoon in which larvae of *R. rostrata* developed consisted of a compacted mass of wet, decaying grass cuttings over which a pasty layer had formed. Populations of microbes will have been high in these materials, as indicated by the occurrence of numerous larvae including the much larger microbe-feeding species, *Myathropa florea* (Linnaeus) (Diptera, Syrphidae) (images at *hoverflylagoons.co.uk/rhingia-rostrata*). From the structure of the mouthparts, the *R. rostrata* larva is, like that of *R. campestris*, a saprophage and filter-feeds on microbes.

Dense amounts of decaying vegetation may be a key requirement of the larva of *R*. *rostrata*. Another feature of the lagoon was the relative freshness of the source material and this may be an additional requirement. It may correlate to the occurrence of a specific set of microbes

associated exclusively with the early stages of decay in green plant material. Natural sites where decaying green plant material accumulates in high density patches possibly include the margins of water bodies, such as, ponds, marshes, seepages, etc.

Neither *Rhingia* species possesses protective sclerotised plates or spines at the anterior end that are often present in tunneling cyclorrhaphan larvae, i.e. larvae that make holes by fragmenting and removing hard, compacted material (Rotheray 1990, Rotheray and Gilbert 1999). Hence their absence in *Rhingia* larvae suggests they are incapable of movement through hard material and they are confined to media soft enough for burrowing, i.e. squeezing through material by pushing it aside with the front of the body (Rotheray 2020). They do, however, possess an inclined plate on the anal segment which is a frequent feature of burrowing and tunneling larvae. The plate helps reduce the risk of the posterior spiracles becoming blocked or inundated. This is achieved by the rim deflecting material away during locomotion (Rotheray 2019).

A feature of both *R. campestris* and *R. rostrata* puparia is dried-on detritus and the complete and uniform manner in which this material coats puparia is striking. Such uniformity suggests less a random accumulation than deliberate behaviour. It is possible that prior to pupariation larvae smear themselves in either saliva or fluids emitted from the anus and these fluids combined with the vestiture and body movements enable the larva to coat itself in detritus that, post-pupariation, dries on. Such behaviours are known in other eristaline larvae (Rotheray and Gilbert 2011). Inside a rigid puparium, pupae are unable to defend themselves by movement, for example from a natural enemy or a drying habitat. Hence, the significance of coating the puparium is possibly protection from desiccation and/or concealment from natural enemies that hunt using visual, tactile or contact chemicals.

#### Acknowledgements

We are grateful to Ashleigh Whiffin for arranging a loan of *R. campestris* early stages from the National Museums of Scotland, Edinburgh. We are also grateful to David, Mia and Henry Mateer for assistance with hoverfly lagoons. Finally, we would like to express our gratitude to our reviewers, Martin Speight and Roger Morris, who suggested useful revisions.

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#### **BOOK REVIEW**

#### Diptera an introduction to flies. By Nikita E. Vikhrev. Published by Phyton XXI Publisher, Moscow, 160 pp. (full colour). ISBN 978–5– 906811–85–1. Available from NHBS at: https://www.nhbs.com/ diptera-an-introduction-to-flies-book. Price: £14.99.

I read this little book from cover to cover and really enjoyed it. The author provides interesting information about flies, their biology and natural history and combines this with some anecdotal information and examples from his own experiences (mostly in Russia).

Originally published in Russian, this book is well arranged and written without too much technical jargon for the beginner, but scientific aspects are well explained and easy to follow. The introductory section explaining the higher classification is especially well done and explained and I enjoyed the addition of footnotes provided by Tony Irwin, which clarify some technical aspects of the text. Having been through the whole text I did not find any glaring technical errors.

The book is divided into two main sections the "Nematocera", which although not a monophyletic grouping is still a useful main division for the purposes of the book and the Brachycera, subdivided into the Orthorrhapha and the Cyclorrhapha. There is an account of each family that begins with an approximate number of known species globally and then gives an account of the family, usually with some examples of European species. Each family account does not include the same information, but is rather a narrative, which outlines some of the more interesting aspects of each family. This enables the author to introduce new general information and concepts about flies as the book progresses and helps keep your interest. Due to limitations on size not all the families of flies are covered in the book, but all the significant families that occur in Europe are and are done very well.

The book is hardbacked, is published on good quality paper and is copiously illustrated with colour photographic images of living flies from various sources. There is some inconsistency in the quality of the images used (as would be expected), but overall, the images are nice and sharp, with good contrast and colour definition. The book includes an index of family, generic and species names, which appears to be quite comprehensive.

The last sentence of the book reads "This book is intended for student zoologists, macro photographers, and for a wide range of nature lovers." In this respect it meets its objective easily and I would go further and say the book is an excellent introduction for anyone either newly interested in the study of flies, or who have an interest in insects in general.

#### ASHLEY H. KIRK-SPRIGGS

#### *Thoracochaeta johnsoni* (Spuler) and *Thoracochaeta valentinei* Roháček & Marshall (Diptera, Sphaeroceridae) in Norfolk

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#### Summary

The occurrence of two little known species of *Thoracochaeta* Duda, *T. johnsoni* (Spuler, 1925) and *T. valentinei* Roháček and Marshall, 2000, in the strandline deposits of Old Hunstanton, West Norfolk V.C. 28 is reported. *T. johnsoni* was by far the commonest sphaerocerid collected during October–December 2020. This species constituted 81% of the 1346 sphaerocerid specimens collected during this period, and 86% of all *Thoracochaeta*. *T. johnsoni* is a non-native species, and it is conceivable that it is experiencing a form of "ecological release". *T. valentinei* ( $6^3_{\uparrow}$ ,  $3^{\circ}_{\downarrow}$ ) was found on four occasions during the same time interval. Photomicrographs illustrate the features used to identify the four *Thoracochaeta* species occurring at Old Hunstanton.

#### Introduction

Seven British species of *Thoracochaeta* Duda are listed in the latest update (January 2021) of Chandler (1998): *T. brachystoma* (Stenhammar), *T. erectiseta* Carles-Tolrá, *T. johnsoni* (Spuler, 1925), *T. lanx* Roháček and Marshall, *T. seticosta* (Spuler), *T. valentinei* Roháček and Marshall, 2000, and *T. zosterae* (Haliday). In their review of Palaearctic members of the genus *Thoracochaeta*, Roháček and Marshall (2000) stated that the native range of *Thoracochaeta johnsoni* is the Pacific coastlines of North and South America. It has also been reported as being abundant at oyster-processing factories in Japan (Hayashi, 1986) and has recently been recorded from China (Su 2011). *T. johnsoni* was assigned non-native status by Roy *et al.* (2012) in their general review of non-native British species.

The first British record of *T. johnsoni*  $(1 \circ, 1 \circ)$  is from Titchwell on the north Norfolk coast on 30.xi.1988 (unknown collector, det. J. Roháček). Other coastal records are those of Ivan Perry:  $1 \circ$  at Holme Dunes NNR, West Norfolk (V.C. 28) on 15.vi.1991;  $1 \circ$  and  $2 \circ$ , respectively, at Porth Joke, West Cornwall (V.C. 1) on 4.viii.2016 and 8.viii.2016;  $1 \circ$  at Gwithian Sands, West Cornwall (V.C. 1) on 6.viii.2016. There are two inland records, both from West Norfolk (V.C. 28):  $1 \circ$  from Roydon Common NNR on 20.iii.2019 (leg. DB, det. DB) and  $1 \circ$  from the adjacent Tony Hallat Memorial Reserve on 21-23.vi.2020 (leg. A. Murray, det. DB). These two inland localities are 9 km from the coast and 21 km from Old Hunstanton beach, which is the study area of the present paper.

*Thoracochaeta valentinei* was described as a new species by Roháček and Marshall (2000) based on specimens from England (Somerset 1990, 25.xi.1990, 83, 89, including holotype; Essex 1992, 8.iv.1992, 33, 19) and Scotland (Barra, 5.viii.1976, 19). They also mention a record of a female from Knock, Belgium on 11.xi.1949. Ivan Perry recorded 13 at Rosemarkie, East Ross & Cromarty (V.C. 106) on 15.vii.1991. DB discovered a further four British records in the collection of the Natural History Museum, London (NHM), all from England: three records from the Isles of Scilly, West Cornwall (V.C. 1) on 26.v.2013 totalling 53 and 149 (leg. D. Whitmore, det. DB); a record of 39 from Bantham, South Devon (V.C. 3) on 29.v.54 (Spooner collection 1996-53, NHM, det. DB). We are not aware of any more records. In this paper, we report the occurrence of these two *Thoracochaeta* species from the strandline deposits at Old Hunstanton, West Norfolk V.C. 28 and consider the possible significance of *T. johnsoni* as the predominant sphaerocerid recorded there during October-December 2020.



Fig. 1. Strandline deposits at Old Hunstanton beach: (a) view looking south of the thicker, most landward deposit; (b) view looking north of a section of the intermittent, patchy, thin strandline lying 15 m seaward of the thicker deposits; (c) a close-up of the heterogeneous material typical of the strandline deposits at Old Hunstanton. Photos: MW.

#### Fieldwork, sampling and examination methods

The strandline deposits at Old Hunstanton beach (Fig. 1) lack a significant wrack component and comprise a heterogeneous aggregate of bryozoan fronds and stems, coral weed, small fragments of bladderwrack, mollusc and bivalve shells, and marram grass (Fig. 1c). It is patchy and discontinuous, <2 m wide and <0.3 m thick. Despite the small, patchy and thin character of some of the deposits (Fig. 1b), they contained plentiful *T. johnsoni*. The surfaces of the patchy deposits dry quickly, although their bases were usually damp or wet. Thicker deposits accumulated against the low sandbanks above high-water mark (Fig. 1a) and are similar in composition and structure to the small, patchy deposits. Beneath the drier surface, the thicker deposits were always very damp or wet.



Fig. 2. (a) Habitus of a male *T. johnsoni* from Old Hunstanton, photo: DB; (b) face of a female *T. valentinei* from Old Hunstanton showing the prominent dull-red facial knob between antennal bases, photo: MW.

During the exceptionally warm fortnight in February 2019, MW visited the strandline at Old Hunstanton beach (TF681426) on 27.ii.2019. In addition to the considerable numbers of *Tephrochlamys tarsalis* (Zetterstedt) (Heleomyzidae), *Helcomyza ustulata* Curtis

(Helcomyzidae), *Scathophaga litorea* (Fallén), *S. calida* Haliday (Scathophagidae) and *Heterocheila buccata* (Fallén) (Heterocheilidae) found, opportunistic sampling by sweeping yielded 21 sphaerocerid specimens, of which 20 were *T. johnsoni* ( $103^{\circ}$ ,  $109^{\circ}$ ) and one  $3^{\circ}$  *T. zosterae* (Haliday). As part of our studies of strandline Diptera, we made six visits to Old Hunstanton between 19.x.2020 and 23.xii.2020 to record sphaerocerids and to see if *T. johnsoni* is a common species there.



Fig. 3. (a) Part of the thoracic dorsum of *T. brachystoma* showing the strong prescutellar dc and median-ac setae and intervening microsetae (arrowed); (b) a similar view of the thoracic dorsum of *T. valentinei* (cleared in 10% KOH) with the microsetae missing. The row of prescutellar setae of *T. brachystoma* is convex towards the scutellum, whereas the prescutellar row of *T. valentinei* is slightly concave towards the scutellum. Photos: MW.

MW made five visits to the strandline between 19.x.2020 and 20.xii.2020. The section of strandline sampled overall during these five visits extended from TF67844238 to TF68144263 and corresponds to ~380 m. Two handfuls of strandline debris at a time were placed onto a 1m-square nylon beating tray, flies pooted individually and each gently blown into a bottle of 70% ethanol. Each inspection lasted about 20 minutes. About ten such debris collections (two handfuls each) were made on each visit. Catches were later poured into a Petri dish and flies extracted and initially sorted into genera or species for further microscopic examination and, in some cases, dissection and slide-mounting using Berlese fluid. Specimens were identified using the key to British Sphaeroceridae of Pitkin (1988) and the key to Palaearctic *Thoracochaeta* by Roháček and Marshall (2000). Photographs of slide-mounted material were taken using a GXSMART compound microscope (GT Vision) at magnifications of ×100 and ×400 and a 5.1Mp GXCAM camera (GT Vision). Photographs of pinned specimens were taken using a GX



Fig. 4. Photomicrographs of the mid-tibiae,  $t_2$ , of the four *Thoracochaeta* species encountered at Old Hunstanton beach: (a) *T. valentinei*, (b) *T. johnsoni*, (c) *T. brachystoma*, (d) *T. zosterae*. Anterodorsal setae of *T. brachystoma* and *T. valentinei* are indicated by blue arrows; the two pairs of basal *ad/pd* setae of *T. johnsoni* are indicated by red arrows; the mid-ventral seta of *T. johnsoni* is indicated by an orange arrow. With the exception of the photomicrograph of *T. valentinei* which is a posterior view, photomicrographs are from an anterior viewpoint. Photos: MW.

DB visited the strandline at TF68144262 on 23.xii.2020 for an hour or so until the weather worsened. Deposits were sieved into a bowl and flies pooted and retained dry. Specimens were determined using a GXM stereoscopic microscope (GT Vision) at ×40 magnification. The habitus image of *T. johnsoni* (Fig. 2a) was taken with a GXCAM Hi-Chrome- SMII (GT vision) using Helicon 7 stacking software.

#### Identification

Diagnostic features of the four *Thoracochaeta* species encountered at Old Hunstanton are shown in Figs 2–8. Roháček and Marshall (2000) gave the following size ranges (body length): *T. brachystoma* 1.0 - 1.8mm; *T. valentinei* 1.3 - 2.0mm; *T. johnsoni* 1.3 - 2.2mm; *T. zosterae* 1.6 - 2.6mm. In the specimens taken at Old Hunstanton, *T. brachystoma* and *T. valentinei* were noticeably smaller than *T. johnsoni* and *T. zosterae*, with bodies less than 2mm long. Another noticeable gross feature of the specimens collected was that *T. johnsoni* and *T. zosterae* had proportionately much longer wings than *T. brachystoma* and *T. valentinei*. Fig. 2 shows the habitus of a male *T. johnsoni* and the face of a female *T. valentinei*, both from Old Hunstanton. The large dull-red facial knob of female *T. valentinei* is a useful identification feature, although for the seven male specimens from Old Hunstanton it is narrower and the red colour is not as clear as it is in the two females. Of the four *Thoracochaeta* species found at Old Hunstanton, only *T. valentinei* lacks the microseta between the prescutellar dorsocentral and acrostichal setae (Fig. 3). Specimens of *T. brachystoma* from Old Hunstanton often lacked one of the prescutellar acrostichal microsetae between the strong *dc* and median *ac* prescutellar setae, but they never lacked both prescutellar microsetae.



Fig. 5. Photomicrographs of male sternite 5 of all four *Thoracochaeta* species found at Old Hunstanton: (a) *T. johnsoni*, (b) *T. zosterae*, (c) *T. brachystoma*, (d) *T. valentinei*. Magnification used ×400. Photos: MW.



Fig. 6. Photomicrographs of female terminalia of the four *Thoracochaeta* species found at Old Hunstanton. All views are dorsal: (a) *T. zosterae*, (b) *T. johnsoni*, (c) *T. valentinei*, (d) *T. brachystoma*. Magnification used ×400. Photos: MW.

The chaetotaxy of the mid-tibiae, t<sub>2</sub>, of the four *Thoracochaeta* species encountered at Old Hunstanton, is shown in Fig. 4 and allows separation of *T. johnsoni* and *T. brachystomal T. valentinei* from all other *Thoracochaeta* species (Roháček and Marshall 2000). *T. brachystoma* and *T. valentinei* both have a basal and a distal pair of *ad* and *pd* setae and a single median *ad* seta. *T. johnsoni* has four pairs of *ad/pd* setae, with the basal pair usually much weaker than the others. Uniquely among the four *Thoracochaeta* species, t<sub>2</sub> of *T. johnsoni* has a mid-ventral seta,

which is a very useful feature for distinguishing this species from the other three. Male sternite 5 and female terminalia were also checked for confirmation in less clear-cut cases where the basal pair of t<sub>2</sub> setae of *T. johnsoni* was weakly developed. Photomicrographs of male sternite 5 and female terminalia of all four *Thoracochaeta* species recorded at Old Hunstanton are shown in Figs 5 and 6 respectively. Surstyli of *T. johnsoni* and *T. valentinei* are shown in Fig. 7. Spermathecae of *T. johnsoni* and *T. valentinei* are shown in Fig. 8.



Fig. 7. Surstyli of *T. johnsoni* (a, b) and *T. valentinei* (c, d) specimens from Old Hunstanton. In 7c the cleft in the sub-anal plate is indicated by a red arrow. Magnification used ×400. Photos: MW.

Male *T. zosterae* were distinguished from all remaining Palaearctic *Thoracochaeta* species (Roháček and Marshall 2000) by examining sternite 5 and surstyli at ×80 magnification, using a stereomicroscope and pins for manipulation, with the specimen under alcohol in a watch-glass. With uncertain views, sternite 5 was slide-mounted and examined using a compound microscope. Female *T. zosterae* were identified by following the key of Roháček and Marshall (2000). In this way, non-British species sharing the t<sub>2</sub> chaetotaxy of *T. zosterae* were not overlooked.

Separating *T. brachystoma* and *T. valentinei*, both of which have an unpaired *ad* mid-seta (Fig. 4), required inspection of prescutellar setae (Fig. 3), male sternite 5 (Fig. 5), female terminalia (Fig. 6) and male surstyli (Fig. 7). The sub-anal plate of male *T. valentinei* also has a characteristic deep cleft (Fig. 7c), with a distinct bristle extending posteriorly from each lobe.

#### Results

Table 1 summarises the sphaerocerids collected from the six visits to Old Hunstanton beach from 19.x.2020 – 23.xii.2020. A total of fifteen sphaerocerid species from 1346 specimens was recorded: *Thoracochaeta brachystoma, T. zosterae, T. johnsoni, T. valentinei, Limosina silvatica* (Meigen), *Rachispoda fuscipennis* (Haliday), *Leptocera nigra* Olivier, *Copromyza equina* Fallén, *Coproica vagans* (Haliday), *C. hirtula* (Rondani), *C. hirticula* Collin, *Pullimosina heteroneura* (Haliday), *P. pullula* (Zetterstedt), *Spelobia clunipes* (Meigen), *Ischiolepta pusilla* (Fallén). *Thoracochaeta johnsoni* was by far the commonest sphaerocerid collected on each occasion. Overall, it constituted 81% of all sphaerocerids and 86% of *Thoracochaeta* collected during the six visits. The discovery of *T. valentinei* at Old Hunstanton is described later in this paper.

A 1-hour visit to Holme beach (TF69464425), 3 km north of Old Hunstanton, on 12.xi.2020 yielded four *T. johnsoni* specimens  $(2 \heartsuit, 2 \heartsuit)$ , and a 20-minute opportunistic sampling of the more wrack-rich strandline at Titchwell RSPB reserve (TF75054498), a further 4 km east of Holme, on 6.xii.2020 yielded a further five *T. johnsoni* ( $2 \heartsuit, 3 \heartsuit$ ). Thus, the species has likely been present at Titchwell since the first confirmed record of it there in 30.xi.1988 (Roháček and Marshall 2000). Its presence at Old Hunstanton, Holme and Titchwell suggests that the species is well-established on the W Norfolk coast.

With the exception of 30 *Coproica vagans* (183, 129) recorded on 12.xi.2020, non-*Thoracochaeta* species were recorded in low numbers (<5 specimens per species per visit). A total of only 80 specimens of non-*Thoracochaeta* species (6%) was recorded from the six visits.



Fig. 8. Spermathecae of *T. johnsoni* (a, b) and *T. valentinei* (c) from Old Hunstanton. The shape of the spermathecae of *T. valentinei* is distinctive among Palaearctic *Thoracochaeta*. Close inspection of the spermathecae of *T. johnsoni* reveals many small pale spots on the surface that appear to be associated with small dimples, as seen in Figure 8b. Magnification used  $\times 400$ . Photos: MW.

#### Thoracochaeta johnsoni

Other than the Old Hunstanton records reported here, there are three records of *T. johnsoni* in Britain, all from West Norfolk: in 1988 (Roháček and Marshall 2000), in 2019 and 2020 (both by DB). There are no records of it in the NBN database (accessed 20.xii.2020). In their review of non-native species in Britain, Roy *et al.* (2012) listed *T. johnsoni* as a non-native "terrestrial marine" species. They also listed *T. seticosta* Spuler as another non-native coastal species.

The two common coastal sphaerocerids in the British Isles are *T. brachystoma* and *T. zosterae*, both associated with seaweed-rich wrack beds (Egglishaw 1958; Roháček and Marshall 2000). However, the West Norfolk coast, with its expansive beaches that extend up to a mile out to sea at low tide, lacks wrack beds. Consequently, the occurrence of *T. johnsoni* in good numbers and being by far the commonest sphaerocerid collected at Old Hunstanton prompted us to start to

explore the phenology of this non-native species, with the aim of understanding how it exploits such a thin, discontinuous strandline, which would seem to contrast with the requirements of *T. brachystoma* and *T. zosterae*.

#### Thoracochaeta valentinei

While sorting through *Thoracochaeta* specimens collected on 19.x.2020, which were predominantly *T. johnsoni* (Table 1), MW noticed a female specimen that resembled *T. brachystoma*, but had clearly different terminalia (Fig. 6) and lacked the microseta between the strong dorsocentral and median acrostichal prescutellar setae (Fig. 3). The terminalia and spermathecae were slide-mounted (Figs 6 and 8) and found to match closely those of *T. valentinei* illustrated by Roháček and Marshall (2000, figs 28-30). Photographs of the terminalia were sent to DB who agreed with the identification. Visits to the thicker strandline at TF67844238 on 4.xi.2020 and 12.xi.2020 provided a further five males and two females. Another male was obtained on 20.xii.2020 from the thin, patchy strandline deposits at TF67834239 (Fig. 1b).

British records of *T. valentinei* are: Berrow Sands, Somerset (1990, leg. J. Valentine) and Essex (1992, leg. J. Valentine); Barra, Scotland (1979, leg. A.R. Waterston); three records from the Isles of Scilly, Cornwall V.C.1 (2013, leg. D. Whitmore, det. DB, NHM collection); a record from Bantham, South Devon V.C.2 (1954, Spooner collection NHM, Det. DB). Further details relating to the Somerset, Essex and Barra records can be found in Roháček and Marshall (2000).

species	19.x.2020		4.xi.2020		12.xi.2020		26.xi.2020		20.xii.2020		23.xii.2020	
	3	Ŷ	3	Ŷ	3	Ŷ	8	Ŷ	8	Ŷ	8	Ŷ
Thoracochaeta brachystoma			48	42	10	4	2	1		2	1	
Thoracochaeta johnsoni	26	20	101	71	37	36	206	141	199	149	47	51
Thoracochaeta valentinei		1	2	2	3				1			
Thoracochaeta zosterae			2	6	4		4	7	21	18		1
Coproica vagans	3	4		1	18	12						
Coproica hirtula				2								
Coproica hirticula			1	2								
Copromyza equina									1			2
Pullimosina heteroneura	1								1	1		3
Pullimosina pullula				1								
Rachispoda fuscipennis	4	3	2		1	1						
Limosina silvatica								1			3	4
Leptocera nigra												1
Spelobia clunipes Ischiolepta pusilla/vaporariorum*					1	2						4

**TABLE 1.** Numbers of species recorded at Old Hunstanton between 19.x.2020 and 23.xii.2020.

\* Pitkin (1988) stated that females of these two species cannot be reliably distinguished from each other. Both specimens recorded here are females.

#### Ecology

Despite the seemingly meagre quality of the strandline deposits at Old Hunstanton and the absence of wrack beds, it appears that *T. johnsoni* thrives compared with the usually common *T. zosterae* and *T. brachystoma*, both of which are relatively scarce at Old Hunstanton. The results of fieldwork carried out in October–December 2020 show that *T. johnsoni* constituted 81% of sphaerocerids recorded, followed by *T. brachystoma* (8%) and *T. zosterae* (5%).

Why is *T. johnsoni* much more prevalent than *T. brachystoma* and *T. zosterae* at Old Hunstanton? Its status as a non-native species may suggest that it is experiencing a degree of "ecological release", whereby its guild of native predators is absent or has no effective counterpart at Old Hunstanton. At present, we can only pose this question. Possible predators and parasites of Diptera larvae occur in the deposits at Old Hunstanton, including several species of staphylinid beetles and parasitic wasps. An answer should eventually emerge from quantifying the invertebrate community of the strandline and investigating the phenology of its Diptera.

Egglishaw (1958) found *T. brachystoma* to be abundant on the Yorkshire coast at Whitburn, but he found no conclusive evidence of the species breeding there, i.e. no immature stages. Thus, presence in large numbers does not necessarily imply breeding, as a species may only be using a strandline opportunistically as a food resource when in transit. We have reared numerous adult *T. johnsoni* from puparia collected at Old Hunstanton during November and December 2020. The puparium of T. *johnsoni* closely resembles that of *T. brachystoma* (Okely 1974) both in terms of its small size (<4 mm) and the pattern of locomotory spicules and tubercles on the ventral surface. The head skeleton of the 3<sup>rd</sup> instar of *T. johnsoni* (our observations from dissected puparia) more closely resembles that of *T. brachystoma* than that of *T. zosterae* (Okely 1974). Our rearing records from puparia collected at Old Hunstanton and the recording of many teneral specimens of *T. johnsoni* are conclusive evidence of a breeding population there.

It is conceivable that a breeding population has been established along the West Norfolk coast for at least 30 years, since the original 1988 record at Titchwell, where this species continues to occur. To gain insight into the reasons for the abundance of *T. johnsoni* at Old Hunstanton, we shall study the *Thoracochaeta* populations, including immature stages, at Old Hunstanton monthly throughout 2021 and thereby obtain a clearer picture of their phenologies. We would welcome any specimens and records of coastal sphaerocerids from the British Isles and Ireland.

#### Acknowledgments

We thank Ashley Kirk-Spriggs for affording DB access to the Diptera collection at the Natural History Museum, London. The reviewers Jindřich Roháček and Ivan Perry are thanked for their helpful comments and the provision of additional records. We also thank Paul Gatt for his comments on the manuscript.

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### A mixed species swarm of the genus *Protearomyia* McAlpine (Diptera, Lonchaeidae) with notes on finding the British species – On

27 May 2020, I encountered a small swarm of *Protearomyia* McAlpine, 1962 at Loton Deer Park, Shropshire (SJ3514). The flies were swarming at the edge of a woodland bordering the deer park; the swarm was situated at the sunlit tip of a beech branch about 5.5 metres above ground level with sycamore and oak branches in close proximity. I was only just able to reach the swarm, using a fully extended anglers' landing net handle (fitted with an insect net) and my completely outstretched arms. It was quite difficult to capture the flies with a sweep across the area where they were swarming, but after a good number of attempts eventually seven specimens, all males, were obtained. These were later determined, by dissection of the genitalia, as four *P. nigra* (Meigen, 1826) and three *P. withersi* MacGowan, 2014. This situation mirrors quite closely the mixed swarming behaviour of various *Lonchaea* species in Canada described by J.F McAlpine and D.D. Munroe (1968. Swarming of Lonchaeid flies and other insects, with descriptions of four new species of Lonchaeidae (Diptera). *The Canadian Entomologist* **100**(11), 1154-1178) and would appear to be the first time a mixed swarm of Lonchaeidae has been noted in Britain.

A third species of *Protearomyia* (*P. jonesi* MacGowan & Reimann, 2021) was added to the British list by I. MacGowan and A. Reimann (2021. A new species of *Protearomyia* (Diptera, Lonchaeidae) with a review of the genus in the Palearctic. *Zootaxa* **4966**(4), 487-493). I have collected all three British *Protearomyia* species exclusively by sweeping tree foliage. A long-handled net, providing a reach of up to 5-6 metres with outstretched arms and a 50cm net bag or a shorter handled net with a 40cm net bag have both been used to good effect. Sunlit trees at woodland edges, trees standing apart from woodland and sunlit foliage within woodland are all productive for *Protearomyia* as well as *Lonchaea* species. The peak period for collecting *Protearomyia* in central England appears to be mid-May to early June (indicative dates 19 May – 3 June).

I would like to thank Sir Michael Leighton for allowing access to record invertebrates at Loton Deer Park and Iain MacGowan for information regarding lonchaeid swarms in North America – **NIGEL P. JONES**, 22 Oak Street, Shrewsbury SY3 7RQ, nipajones@talktalk.net

#### Rachispoda uniseta (Roháček) (Diptera, Sphaeroceridae) new to

**Britain** – *Rachispoda uniseta* (Roháček, 1991) was originally described from three male specimens, two collected in Tunisia and one in Morocco (Roháček 1991). Since that time, a few male specimens have also been reported from Switzerland (Gatt, P. 2006. Two remarkable species of *Rachispoda* Lioy (Diptera, Sphaeroceridae) new to Switzerland. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **79**, 75-76) and Italy (Gatt, P. 2010. A further six additions to the lesser dung flies (Diptera, Sphaeroceridae) of Italy with new distributional data on the fauna of peninsular (southern) Italy. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **79**, 15-76) and other specimens, both male and female have more recently been collected from the Mediterranean (P. Gatt *pers comm.*, 2021), the female remains undescribed (P. Gatt *in prep.*).

A single female specimen of *Rachispoda uniseta* was collected by DB on 3 March 2017 from a green lane in North Creake (TF857390), North Norfolk, next to a wet meadow and inside the cover of a group of ash, *Fraxinus excelsior* and oak *Quercus robur*. The area swept was muddy and deeply rutted by tractor tyres. A single male specimen of *R. uniseta* was collected by PC on 19 July 2018 from the Highstanding Hill area of Windsor Forest, swept along the stream bed of Badger's Brook (SU930739), which was mainly dry, but steep-sided in parts within beech woodland, so was still providing high humidity compared with the surrounding woodland. Fourteen other species of Sphaeroceridae, including *Rachispoda anceps* (Stenhammar, 1855) (elsewhere found in forests, marshes, alongside brooks and lake shores) (Roháček, J. 1991. A monograph of *Leptocera* (*Rachispoda* Lioy) of the West Palaearctic area (Diptera, Sphaeroceridae). *Časopis Slezského zemského Muzea, Opava* (A) **40**, 97-288), were also collected at the same time.

One male *R. uniseta* was swept from alder (*Alnus glutinosa*) carr on the edge of *Sphagnum* bog by Ivan Perry on 18 August 2018 in Flitwick Moor (TL046352), Bedfordshire. Another male was swept from the remains of an old moat with seasonal standing water, again by Ivan Perry, on 5 April 2019, in Fulbourn Fen (TL528562), Cambridgeshire.

A further male specimen has since been discovered in the collection of the Natural History Museum (NHM); this specimen was collected from Gissing Common (TM147876), Norfolk, on 15 July 1975 by John Ismay.

Little is known about the biology of the species to date, although one of the male paratypes was collected along the riparian zone of a river (Roháček *op. cit.*). The specimens reported in this paper were collected between March and August. These records from Britain represent the northernmost known distribution of the species.

Male specimens of *R. uniseta* can be identified using Roháček (*op. cit.*). If using the key in Pitkin (1988. Lesser Dung Flies. Diptera: Sphaeroceridae. *Handbooks for the Identification of British Insects*. Volume 10 Part 5e), specimens will key to *Rachispoda cryptochaeta* (Duda, 1918); clearing and dissection of the post-abdomen is required to differentiate between the species.

We thank Paul Gatt (Wickford, UK) for confirming the identity of all specimens, information on distribution, and suggesting improvements to a draft of the manuscript; also Jindřich Roháček (Opava, Czech Republic) for guidance in the initial identification. DB would like to thank Ashley Kirk-Spriggs for access to the Diptera collection of the NHM and Ivan Perry, for supplying specimens from Cambridgeshire and Bedfordshire. For permission to record at Windsor Forest, PC would like to thank the Crown Estate and Natural England – DAVE BRICE, 100 West St, North Creake, Fakenham, Norfolk NR21 9LH, ischiolepta20@gmail.com and PETER CHANDLER, 606B Berryfield Lane, Melksham, Wilts SN12 6EL

#### Fourth Scottish locality for Mallota cimbiciformis (Fallén) (Diptera,

**Syrphidae)** – *Mallota cimbiciformis* (Fallén, 1817) is predominantly an English species with few records for Scotland (Ball, S. and Morris, R. 2021. Hoverfly Recording Scheme Maps. http://www.hoverfly.uk/hrs/). Its 'long-tailed' larva develops in wet rot-holes on broadleaf trees, and can be identified in the field (Rotheray, G.E. 1993. Colour guide to hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterists Digest (First Series)* **9**, 1-155). It is one of a number of syrphids whose recording is as effective in their early stages as the adult stage, if not more so.

The first Scottish record came from Motherwell in 1994, based on an empty puparium found in a rot-hole on horse-chestnut *Aesculus hippocastanum* (Barr, B. 1996. *Mallota cimbiciformis* (Diptera, Syrphidae) in Lanarkshire. *Dipterists Digest* (*Second Series*) **3**, 4). The second record was from Glasgow, based on 20 larvae found in rot-holes on horse-chestnut and sycamore *Acer pseudoplatanus* (Gemmell, L. *et al.* 2011. A second Scottish record of *Mallota cimbiciformis* (Fallén) (Diptera, Syrphidae). *Dipterists Digest* (*Second Series*) **18**, 71-72). The third Scottish record was an adult female reported from Brechin, Angus in 2017 and represented a significant northward extension to the known British distribution. Furthermore, the rot-holes occupied by *M. cimbiciformis* larvae in Glasgow in 2010 were revisited in January 2018 and their continued presence confirmed (Wilkinson, G. 2017. Third record of *Mallota cimbiciformis* for Scotland with a note on the early stages (Diptera, Syrphidae) *Hoverfly Newsletter* **65**, 11-13).

A fourth locality for *M. cimbiciformis* was found by the author at Baldovie Den (NO6972255502), near Montrose in Angus, on 17 February 2021. The den is a maturing line of trees that forms a field boundary, mostly composed of beech *Fagus sylvatica* and sycamore. A mature larva and two empty puparia were found in a large rot-hole (~ 50 cm width, 40 cm depth) at the base of a sycamore tree (Figs 1-3). The puparia were found among drier debris at the margins of the rot-hole and the larva was dislodged to the surface by swirling the wet porridge-like contents with a stick. The larva and puparia were retained as voucher specimens.



Figs 1-3. Mallota cimbiciformis larva, rot-hole and puparium.

There is little broadleaf woodland in Angus, especially in the low attitude regions dominated by intensive agriculture. However, there are small woods of planted beech and sycamore around large houses, and tree belts along field boundaries and roadsides with increasing numbers of mature trees that will likely provide some larval habitat over the coming years – **GEOFFREY WILKINSON**, 23 Beacon Terrace, Ferryden, Montrose, Angus, DD10 9RU

#### A new Napomyza Westwood (Diptera, Agromyzidae) species of the lateralis-group

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#### Summary

A new *Napomyza* Westwood (Diptera, Agromyzidae) species, *Napomyza crepidicaulis* sp. n., is described based on a series of adults reared from puparia obtained from the stems of *Crepis capillaris* in England and Germany, and specimens within a Malaise trap sample from Italy. Description and illustrations of the larval stage and adult are provided, along with a comparison to other species in the *lateralis*-group. Details of the species' associated parasitoids [Braconidae] are also discussed.

#### Introduction

In May 2020, a male *Napomyza* was collected from a newly created flood alleviation site in Anlaby, East Yorkshire [V.C. 61], TA033278, England. Upon initial examination, *Napomyza carotae* Spencer, 1966 seemed most likely owing to the specimen possessing second cross-vein, dark scutellum, all knees yellow and third antennal segment with short but noticeable [not long as in *Napomyza hirticornis* Hendel, 1932] pubescence. When dissected, the male genitalia, although superficially similar, do not agree well with *N. carotae*: head of distiphallus smaller, neck of distiphallus with very little curvature, postgonite of different shape.

Using the keys of Spencer (1966, 1976) and Papp and Černý (2019), the male runs to couplets [depending on interpretation of third antennal segment pubescence] which suggest *N. carotae*, *N. cichorii* Spencer, 1966, *N. lateralis* ((Fallén, 1823), *N. scrophulariae* Spencer, 1966 or *N. tripolii* Spencer, 1966. The male was compared to reared *N. lateralis* and *N. scrophulariae* material; the male genitalia [inner and outer] are sufficiently different to the latter species for it not to be considered, whilst although *N. lateralis* is known to be rather variable, several characteristics do not agree and therefore, the male was deemed unlikely to be *N. lateralis*. *N. carotae*, *N. cichorii* and *N. tripolii* were not considered owing to slight but important differences in external and internal morphology [particularly so with *N. tripolii*].

The collection site possesses several of the host plant genera stated to be utilised by *N. lateralis* (Benavent-Corai *et al* 2005, Zlobin 1994a). Detailed examination of many stems belonging to the genera *Bellis*, *Carduus*, *Centaurea*, *Crepis*, *Matricaria* and *Senecio* resulted in *Napomyza* puparia being obtained from only *Crepis* and *Matricaria*. Two male *Napomyza* emerged from puparia ex *Matricaria discoidea*, which upon examination of the genitalia, proved to be *N. lateralis* [based on the illustrations by Papp and Černý (2019) and Zlobin (1994a)].

Adults were also successfully reared from puparia obtained from *Crepis capillaris* stems; upon examination of the male genitalia, these agreed with the collected male and not *N. carotae*, *N. cichorii*, *N. lateralis*, *N. scrophulariae* or *N. tripolii*.

The collected and reared [from *C. capillaris*] males belong to the *lateralis*-group [based on Zlobin's definition of the group], owing to: the uniform body colouration [essentially as in *N. lateralis*], presence of second cross-vein, frons projecting above eye in profile, true surstyli absent, postgonite without long, hook-shaped, projection at ventral side, distiphallus unpaired, larvae usually feeding as stem-borers or feeders in developing seeds of flower heads, puparium elongated and known host plants belonging in the Asteraceae family.

Of the 59 valid *Napomyza* species, worldwide, the following are placed in the *lateralis*group: *N. achilleanella* von Tschirnhaus, 1992, *N. acutiventris* Zlobin, 1993, *N. angulata* Zlobin, 1993, N. arcticola Spencer, 1969, N. bellidis Griffiths, 1967, N. carotae Spencer, 1966, N. cichorii Spencer, 1966, N. curvipes Zlobin, 1993, N. dubia Zlobin, 1994, N. filipenduliphila Zlobin, 1994, N. genualis Zlobin, 1994, N. grandella Spencer, 1986, N. hirta Zlobin, 1994, N. hirticornis (Hendel, 1932), N. immanis Spencer, 1969, N. immerita Spencer, 1969, N. hirta Zlobin, 1994, N. hirticornis (Hendel, 1932), N. immanis Spencer, 1969, N. immerita Spencer, 1969, N. inquilina (Kock, 1966), N. kandybinae Zlobin, 1994, N. lacustris Zlobin, 1994, N. lateralis (Fallén, 1823), N. laterella Zlobin, 1994, N. manni Spencer, 1986, N. maritima von Tschirnhaus, 1981, N. merita Zlobin, 1993, N. mima Zlobin, 1994 N. mimica Zlobin, 1994, N. mimuta Spencer, 1986, N. minuta Spencer, 1981, N. minuta Spencer, 1981, N. minuta Spencer, 1981, N. minuta Spencer, 1969, N. pinima Zlobin, 1994, N. neglecta Zlobin, 1994, N. nigriceps van der Wulp, 1871, N. nugax Spencer, 1969, N. prima Zlobin, 2001, N. pusztae Papp, 2019, N. schusteri Spencer, 1981, N. scrophulariae Spencer, 1966, N. strana Spencer, 1960 and N. tripolii Spencer, 1966. In addition, one undescribed species develops in the stems of certain genera of European Lamiaceae (M. von Tschirnhaus pers. comm.)

Zlobin (1994a) divided the *lateralis*-group into three 'sections', based on characteristics of the male and female genitalia: 1) species having lower margin of postgonite distinctly concave; side-arms of hypandrium without significant prominences; neck of receptaculum seminis short, without lateral curves; spermathecea small, 2) lower margin of postgonite with more or less defined notch or hook; hypandrium with distinct prominences; neck of receptaculum seminis short, without lateral curves; spermathecea small and 3) lower margin of postgonite slightly concave or weakly wave-shaped; hypandrium without strong prominences laterally; head of distiphallus usually strongly elongated; neck of receptaculum seminis long, with lateral curves; spermathecea large.

The collected and reared *Napomyza* can be placed within Zlobin's first 'section'. The described Palaearctic species which are placed within this section include *N. acutiventris*, *N. carotae*, *N. cichorii*, *N. filipenduliphila*, *N. hirta*, *N. hirticornis*, *N. lateralis*, *N. laterella*, *N. minima*, *N. minutissima*, and *N. neglecta*.

Detailed examination of the female and male genitalia [particularly the postgonite, its shape is one of the most important characters in the differentiation of species (Papp and Černý 2019)] confirmed that the collected and reared adults do not belong to any of the above species.

When referring to the keys and publications discussing and illustrating all other members of the *lateralis*-group and other worldwide *Napomyza* (Chen and Wang 2003, Griffiths 1967, Hendel 1931-36, Kock, 1966, Sasakawa 1955, Spencer, 1969, Spencer, 1973, Spencer, 1976, Spencer, 1981, Spencer, 1990, Spencer and Steyskal 1986, von Tschirnhaus 1981, von Tschirnhaus 1992, Zlobin, 1993a, Zlobin 1993b, Zlobin 1994a, Zlobin 1994b, Zlobin 1994c, Zlobin 2001), no species agree with the specimens discussed here, indicating they belong to an undescribed species.

Images and morphological observations were sent to Dr Michael von Tschirnhaus who confirmed that this *Napomyza* is an undescribed species and almost certainly the same as his *Napomyza* 'spec. 4'; von Tschirnhaus successfully reared a long series [633, 492] from puparia collected from the stems of *Crepis capillaris* and also obtained the same species via the collection of adults on the wing [see Distribution section for details]. To confirm that the British collected and reared specimens are conspecific with the von Tschirnhaus material, his reared and collected adults were sent to me, which upon detailed examination of external morphological features and the male genitalia, confirmed the specimens to be the same species.

In total, seven  $[3 \circlearrowleft, 4 \heartsuit]$  adults were successfully reared from puparia found in *C. capillaris* stems at the site in England, with thirteen parasitoids emerging.

#### *Napomyza crepidicaulis* Warrington sp. n. urn:lsid:zoobank.org:act:45985EDD-57A0-40E8-A8A0-EC571A15BB54 Description

**Head** (Fig. 1): Frons 1.5x width of eye, projecting above eye in profile, with 2 strong reclinate *ors* and 2 strong, incurved *ori* [in all seven specimens]. Orbital setulae in a single row, relatively sparse, infrequently increasing to two rows at level of lower *ori*. Cheeks forming broad ring below eye. Gena deep, angular, 1/2 to 1/3 height of eye [measured in 153, 159]. Orbits wide with lunule broad, semi-circular. Ocellar triangle reaching to level of upper *ors*. Third antennal segment marginally longer than broad, slightly cut away below, with short but noticeable pubescence. Palpi normal, indistinctly widening distally. Epistoma normal, narrow.



Fig. 1. Napomyza crepidicaulis sp. n., male head detail; left, frontal view; right, face and epistoma detail.

**Mesonotum** (Fig. 2): 1+3 strong dorsocentral [dc] bristles, with acrostichals [acr] in two rows up to level of third dc, sometimes acr in four, irregular, scattered rows, up to fourth dc.



Fig. 2. Napomyza crepidicaulis sp. n., male viewed from above.

**Wing:** Hyaline, length 2.2mm – 2.5mm in male, 2.5mm – 3.0mm in female, with costa extending to, or slightly surpassing, vein R<sub>4+5</sub>. Second cross-vein [*tp* or M-M or *dm-Cu*] in continuation of first. Radial veins mainly dark. Costal sections (2-4) of 30 specimens [ $15^{\circ}_{\circ}$ ,  $15^{\circ}_{\circ}$ ] were measured, with an average ratio of 100:41:65.

**Colour:** Frons yellow, slightly darker adjoining lunule. Orbits and lunule paler than frons. Cheek and gena pale yellow, with slight greyish tinge. Face greyish [sometimes paler], palpi black. All antennal segments and arista black. Hind margin of eye black, with inner *vt* seta on border of yellow and dark ground. Mesonotum and scutellum matt, ash-grey. Squama whitish-grey, with pale margin and dark fringe, brownish. Legs black, with all knees bright yellow. Abdomen dark, caudal margins of tergites with yellow stripes, abdominal membrane yellow.

**Male genitalia:** Surstylar lobe (Fig. 3, upper) broadly rounded apically. Arms of hypandrium (Fig. 3, lower) rounded, without significant prominences. Tip of hypandrium with distinct projection in lateral view. Postgonite (Fig. 4, centre) broadest at its apical <sup>3</sup>/<sub>4</sub>, ventral edge broadly rounded, distal third straighter. Phallus (Fig. 5): basiphallus sclerites thin, left sclerite with long ventrobasal process; paramesophallus with distinct curvature, basal section broad [distal and centre section noticably narrower]; mesophallus relatively thin, with distinct dorsal 'attachment'; hypophallus strong, relatively long, mostly straight, with only slight curvature distally; medial lobe of hypophallus distinct, sclerotised; neck of distiphallus with only slight ventral curvature; head of distiphallus elongated distally. Ejaculatory apodeme (Fig. 4, right) typically variable, in general blade and neck broad, asymmetrical, with small dark sign on bulbus [which is variable].



Fig. 3. *Napomyza crepidicaulis* sp. n.: upper, epandrium and hypandrium in left lateral view; lower, epandrium and hypandrium viewed from below.



Fig. 4. *Napomyza crepidicaulis* sp. n. [not to scale]: left, epandrium complex in caudal view; centre, postgonite [with part of pregonite] in broadest extension (sub-lateral view); right, ejaculatory apodeme, lateral view.



Fig. 5. *Napomyza crepidicaulis* sp. n., phallus: upper, phallus in left lateral view; lower, phallus viewed from below.

The genitalia of the male specimens reared by von Tschirnhaus highlight a degree of natural variation within the species: mesophallus sometimes broader and lacking dorsal 'attachment', neck of distiphallus may be more ventrally curved or almost straight (Fig. 6), head of distiphallus can be directed downwards (Fig. 6). Nevertheless, the von Tschirnhaus material also confirms that some features are stable within the species: curvature of paramesophallus, head of distiphallus when viewed from below (Fig. 7) and postgonite.



Fig. 6. Napomyza crepidicaulis sp. n., variation in neck of distiphallus curvature.



Fig. 7. *Napomyza crepidicaulis* sp. n., phallus viewed from below [material and photograph(s) of von Tschirnhaus].

**Female genitalia:** Spermathecae (Fig. 9, left) small, unequal in size, slightly broader than high, rounded above, dark brown, almost black. Neck of receptaculum seminis (Fig. 9, right) without lateral curves. Head of receptaculum seminis large, hind wall with distinct projection, never rounded, lower margin close to neck.



Fig. 8. Napomyza crepidicaulis sp. n., female cerci: upper, viewed from above; lower, viewed from below.



Fig 9. Napomyza crepidicaulis sp. n., female genitalia; left, spermathecae; right, receptaculum seminis.

**Early stages:** Larva 3mm-5mm long, thin, white. Puparium (Fig. 10), elongate, tapered, pale yellow [one puparium pale grey], 2.8mm-3.9mm in length. Posterior spiracles (Fig. 11) on short projections, rectangular, brown, each with 10-13 bulbs in two rows.



Fig. 10. Napomyza crepidicaulis sp. n., puparium viewed from above.



Fig. 11. Napomyza crepidicaulis sp. n., puparium posterior spiracles.

#### Host plant: Crepis capillaris [Asteraceae]

**Host-range and distribution:** *Crepis capillaris*, commonly referred to as smooth hawk's-beard, is a low-growing annual [may also be biennial]. An early colonist of open ground, found in thin grassland, road verges, lawns, spoil heaps, rocky banks and other open habitats. It is common throughout Great Britain and the rest of Europe.

**Biology:** Unknown in detail, a stem-borer. Larva feeding, in an upward or downward direction, within the stem, mostly just a few centimetres [2-3cm] above ground level. Pupariation takes place at the root neck (Fig. 12) but some puparia were to be found higher up the stem. No larvae or puparia were found in the inflorescence or roots. Only one larva per plant. Larvae and puparia were found between 6 and 19 June [August in Germany].

As the reared British adults emerged during June, it would be reasonable to assume that *Napomyza crepidicaulis* sp. n. is bivoltine, possibly trivoltine. Adults reared by von Tschirnhaus emerged in August and September, supporting the possibility that the species is trivoltine [when seasonal conditions are optimal].



Fig. 12. Napomyza crepidicaulis sp. n., puparium at root neck in Crepis capillaris stem.

**Biotope:** Puparia were obtained from plants within a newly created flood alleviation site (Fig. 13). The area contains [newly planted] native trees and shrubs, with the ground flora containing the following genera: Achillea, Artemisia, Bellis, Brassica, Carduus, Centaurea, Cirsium, Crepis, Daucus, Echium, Lathyrus, Leucanthemum, Matricaria, Medicago, Melilotus, Onobrychis, Petasites, Ranunculus, Rhinanthus, Salvia, Senecio, Sonchus, Taraxacum, Trifolium, Urtica and Vicia. Various Poaceae genera are also present.

Prior to the creation of the site, the area was arable land. In the brief time the area has being free from engineering works, several notable species of Agromyzidae have also been recorded: *Agromyza macedonica* Černý, 2011, *Ophiomyia senecionina* Hering, 1944 and *Cerodontha vinokurovi* Zlobin, 1994 [*pers. obs.*].

The material of von Tschirnhaus was obtained from the following biotopes; dune [bird island of Memmert in the North Sea, Germany], forest clearing [near Schierensee, west of Kiel, Germany], Malaise trap [South Tyrol, Italy], sweeping from lawn [Niedersachsen, village Klein Süntel, Germany] and yellow pan traps [Schleswig-Holstein, city of Kiel, Germany].



Fig. 13. Napomyza crepidicaulis sp. n., biotope

**Etymology:** The specific epithet refers to the species feeding in the stems [*caulis*] of its host plant genus *Crepis*.

#### Discussion

Prior to Zlobin's (1993a, 1993b, 1994a, 1994b, 1994c) [and to some extent Spencer (1966, 1976)] excellent review of the *lateralis*-group, *N. lateralis* was considered to be a widespread, apparently polyphagous [see Benavent-Corai (2005), Hendel (1931-36: 528-559)], species; however, his work, based upon species-specific genitalia features [epandrium, hypandrium, phallus, postgonite, receptaculum seminis, spermathecae] revealed that there are several sibling species in what is clearly a larger complex. Although species of the *lateralis*-group are superficially extremely similar, thanks to the work of Spencer and Zlobin, differentiation of species is possible.

Distinctive characteristics of *N. crepidicaulis* male genitalia include: relatively long, apically rounded, caudally directed, surstylar lobe; basal part of paramesophallus strongly upcurved in lateral view; neck of distiphallus with only slight ventral curvature [although can be variable]; postgonite broad, ventrally rounded, straight on distal third. The short third antennal segment, slightly cut away below and its short pubescence [different from other species] are also characteristics of this species.

Females can only be safely associated with the correct males after detailed rearing, as nothing is known about the potential sibling species in all other '*N. lateralis*' hosts; the receptaculum seminis of *N. crepidicaulis* sp. n. appears to be distinct but it is a very simple
structure and should be treated with caution when identifying this species [until other workers undertake such complicated dissections and macerations of reared material from other hosts].

The genitalia of *N. crepidicaulis* sp. n. suggests a close relationship to *N. cichorii* and this is supported by its biology; both larvae mine in the stems of Asteraceae in the Tribe Cichoriae and both are attacked by the same species of parasitoid wasp [see Additional information].

# **Additional information**

In total, 13 parasitoids of two species were successfully reared, both Braconidae [Alysiinae, Dacnusini];  $6^{\circ}$ ,  $6^{\circ}$  *Chorebus glaber* (Nixon, 1944), a known parasitoid of *Napomyza* spp. This parasitoid has not been reared before in the UK and is a relatively uncommon species. In continental Europe, *C. glaber* is a common parasitoid of *N. cichorii* (Griffiths, 1968), which attacks commercial chicory [*Cichorium intybus*], whilst it has been reared once from *N. carotae* in Spain (Docavo *et al.* 1994).

The final reared parasitoid was a single male *Dacnusa* sp., probably *D. pubescens* (Curtis, 1826), a species which is known from *N. lateralis* and other agromyzids, typically those feeding in stems and midribs. Initial molecular [DNA barcoding] studies suggest there may be a number of species under the name *pubescens* and only further work and additional specimens would confirm the identification of this specimen [H.C.J. Godfray *pers. comm.*].

# Distribution

*Napomyza crepidicaulis* sp. n. is known from Great Britain, Germany and Italy. Details of the von Tschirnhaus collection is hereby included;

K113 7.viii.1970 leg. M von	North Germany	Mass rearing from Crepis
Tschirnhaus	Schleswig-Holstein	<i>capillaris</i> [63 $3$ ,49 $2$ ], adults
	Kiel	emerging; 12.viii.1970 1♂
	54°19'42"N, 10°08'34"E	15.viii.1970 2♂
		18.viii.1970 2♂, 1♀
		20.viii.1970 4♂, 2♀
		25.viii.1970 5♂, 10♀
		26.viii.1970 4♂, 2♀
		30.viii.1970 11∂, 11♀
		2.ix.1970 3♂
		[not all dates of emergence
		could be noted].
F196-F202 25.v15.vii.1970	Data as above	$63, 1^{\circ}$ series of yellow and
leg. M von Tschirnhaus		light yellow pan traps
		emptied fortnightly.
550 leg. M von Tschirnhaus	North Germany,	23, 52 - swept from lawn.
0	Niedersachsen (Lower	
	Saxony)	
	village Klein Süntel,	
	52°10'10"N, 9°26'07"E	
X0153 15.x.1976 leg. Hans	Italy	$2^{3}$ , $2^{\circ}$ ex Malaise trap.
Stockner	South Tyrol	
	Kaltern, 9 km SW of	
	Bolzano	
	46°24'N, 11°14'E	

**Type material: Holotype**  $\mathcal{J}$  ENGLAND, East Yorkshire, V.C. 61, Anlaby, TA033278 [53.736365 -0.43543769], emerged 15 June 2020, ex puparium collected 6 June 2020. Pinned, with its puparium in a gelatin capsule and genitalia preparations in Euparal pinned below the specimen. Deposited at Natural History Museum, London.

**Paratypes:**  $\bigcirc$  ENGLAND, East Yorkshire, V.C. 61, Anlaby, TA033278 [53.736365 - 0.43543769], emerged 16 June 2020, ex puparium collected 6 June 2020. Pinned, with its puparium in a gelatin capsule and genitalia preparations in Euparal pinned below the specimen. Deposited at Natural History Museum, London.

343, 319 GERMANY, Schleswig-Holstein, (city of) Kiel,  $54^{\circ}19'42"N$ ,  $10^{\circ}08'34"E$ , leg. 7.viii.1970 M. von Tschirnhaus, **K113**, in vial containing data label [in 96% ethanol]; 13' GERMANY, Schleswig-Holstein, (city of) Kiel,  $54^{\circ}19'42"N$ ,  $10^{\circ}08'34"E$ , leg. 7.viii.1970 M. von Tschirnhaus, **K113**, in vial containing data label and genitalia [in 96% ethanol]; 53', 19' GERMANY, Schleswig-Holstein, (city of) Kiel,  $54^{\circ}19'42"N$ ,  $10^{\circ}08'34"E$ , leg. 7.viii.1970 M. von Tschirnhaus, **F196-F202**, in vial containing data label [in ethanol]; 23', 59' GERMANY, Niedersachsen, village Klein Süntel, 8.5 km NW of Hameln/Weser  $52^{\circ}10'10"N$ ,  $9^{\circ}26'07"E$ , leg. M von Tschirnhaus, **550**, in vial [in ethanol]; 23', 29' ITALY, South Tyrol, Kaltern, 9km SW of Bolzano,  $46^{\circ}24'N$ ,  $11^{\circ}14'E$ , 15.x.1976 leg. Hans Stockner, **X0153**, in vial containing data label [in ethanol], genitalia preparation no. 306 by M.v.T, preserved in two micro craters with glycerin on glass slide, within separate vial. Types in the MvT collection to be deposited in the Zoologische Staatssammlung München (= Munich), GERMANY.



Fig. 14. Napomyza crepidicaulis sp. n., male

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The sheep nostril fly, *Oestrus ovis* Linnaeus (Diptera, Oestridae), from a garden vane trap in Dorset – Between 1 June and 16 October 2020 a vane (flight interception) trap was placed next to a log store in the garden with a view to recording Coleoptera emerging from, or being attracted to, the logs. When recently working through the sample it was a surprise to find a single female of the sheep nostril fly *Oestrus ovis* Linnaeus, 1758. The trap was in a south-east facing garden within the parish of Bothenhampton on the south-eastern outskirts of Bridport in Dorset (SY471926).

With improved modern animal husbandry and veterinary procedures, this rarely-found fly has become very scarce, and is ultimately under threat of national extinction - it is assigned pNear Threatened status (Falk, S.J. and Pont, A.C. 2017. *A Provisional Assessment of the Status of Calypterate flies in the UK*. Natural England. Commissioned Reports, Number 234) though no conservation measures were considered appropriate in view of its potential pest status. Andrew Grayson informs me that only very few records are submitted to the Oestridae Recording Scheme and that the only other Dorset record in the scheme is from Church Knowle on Purbeck in 2010. Furthermore, Bryan Edwards reports that there are no modern records held at Dorset Environmental Records Centre (DERC), though there are historic records from Glanville's Wootton by C.W. Dale (1878. *History of Glanvilles Wootton*. London) - "*Cephalemyia ovis*, Linn. Sheep Fly. Rare in the perfect state. Taken by my father [J.C. Dale], August 16th, 1820, and June 22nd, 1829; also by myself in Sandhills, July 7th, 1870". It appears that the Bridport example represents only the second modern record for Dorset.

There are some parallels between the Bridport record and observations reported by P. Roper and B. Yates (2003. On the behaviour of the sheep nostril fly, *Oestrus ovis* Linnaeus (Diptera, Oestridae) at Rye Harbour, East Sussex. *Dipterists Digest (Second Series)* **10**, 40), who noted two individuals resting on a white painted pebble-dash wall of a building, with one seen over a period of several days, and that the nearest sheep-grazed area was located at least 300 metres away. In Bridport, the nearest likely source of the specimen is a sheep-grazed hillside to the south-east, again at least 300 metres away (ca SY474921), and perhaps of relevance is that the front of the house also has a white painted pebble-dash wall, with the vane trap located less than 2 metres away. Perhaps the fly had been attracted to the white wall here as well.

My thanks to Andrew Grayson for confirming the female *O. ovis* from a photograph, comments on a draft of this note and for the other modern Dorset record, also to Bryan Edwards and Alison Stewart of DERC for checking data held there – **ANDY P. FOSTER**, 42 Crock Lane, Bothenhampton, Bridport, Dorset, DT6 4DF

# Further records of Villa cingulata (Meigen) (Diptera, Bombyliidae)

**from Dorset** – On 29 June 2019, APF observed a single example of *Villa cingulata* (Meigen, 1804) flying low over the grassland sward within a large glade at Turnworth Common, Dorset (ST815084). During a return visit on 14 June 2020, APF observed at least three individuals - all in view at once in a neighbouring glade (ST815085), followed shortly afterwards by a copulating pair (Fig. 1) on a nearby ant hill. BE then made a visit to the same area on 24 June 2020, when there was a minimum of 15 individuals, all females, scattered through the sheltered south-facing chalk grassland clearings, indicating a thriving population. It was interesting to see how they were using the site, being observed flying low and ovipositing in the short turf, nectaring on bramble blossom at the clearing edges, and at pinch-points, where the cattle go between clearings and create tracks, up to four at a time were noted on the bare ground 'collecting' soil particles. The only other flower *V. cingulata* was observed on was *Potentilla reptans*.

The first Dorset record was provided by M. Parker (2014. Villa cingulata (Meigen) (Diptera, Bombyliidae) in Dorset. Dipterists Digest (Second Series) 21, 171) after several individuals had been observed in the Cranborne Chase area in the north-east of the county on various dates in late July 2014. Mick Parker has subsequently provided further records from the same area: 27 June 2015, 19 June 2017 (when 9 were seen) and 10 July 2019 (good numbers). Also, a single female was seen by him on 17 July 2017 at the nearby Great Shaftsbury Coppice (ca ST9719) - possibly a wanderer from the original site. Another record from the Cranborne Chase area is held by Dorset Environmental Records Centre - 2015, Stubhampton Bottom (ST8915) by Peter Orchard. This locality largely comprises replanted ancient woodland, managed by the Forestry Commission, with chalk grassland glades on the south-facing side of a sheltered valley. And further nearby records recently submitted to the Soldierflies and Allies Recording Scheme via iRecord (M. Harvey pers. comm.) are 7 June 2020, Garston Woods RSPB Reserve (SU001194) by Philip Saunders, and 8 August 2020, Chase Woods (ST9919) by Colin Lamond. The latter site is possibly just over the border into Wiltshire. Like Turnworth and Stubhampton, these wooded sites support a network of open rides or glades. It is evident from this cluster of records in hectads ST81, ST91 and SU01 that V. cingulata is firmly established in the Cranborne Chase area of Dorset bordering Wiltshire, while the Turnworth site is currently an outlier located approximately12km to the south-west.

Turnworth is owned by the National Trust and supports a mosaic of pasture woodland and unimproved grassland, the latter including neutral and calcareous swards. It is clear that the sheltered glades provide suitable habitat for *Villa* and there may be some similarities with the Cranborne Chase localities – also supporting sheltered calcareous grassland glades within a wooded habitat. These sites closely resemble habitat for the species described by A. Stubbs and M. Drake (2014. *British Soldierflies and their allies: an illustrated guide to their identification and ecology.* British Entomological and Natural History Society), although the original Cranborne Chase locality (Parker 2014 *loc. cit.*) is described as a more open environment – a trackway with a calcareous grassland flora running through an improved farm landscape.



Fig. 1. Pair of Villa cingulata at Turnworth Common, Dorset, 14 June 2020.

This group of recent records in Dorset would suggest that sites elsewhere in the county with suitable unimproved calcareous or neutral grassland swards, particularly those sheltered by scrub or trees, could also support *V. cingulata*. Our thanks to the National Trust for permission to sample invertebrates at Turnworth – *V. cingulata* was initially discovered by casual observation during a saproxylic invertebrate survey of the site, and to Mick Parker and Martin Harvey for comments on the draft of this note and providing additional records – **BRYAN EDWARDS**, Dorset Environmental Records Centre, Dorset History Centre, Bridport Road, Dorchester DT1 1RP and **ANDY P. FOSTER**, 42 Crock Lane, Bridport, Dorset, DT6 4DF

# A casual observation of the occurrence of *Villa cingulata* (Meigen) (Diptera, Bombyliidae) at a previously unreported site in North

**Dorset** – On 1 July 2021, the author observed a fly feeding on what is believed to be a selfseeded wild carrot (*Daucus carota*) plant within the front garden of his property situated within the village of Iwerne Minster, North Dorset (ST865139). Several photographs were taken at this time before the insect flew away. The conclusion from available sources that this was *Villa cingulata* (Meigen) was confirmed by submitting the images (including that in Fig. 1) to the UK Diptera group on Facebook, from which Mick Parker confirmed the identification. Since this original observation, a further two females were seen together, on 5 July 2021, at Tower Hill (ST875145), which is approximately one mile east of the original site.



Fig. 1. A female Villa cingulata at Iwerne Minster, North Dorset, 1 July 2021.

The first Dorset record was provided by M. Parker (2014. *Villa cingulata* (Meigen) (Diptera, Bombyliidae) in Dorset, *Dipterists Digest (Second Series)* **21**, 171), after several individuals had been observed in the Cranborne Chase area in the north-east of the county. Between 2015 and 2019 further observations were made in that area by Mick Parker, and further records from the county include those from 2015 to 2020 reported in the above note by Bryan Edwards and Andy Foster. These include a cluster of hectads (ST81, ST91 and SU01), which suggest that *V. cingulata* is firmly established in the Cranborne Chase area of Dorset and the bordering area of Wiltshire. The location of the observations in this note is to the west of the current known sites for *V. cingulata* and may suggest that further movement away from the original sites may be occurring.

Thanks are due to Mick Parker for confirmation of the initial identification and to Peter Chandler for help with preparation of this note – **HARRY M. MCBRIDE**, zacsid@aol.com

# *Pseudolynchia canariensis* (Macquart in Webb & Berthelot) (Diptera, Hippoboscidae) new to Britain

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#### Summary

The pigeon louse fly, *Pseudolynchia canariensis* (Macquart in Webb & Berthelot, 1839) is recorded as new to the British fauna and its identification is discussed.

# Identification

The identification of *Pseudolynchia canariensis* (Macquart in Webb & Berthelot, 1839) is discussed in the Royal Entomological Society handbook to keds, flat-flies and bat-flies (Hutson 1984), in which the eventual discovery of *P. canariensis* in Britain was assumed. A second species of the genus, *P. garzettae* Rondani, was added to the British list as a vagrant by Palmer (1987). These two species are also keyed in the paper on the genus *Pseudolynchia* Bequaert by Maa (1966). Amongst the bird-associated Hippoboscidae, *Pseudolynchia* is the only genus to have just one cross-vein (r-m). *Pseudolynchia canariensis* may then be determined by the long pale setae present on the prescutum, and the scutellum has a distinctive rectangular shape, with its median length about a quarter the distance between the bases of the scutellar bristles.

#### Discussion

An individual of *P. canariensis* (see cover illustration) was potted on 6 December 2020, after flying through an open window of the author's car in Isleworth (TQ17), London. Commonly known as the pigeon louse fly or just pigeon fly, *P. canariensis* has been recorded from a range of avian hosts across multiple orders (Maa 1969). It, however, appears to be most common amongst domestic pigeons. Considering the urban environment, the fly was found in, it could be assumed that the host was a feral pigeon (*Columba livia domestica* Gmelin, 1789). From communications with Denise Wawman regarding this species, it was noted that wood pigeons (*Columba palumbus* Linnaeus, 1758) have been checked for *P. canariensis* by a team of "flat fly collectors" and all hippoboscids found have proven to be *Ornithomya avicularia* (Linnaeus, 1758). Further research on British flat flies found on *Columba* species may change this, and the recently formed UK Hippoboscidae and Nycteribiidae Recording Scheme will complement such efforts.

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# Two species of Lonchaeidae (Diptera) new to the British Isles and further records of the family in Scotland

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# Summary

Two species of Lonchaeidae, *Dasiops facialis* Collin, 1953 and *Lonchaea angelina* MacGowan, 2014, are added to the British fauna based on specimens captured in a Malaise trap in Lochaber, Highland. The taxonomic history and geographical range of these species are discussed and comparisons are made between them and other British species of Lonchaeidae. Additional records are provided for *Lonchaea deutschi* Zetterstedt, 1837 which was added to the British fauna in 2020 and for *Lonchaea ultima* Collin, 1953 which is recorded from Scotland for the first time.

# Introduction

During a rather remarkable period in May 2020 a Malaise trap operated in a garden at Upper Inverroy, Lochaber, captured four specimens of Lonchaeidae, representing two species, both of which were new to the British Isles.

Inverroy is a crofting township with unimproved and semi-improved grasslands and patches of deciduous woodland. It is underlain in part by limestone and supports a locally rich flora. The trap was located in a semi-wild garden with herb-rich grassland and rush pasture, lawns, flower-beds and a fringe of dry and wet woodland with a range of native trees and shrubs. These include over-mature goat willow *Salix caprea* and birch *Betula* spp as well as ash *Fraxinus excelsior*, rowan *Sorbus aucuparia*, hazel *Corylus avellana*, alder *Alnus glutinosa*, aspen *Populus tremula* and others. Ferns, bryophytes and lichens are abundant and there is a pond with emergent vegetation.

The Malaise trap specimens, which were originally stored in alcohol, are now micropinned and staged. The male terminalia of *L. angelina, L. deutschi* and *L. ultima* have been dissected and cleared and are stored in glycerol-filled microvials attached to the specimen pins. All specimens are now in collections of National Museums of Scotland.

# Accounts of the species new to Britain.

# Dasiops facialis Collin, 1953.

Three females of this species were captured during late May 2020. *Dasiops facialis* is a relatively large species of *Dasiops* with a wing length of approximately 3.6mm. With a scutellum which is entirely bare apart from the four marginal setae, first tarsomere yellowish, one seta on the proepimeron (= one stigmatical bristle) and dark grey calypters with a black fringe, this species would key out in the British Handbook (MacGowan and Rotheray 2008) to *D. trichosternalis* Morge, 1959. The easiest means of separating these two species is by examination of the female aculeus. In *D. facialis* the apical segment has a 'shouldered' appearance with a very acute apex and several pairs of lateral setae (Figs 1 & 3). In *D. trichosternalis* the apical segment smoothly tapers towards a blunter, slightly rounded apex and there is usually only one pair of relatively short lateral setae (Fig. 4).

*Dasiops facialis* has a boreo-alpine distribution. Morge (1959) gave the type locality as Finland, with additional records from the St. Petersburg region of Russia, and Styria and Admont in Austria. It is also recorded from the Italian Alps at altitudes of 940m and 1220m (MacGowan 2016) and from Switzerland. In Sweden it seems to be well-distributed with records from seven provinces, ranging from Torne lappmark in the north to Småland in the south (MacGowan 2019). The larval biology is unknown, but the acutely pointed apex of the aculeus may indicate an association with the stems of herbaceous plants.

**Records. Highland:** Inverroy, NN255818, Malaise trap, 21.v.2020, 2; 30. v. 2020, 1, leg. I. Strachan.



Figs 1-2: 1, apex of the female aculeus of *Dasiops facialis*; 2, internal view of the surstylus of *Lonchaea angelina* showing the characteristic linear row of strong, ventrally-directed setae.



Figs 3-4: 3 (above), female aculeus of *Dasiops facialis*; 4 (below), same of *Dasiops trichosternalis* (both after Morge 1959).

The name *D. facialis* has had a slightly complicated past. It was originally created by Collin (1953: 85) in his review of the British Lonchaeidae as a new name for *Lonchaea albiceps* Frey, 1930 as this name was already occupied by *L. albiceps* Malloch, 1914 (Collin recognised that both these species were actually in the genus *Dasiops*). Collin went on to give a brief description of *D. facialis* and provided British records. Later, Collin (1957) in discussion with Morge recognised that his *D. facialis* was not in fact the same species as *L. albiceps* Frey and subsequently Morge (1959) described Collin's '*D. facialis*' as a new species which he called *Dasiops trichosternalis*. As a result of these changes *D. facialis* Collin was removed from the British checklist with previous records being attributed to *D. trichosternalis*.

#### Lonchaea angelina MacGowan, 2014.

*Lonchaea angelina* is a member of the *Lonchaea fraxina* species-group, whose members are uniquely distinguished by the presence of hairy eyes, multiple rows of anterior genal setae, dark fringes on the calypters and entirely black legs. They can all show variation in the number of setae or setulae on the proepimeron, the presence and number of setulae on the orbital plates and scutellar disc and in the density and length of eye hairs: all features which can make species-level identification difficult.

The group was reviewed by MacGowan (2014), who used the characters of the male terminalia, in particular the number and distribution of setae on the inner surface of the surstylus, to confirm species identification. This paper also provided a key to the five Palearctic members of the group, two of which, *Lonchaea fraxina* MacGowan & Rotheray, 2000 and *Lonchaea iona* MacGowan, 2001, were known from the British Isles at that time.

Lonchaea angelina is one of the smallest of the Palearctic Lonchaea species with a wing length of approximately 2.8mm. Its small size, densely long-haired eyes and relatively pale wings give an initial indication of its identity but examination of the male terminalia is essential for confirmation. The key feature is the linear row of 5-6 strong, ventrally-directed setae on the inner surface of the surstylus (Fig. 2). In the Handbook to British Lonchaeidae this species would key out to L. iona but use of the more detailed key to the species group, mentioned previously, is recommended.

The addition of a third species, *L. angelina*, to the British list has come as something of a surprise as it was only previously known from two male specimens, the holotype taken in Sweden in May 2005 as part of the Swedish Malaise trap project and the paratype, also taken by a Malaise trap in May 2005 in Greece. With so few records it is difficult to say much about the biology of the species. The Swedish specimen came from old mixed deciduous forest in a stream ravine. Only one member of the species-group has been reared, *L. fraxina*, whose larvae have been found under the bark of decaying ash *Fraxinus excelsior*, and it is most likely that *L. angelina* is also saproxylic and associated with ash or similar tree species, such as aspen *Populus tremula*, with a relatively thick sub-cortical layer.

**Record. Highland:** Inverroy, NN255818, Malaise trap, 1-4.v.2020, 1∂, leg. I. Strachan.

The addition of these two species to the British fauna of Lonchaeidae brings the total number to 51 species in 5 genera: *Dasiops* Rondani, 1856, 9 species; *Protearomyia* McAlpine, 1962, 3 species; *Earomyia* Zetterstedt, 1842, 4 species; *Lonchaea* Fallén, 1820, 34 species and *Silba* Macquart, 1851, 1 species.

# Other notable Scottish records

# Lonchaea deutschi Zetterstedt, 1837.

First identified as British in 2020 from specimens taken by sweeping birch (*Betula* spp) in Fungarth Wood, Perthshire (MacGowan 2020). We can now record this species from a second British site in the Caledonian pinewoods of Glen Mallie on the shores of Loch Arkaig, Inverness-shire. This is also a woodland where birch is common and indicates a strong association of this species with birch woodland. The locality of this site in the north-west Highlands would also tend to indicate that this species could be widespread in the Highlands.

**Record. Highland:** Lochaber, Arkaig Pinewoods, Glen Mallie, NN128876, Malaise Trap, 21.v-10.vi.2018,  $1 \stackrel{\circ}{\circ} 5 \stackrel{\circ}{\ominus}$ , leg. I. Strachan.

# Lonchaea ultima Collin, 1953.

This species was listed as occurring in southern counties of England by MacGowan and Rotheray (2008) with more recent records on the NBN Atlas from the Shrewsbury area and mid-Wales. This record represents the first for Scotland and a considerable northern extension of its known British range.

**Record.** Perth & Kinross: Fungarth Wood (NO0442) near Dunkeld, 15.v.2020,  $13^{\circ}$ , by sweeping birch, leg. I. MacGowan.

#### Acknowledgements

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# Recent records of *Minilimosina secundaria* (Duda) (Diptera, Sphaeroceridae) from Berkshire

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#### Summary

The first British record of *Minilimosina secundaria* (Duda, 1918), an extremely rare sphaerocerid, was of a single female specimen caught over a hundred years ago in a wood in Cambridgeshire (Richards 1930), and the species was provisionally classed as extinct in the British Isles (Falk *et al.* 2016). It is therefore of interest to report two recent new British records of this species: a female was identified in 2017 from a 1993 sample collected in Windsor Forest and another female was collected last year (2020) from Besselsleigh Wood; both woodlands are situated in Vice County Berkshire (V.C. 22). In light of these new records *M. secundaria* status has changed from presumed Extinct to Data Deficient.

# Introduction

A single female specimen of *Minilimosina* (*Allolimosina*) secundaria (Duda, 1918) was swept from vegetation in Besselsleigh Wood, Berkshire (Grid Reference: SP450014) on 2 June 2020 by RM. The specimen was identified by DB from mixed sphaerocerid material stored in 70% ethanol. There was only one previous record of this species from Britain, a single female from Woodditton Wood, Cambridgeshire, collected by J.E. Collin on 23 May 1909 (Richards 1930). Due to the lack of further data on this species in Britain, it was provisionally classed as Extinct by Falk *et al.* (2016). Since the publication of this report a male specimen of *M. secundaria* was identified by Paul Gatt in 2017 from a Malaise trap sample for the period 16-27 July 1992 at Windsor Forest, Berkshire, in the South Forest area (Grid reference: SU945705); the trap was operated by Keith Porter in open dry deciduous woodland (Chandler *in prep.*). Currently there are European records from the Czech Republic (Roháček 2005), Germany (Duda 1918), Great Britain (Richards 1930), Hungary (Papp 1976, 1990), Lithuania (Dumčius and Pakalniškis 2006), Spain (Carles-Tolrá 1990) and Sweden (Florén 1989), all of which are listed in Marshall *et al.* (2011). The specimen recorded by RM is temporarily retained and stored in DB's personal collection and that from Windsor is in Paul Gatt's collection.

# Ecology

There is little information available on the ecology of *Minilimosina secundaria*. The type specimen, a female, was caught on a window in Germany (Duda 1918). The second record of this species, also a female, was from a soil trap in a boggy meadow in Hungary (Papp 1976). Roháček (1993) examined females from Hungary, which were collected in a valley of a brook and on a refuse heap and thought that the species was mostly polysaprophagous. Six males and eight females were taken on human excrement in Spain by Carles-Tolrá in 1984, who in the same paper described the male for the first time and figured the male genitalia (Carles-Tolrá 1990). Swedish records of two males were from a window and from a wet pasture and a potato field (Florén 1989, Roháček 1993). The three male records in the Czech Republic were collected by Malaise Traps (23) and a Car-net (13) in warm deciduous forests (Roháček *et al.* 2005); this habitat is similar to the recent British records of *M. secundaria*. Currently all three British records are from woodland sites in southern England; however, due to the paucity of records, both in Britain and in mainland Europe, the distribution and biology of this species is still very poorly

known. The habitat at Besselsleigh Wood is a small area of semi-ancient woodland (10 hectares) with two distinct areas: oak and hazel woodland on the northern slope with sycamore, birch and wild cherry – this area has open rides (Fig. 1), and marshy areas present at the base of the slope with old alder and crack willow coppice (Fig. 2). The southern part of the wood is predominantly sycamore and less sloping with a replanted mix of native species; the understorey is dominated by bluebells, with very few other species present. Dead wood, in various stages of decomposition, is a prominent feature throughout the site (Fig. 3). The 1992 male record from Windsor Forest seems to share some similar characteristics in its habitat to Besselsleigh Wood.



Figs 1-3, Besselsleigh Wood: 1, open glade; 2, streams and marshy areas; 3 dead wood debris (photos RM).

# Identification

The Besselsleigh specimen was identified by DB using the keys, description and illustrations for the female in Roháček (1983) and Pitkin (1988). Male identifications should be confirmed after comparing the genitalia with figures provided by Carles-Tolrá (1990), redescribed and refigured by Roháček (1993).

# **Conservation status**

This recent record of *M. secundaria* at Besselsleigh Wood and the 1992 record from Windsor Forest change the status of this species from Extinct and in any future status review it would be designated as Data Deficient.

# Acknowledgements

Both authors are grateful to Peter Chandler for very kindly making available to us the unpublished record of this species from Windsor Forest for inclusion here. We also thank Paul Gatt and Jindřich Roháček for their helpful review and comments on this paper.

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Aphaniosoma melitense Ebejer (Diptera, Chyromyidae) in Essex and some recent records of A. socium Collin – On 23 June 2020, I swept numerous specimens of both sexes of Aphaniosoma melitense Ebejer, 1993 at Walton-on-Naze, Essex (TM263247). They were restricted to a small area of bare ground between patches of Juncus gerardii at the edge of what had been a brackish pool. Sometime in the recent past the area had been inundated by the sea, which had resulted in the death of some of the vegetation, with Bolboschoenus maritimus being particularly badly affected. I had visited the site several times in the past and was shocked to see the changes that had taken place, although *A. melitense*, which I think must be a recent arrival there, may have benefited from this in some way. When I visited the site again on 11 July 2020, *A. melitense* was still present in the same restricted area, although in much reduced numbers. At Dingle Marshes (TL480714) on the Suffolk Coast on 20 June and 17 July 2020, I swept single females of what appeared to be *A. melitense*, although the capture of a male would be necessary to confirm its presence there. They were associated with sparsely vegetated shingle behind the shingle ridge and here again there had been some recent breaches of the sea defences, although with no obvious damage to the vegetation.

Aphaniosoma melitense was first recorded in Britain in 1999, when it was swept from mown grass adjacent to a brackish canal at Queenborough Lines, Sheppey, Kent (Ismay, J.W. and Clemons, L. 2001. A third British Species of Aphaniosoma Becker (Dipt. Chyromyidae). Entomologist's Monthly Magazine 137, 211-214). Further specimens from North Kent were taken at Barton's Point Coastal Park (TQ92857435), Sheerness on 13 June 2002 (Clemons, L. 2003. Retrospect of a Kent Dipterist, 2002. Bulletin of the Kent Field Club 48, 94-104), Rushenden Marshes (TQ903711), Queenborough on 9 July 2012 (Clemons, L. 2013. Kent Diptera 2012. Bulletin of the Kent Field Club 58, 117-135) and Brett's Gravel Workings (TR011628), Oare on 6 August 2013 (Clemons, L. 2014. Kent Diptera 2013 Bulletin of the Kent Field Club 59, 100-112). The respective site descriptions were a grassy bank bordering Queenborough Lines, pulverised ash infill with brackish pools and a sandy track with Phragmites.

It is quite a coincidence that *A. melitense* should be found at Walton, as it is the locality from which *A. socium* Collin, 1949 was described (Collin, J.E. 1949. On the Palaearctic species of the genus *Aphaniosoma. Annals & Magazine of Natural History* (12)**2**, 127-147). J.E. Collin found both sexes in the flowers of *Convolvulus* in 1912 and gave the locality as Frinton-on-Sea, although the specimens are labelled Walton-on-Naze (Pont, A.C. 1995. *The type material of Diptera (Insecta) described by G.H. Verrall and J.E. Collin.* Clarendon Press, Oxford. 233 pp) and Walton is given as the locality in an earlier paper (Collin, J.E. 1913. Thirty additions to the list of British Diptera. *Entomologist's Monthly Magazine* **49**, 130-135) when *A. socium* was mistaken for *A. approximatum.* I, too, found *A. socium* at Walton when, on 10 July 2010, one female was found close to where *A. melitense* occurred and males and females were found associated with soft cliff seepages a little to the south (at TL267238). The habitat was similar at Hordle Cliff, Hampshire (SZ265922) on 22 June 2015, when some major slumping had left large areas of bare, wet clay and *A. socium* was found to be numerous there. Indeed, apart from a few Ephydridae, in that situation it was the only dipteran present.

The biology of *Aphaniosoma* is poorly known, although a species was reared from a mouse nest in Spain (Ebejer, M.J. and Deeming, J.C. 1997. Chyromyidae. (Diptera, Schizophora) new to Spain with descriptions of the adult and puparium of a new species of *Aphaniosoma*. *Entomologist's Monthly Magazine* **133**, 157-160) and three species were reared from loose soil at the base of low-growing dense vegetation (mainly *Phragmites* and *Salicornia*) at Salina salt marsh in Malta (Ebejer, M.J. 1996. Chyromyidae (Diptera: Schizophora) from the Arabian Peninsula with descriptions of twelve new species. *Fauna of Saudi Arabia* **15**, 280-299.). A few puparia were subsequently found in the latter location; these are minute and covered with debris, which renders them very inconspicuous (Martin Ebejer *pers. comm.*). Martin's experience of this genus is for adults to have usually been collected in marshy and sandy localities, often in the vicinity of reeds and tamarisk trees. Apart from the flowers of tamarisk, he has also collected them from the flowers of *Salicornia, Euphorbia* and *Foeniculum*.

If these habitats and development sites are typical of the genus it is somewhat at odds with my own limited experience, which suggests that the adults at least, are very much associated with bare ground and early successional habitats – **IVAN PERRY**, 27 Mill Road, Lode, Cambridge, CB25 9EN

# The biting midge *Forcipomyia tenuis* (Winnertz) (Diptera, Ceratopogonidae) new to Britain

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#### Summary

Forcipomyia tenuis (Winnertz, 1852) is added to the British checklist, based on specimens collected in Worcestershire and north Devon.

#### Introduction

There are 28 species of the genus *Forcipomyia* recorded from the British Isles (Chandler 2021) The subgenus Forcipomvia (s.s.) has 13 species, all of which are in nine subgenera. predominantly brown or black. Adults of both sexes of this subgenus are distinguished by the following characters: a nipple at the end of the terminal antennal segment; sensilla coeloconica absent on the first flagellomere; legs with long empodia; and males have symmetrical parameres and the tibiae lack lanceolate scales (definition from Navai and Szadziewski 2016). Within this subgenus, three previously recorded British species have long slender parameres (= submedian process of some authors) which are broad basally but filiform in the distal half. The parametes appear to be 'free' at the base but are in fact attached by a very lightly sclerotised band, articulating with the coxite apodeme. They are: F. bipunctata (Linnaeus), F. pulchrithorax (Edwards) and F. squamigera Kieffer (Szadziewski et al. 2007). This lightly sclerotised band at the base of the parameters is very difficult to see in some preparations and therefore can give misleading results when using Alwin and Szadziewski's (2013) key to subgenera (couplet 8, p. 125) or Navai and Szadziewski (2016, couplet 7, p. 92). The common British species Forcipomyia (s.s.) ciliata is included in this slender parameter group by Szadziewski et al. (2007) but is easily distinguishable in the male by the broadly joined base of the parametes.

Here we record a further species of this group, *Forcipomyia tenuis* (Winnertz, 1852), based on material collected in recent years. It has not been recorded previously in the British Isles. Walker (1856: 213) gave a description of this species as '*Ceratopogon tenuis*', based on Winnertz' monograph, but this was on the assumption that it might occur in Britain as he had not seen any material (on p. 209 he stated "I have not been able to ascertain clearly that all the species here described are British insects; but it is most probable that they will be proved to be so"). Edwards (1926) evidently excluded it from consideration as a British species on that basis, no British material being available to him.

#### **Occurrence in Worcestershire**

On 15 June 2018, a fogging operation was carried out on a yew tree in the Wyre Forest. The experiment was carried out by Alice James (Natural England) in collaboration with the Forestry Commission, and the Wyre Forest Study Group. The yew tree was growing near the edge of the old railway track and opposite the Great Bog of Wyre at SO748764. It appeared to be a healthy tree with a tight, dense canopy, isolated from other yew trees but surrounded by oaks. The Diptera were referred to MB for identification. The catch contained extremely large numbers of biting midges (Ceratopogonidae), comprising a number of species and forming numerically the largest group amongst the Diptera in the sample. The first specimen removed from the sample bore a

close resemblance to *Forcipomyia tenuis* in Remm (1962) and this identification was kindly confirmed by Ryszard Szadziewski.

MB had been encountering this species over several years (without previously confirming the identification), so it is probably not rare in Worcestershire. The following records result from the examination of stored photographs:

4 April 2012. SO933665. Upton Warren Flash Pools near Droitwich, Worcestershire. Two male specimens taken from a Malaise trap set near the edge of one of the brine pools in a patch of rather tall lush grass surrounded by reeds and bushes.

18 April 2018. SO771763. Wyre Forest; the newly established Helen Mackaness nature reserve of the Worcestershire Wildlife Trust. One male netted from about ripe *Salix* catkins. It was accompanied by *F. sphagnophila* Kieffer, 1925 which seems to be the most abundant *Forcipomyia* in the Wyre Forest, especially in the spring and autumn.

#### **Occurrence in Devon**

As part of a long-term sampling programme at a site in north-western Devon, Robert Wolton sent a collection of 'midges' to RPL for identification. Flies were collected using a Malaise trap near a pond at Locks Park Farm, Hatherleigh, Devon [SS51670238, Lat 50° 48' 07" N, Long 004° 06' 23" W] in two periods: 6.iv-17.vi.2020 and 21.vi-14.vii.2020. The general habitat is acid grassland on heavy clay soils with adjacent woodlands (see Wolton *et al.* 2014 for a general description of the locality). It is within the North Devon UNESCO Biosphere reserve. Midges were stored in 70% ethanol before being slide-mounted in Euparal. Midges were initially identified using an unpublished key by John Boorman and Alwin and Szadziewski (2013) for subgenera and subsequently using literature from continental Europe, particularly Remm (1962). Two males of *Forcipomyia tenuis* were identified, one in each of the collection periods. Patrycja Dominiak verified the identification and sent illustrations to Ryszard Szadziewski for further confirmation. Subsequently, four males were identified from Devon: Tiverton, Cowleymoor, (SS965135), collected by Andrew Cunningham on 1.iv.2020, by sweeping in a suburban garden.

a b b

Fig. 1. Male genitalia of *Forcipomyia tenuis*: (a) ventral view of genitalia showing shield shaped aedeagus; (b) detail of parameres, arrow indicating spiral sculpturing characteristic of this species.

# Identification

*Forcipomyia tenuis* Winnertz has a wing length 1.8 to 2 mm. The body is blackish, with all body hairs long and black, giving a shaggy appearance. The third palp segment is slender. The leg hairs are very long. Tarsi are paler; the tarsal ratio is 1.0. The wings are hyaline with no yellow costal spot over the second radial cell and no yellow at the wing base. There is a white spot on the tip of the halteres. It is easily distinguished from other Palaearctic species of *Forcipomyia* (*s.s.*) with long slender parameres by a very characteristic 'spiral' effect mid-way along the parameres (Fig. 1b). The aedeagus is shield-shaped with a strong central longitudinal ridge and two less sclerotised parallel ridges either side of the central ridge (Fig. 1a) – these are faintly marked in Remm's (1961) figure but are distinct in the Devon specimens.

*Forcipomyia tenuis* occurs widely in continental Europe: France, The Netherlands, Germany, Hungary, Estonia, Lithuania and Poland (Borkent *et al.* 2013) and Finland (Stur and Borkent 2014).

#### Acknowledgements

MB wishes to express his gratitude to Alice James for permitting him to examine the results of her experiment. RPL would like to thank Rob Wolton for kindly sending him the samples and details of the Devon site. We are grateful to John Boorman for use of his unpublished key, and Patrycja Dominiak (Tromsø University Museum) and Professor Ryszard Szadziewski (Gdansk University, Poland) for confirming our identifications. We would also like to thank Peter Chandler for integrating our two original papers.

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# The enigmatic head of the cyclorrhaphan larva (Diptera, Cyclorrhapha)

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#### Summary

The most diversified part of a Diptera larva is the head and it reaches a peak of disparity in the Cyclorrhapha (Diptera). So much so that the cyclorrhaphan larval head has proved contentious and difficult to resolve, i.e. working out the origins and relationships of its component structures. Only recently has progress been made to breach this longstanding barrier. In this brief review, some of these developments are outlined in order to help others recognise structures and directions of change and, thereby, encourage investigation and analysis of this key component.

#### Introduction

The dipteran larval head is important for perception, feeding, locomotion, defence, etc. Understanding it is pivotal to understanding these functions and explaining how larvae live. The larval head is also a source of morphological diversity and may play a significant role in divergence (Rohdendorf 1974, Schneeberg and Beutel 2014, Rotheray 2019a).

In the case of the Cyclorrhapha (Diptera), the larval head has, unfortunately, proved contentious and difficult to resolve. This is due to its disparity relative to the heads of other dipteran larvae and confusion about it has persisted for more than a hundred years (Keilin 1915, Snodgrass 1953, Teskey 1981, Sinclair 1992, Courtney *et al.* 2000, Rotheray 2019a). Specifically, the disparity of the cyclorrhaphan larval head makes it difficult to work out the origins and relationships, i.e. the homology, of its component structures and what nomenclature to apply. For instance, Ludwig (1949) viewed the pair of hook-shaped mandible equivalents at the front of the head as mandibular in origin, but Cook (1949) considered that they also contained maxillary elements. Snodgrass (1953) thought that this paired structure was an innovation while Menees (1962) and Matsuda (1965) argued it came solely from the maxilla. Modern developmental studies support a maxillary origin and morphological studies a mandibular one. In an attempt to accommodate the conflict, Courtney *et al.* (2000) raised the possibility that the base is derived from the mandible and the apical hook from the maxilla.

Faced with uncertainties such as these, a convention often adopted is to use terms that make no reference to origins or homology. In the case of the mandible equivalent, a term that indicates location and shape yet avoids any hint of origin or homology, is 'mouthhook' (Headrick and Goeden 1996). Lack of homologies that enable head structures to be recognised, named and compared is a significant barrier to progressing understanding of cyclorrhaphan larvae (Hartley 1963, Teskey 1981, Headrick and Goeden 1996, Courtney *et al.* 2000).

Relatively few lower cyclorrhaphans (= Aschiza) have been included in analyses of larval heads and Hartley (1963) and Courtney *et al.* (2000) suggested that a solution to the problem of names and homologies might be found here. Recent assessments of lower cyclorrhaphan larvae within the Lonchopteridae, Platypezidae, Phoridae, Pipunculidae and Syrphidae, support this suggestion (Sinclair 1992, Rotheray and Gilbert 2008, Rotheray and Lyszkowski 2015).

In this brief review, some of these developments and directions of change in the cyclorrhaphan larval head are outlined. The aim is to encourage others to better understand, and investigate this pivotal component and more broadly, to motivate studies of cyclorrhaphan larvae. This paper links with others towards these ends that include an assessment of techniques for

finding larvae in the field (Rotheray 2016a) and evaluation of a promising assessment method that combines morphology with movement (Rotheray 2020).

# Head partitioning

Among Diptera, a tendency exists for the larval head to reduce, desclerotise and invert into the body and among others, Teskey (1981), Sinclair (1992), Courtney *et al.* (2000) and Schneeberg and Beutel (2014) evaluated these widely referenced traits that are particularly developed in the Cyclorrhapha. Consequently, a marked contrast exists between the conspicuous, hard, sclerotised, brown to black, caterpillar-like heads of many nematoceran larvae and the small, inconspicuous, soft, translucent heads of cyclorrhaphans (Fig. 1).



Fig. 1. *Palloptera anderssoni* Rotheray & MacGowan (Pallopteridae), saprophage, preserved, third stage larva; lateral view of head and front of thorax; length about 1.5mm: a = antenna; hs = head skeleton; mp = maxillary palpus; ms = mesothorax; pr = prothorax; ps = pseudocephalon; t = trachea terminating at the anterior spiracle.

Brauns (1954) referred to the nematoceran larval head as the eucephalic state, the cyclorrhaphan as acephalic, and the intermediate, part-sclerotised, part-fleshy head typical of lower brachycerans, as the hemicephalic. Several workers, Courtney *et al.* (2000) included, point out that 'acephalic' is unfortunate in its literal meaning of lacking a head. Campos-Ortega and

Hartenstein (1997) suggest the alternative term, 'cryptocephalic', meaning hidden head, but this is not the contrast Brauns (1954) intended. He was drawing attention to levels of incompleteness in external heads evidenced by reduced sclerotisation and for cyclorrhaphans, a term that alludes to this is 'laevicephalic', from the Latin 'laevis' meaning soft or lightweight (Rotheray 2019a).

These terms are not often used and for cyclorrhaphan larvae, there is a significant but little referenced feature, a partitioned head (Rotheray 2019a). Head partitioning or decoupling between the overlying cranium and its internal tentorial apparatus, the system of sclerotised apodemes, struts and associated feeding structures, does not occur, or not to the same extent, in other Diptera larvae. The external, fleshy part is termed the pseudocephalon after Henneguy (1904) and the internal mostly sclerotised one, is the cephaloskeleton or head skeleton (Fig. 1) (Courtney *et al.* 2000). Although partitioned, the two sections are not entirely separate and understanding their connections is crucial to resolving the origins and functions of the head.

In most Cyclorrhapha a marked discrepancy in size exists between the two partitions. The head skeleton is about three times as long as the pseudocephalon and reaches into the thorax as far as the mesothorax and sometimes beyond (Fig. 1). Furthermore, and except for the Lonchopteridae, the head skeleton can move independently of the pseudocephalon. Substantial differences in size, sclerotisation and mobility between the two partitions are evidence of major functional re-organisation. Sclerotisation and size are means of optimising chitinous structures relative to mechanical demand, i.e. the capacity to withstand force or pressure. Mechanical demand in the head skeleton is high, due primarily to supporting musculature and low in the pseudocephalon, due to supporting flexibility.

# Pseudocephalon

Connections between the pseudocephalon and the head skeleton mean that the fleshiness of the former is important for movement in the latter. This is because, as the head skeleton moves, the pseudocephalon folds and unfolds or expands and contracts with body fluids. Hence, its size and flexibility both facilitate and limit head skeleton movement. Another potential limit is the gut which is attached to the head skeleton and to the body wall, certainly at the anus and also to tissues and organs at various points along its length. Moreover, the gut fills with food, wastes and may have membranes within it. Despite this, the gut flexes to accommodate head skeleton movement and observations show that it is the foregut that does this. The foregut is longer than the distance between the head skeleton and the midgut, and in time with a moving head skeleton it folds and unfolds. This can be observed directly due to the translucency of larval bodies, particularly in first, second and early third stages that have not built up obscuring levels of fat or, in larvae that are starved and have used up fat reserves (Rotheray 2019a).

The major sense organs of the larva, the antenna and the maxillary palpus, are on the dorsum of the pseudocephalon (Fig. 1), and at the apex or on the underside is a pouch or pocket, the preoral or oral cavity, at the back of which is the mouth (Fig. 2). Postero-ventrally, the pseudocephalon is usually concealed within a deep fold at the boundary with the prothorax and a similar fold exists between the prothorax and mesothorax. These confer a downwards orientation to the head and thorax and if they unfold during feeding or locomotion and expose the full length of the pseudocephalon, they do so for brief moments only. In preserved larvae these folds are invariably retained, which complicates examination. The pseudocephalon can be revealed by excising the anterior end of a preserved larva and placing it for several minutes in potassium hydroxide solution. After which, with the aid of pins and forceps, obscuring tissue and fat can be removed to reveal the full extent of the pseudocephalon or it can be pulled out with forceps.

The pseudocephalon not only facilitates head skeleton movement and food gathering, it may have played a role in the development of the puparium. Puparia are not unique to the Cyclorrhapha, but they are scarce in other Diptera, for instance, among the lower Brachycera they

are present in the Stratiomyidae (Stubbs and Drake 2001). Dense media characterise Diptera development sites (Schneeberg and Beutel 2014), and within them soft, naked pupae risk being compressed or crushed. Naked pupae are capable of wriggling, which provides a means of escape. Inside a puparium, however, pupal wriggling is constrained. Probably for physical protection, cyclorrhaphan and stratiomyid puparia are rigid compared to naked pupae. In the cyclorrhaphan puparium rigidity is enhanced by contraction of the head and anal ends via segments folding up and corrugating. During these processes, the rigid head skeleton retracts out of the way and with it, the pseudocephalon and prothorax invert into the puparium as far as the anterior spiracles. Inversion ends at the anterior spiracles because the pupa depends on these spiracles for respiration (Keilin 1944, Roddy 1953). Facilitated by a fleshy pseudocephalon, inversion distinguishes the cyclorrhaphan puparium from those of other Diptera (Rotheray 2019a).



Fig. 2. *Coelopa frigida* (Fabricius) (Coelopidae), saprophage, preserved, third stage larva; underside of the pseudocephalon; length about 1.5mm: is = intermediate sclerite; la = labial apparatus (faint); m = scalloped mandible hook with apex outside its sheath; oc = oral cavity with sides sculptured with cirri posteriorly and fringed scales anteriorly (= facial mask); pr = prothorax; ps = pseudocephalon; v = ventral bridge of intermediate sclerite.

Nonetheless, puparial rigidity varies across the Cyclorrhapha and some puparia may be tolerant of denting or flattening. For instance, Hartley (1961) mentioned that the puparium of the syrphid *Parhelophilus versicolor* (Fabricius) (Diptera, Syrphidae), is invariably flattened in the narrow space the aquatic larva of this species tends to use for pupariation; tight-fitting leaf bases of *Typha* plants. Rotheray and Hewitt (2015) found that puparia of *Palloptera scutellata* 

(Macquart) (Diptera, Pallopteridae) are often dented. Compared to puparia of congenerics, that of *P. scutellata* is thin and, typically, several larvae occupy an individual development site, *Juncus* stem bases. A deformable puparium is probably a modification in this species enabling them to tolerate being squashed as teneral adults squeeze past to reach an escape hole at the apex of the hollowed out stem.

The pseudocephalon is often overlooked. This might be due to investigators tending to work within the limits of one or a small set of closely related families where variability and contrasts may not be obvious. For such a large and diverse lineage as the Cyclorrhapha taxon-specific working is understandable although to improve recognition of shared and contrasting features, identify errors and shortfalls and inform directions of research, wider taxon comparisons are helpful (Rotheray 2019a). In summary, the small size and fleshiness of the pseudocephalon belies its significance and it deserves better appreciation and study.

#### Significant components

#### 1. Antennomaxillary organs

On the antero-dorsal margin of the pseudocephalon in larvae of the Eumuscomorpha (Syrphidae + Pipunculidae + higher Cyclorrhapha (= Schizophora)) are two pairs of approximated sensory organs (Fig. 1). Working out their sensory roles has been less controversial than determining their origins. The more dorsal pair includes olfactory receptors and the ventral pair, contact chemoreceptors; both are involved in finding and recognising food (Cobb 1999).

The difficulty over whether these structures are homologous with the antenna and maxillary palpus of lower brachycerans and empidoids is because in these taxa these organs are on different structures, the cranium and maxilla respectively (Roberts 1969, Teskey 1981, Sinclair 1992). Furthermore, developmental studies suggest that in higher cyclorrhaphan larvae these sensory structures are mixed. Under these circumstances, the term 'antennomaxillary organs' seems a reasonable compromise (Courtney *et al.* 2000). Nonetheless, uncertain origins means that authors often stipulate ad hoc terminology, for instance, Oppliger *et al.* (2000) refer to these sensory structures as the dorsal and terminal organs.

Lower cyclorrhaphan morphology indicates, however, that the origin of the dorsal organ is indeed the outgroup antenna and the terminal one is the outgroup maxillary palpus (Rotheray and Gilbert 2008). In basal lower cyclorrhaphan taxa, such as the Lonchopteridae and Platypezoidea, the antenna and maxillary palpus are not approximated at the apex of the pseudocephalon, but are separate and similar in shape and relative position to those of empidoids. These similarities not only indicate origins for these sensory structures, they provide morphological evidence that the pseudocephalon is a composite structure comprising some or all of a desclerotised cranium and part of the maxilla, a result supported by developmental studies (Campos-Ortega and Hartenstein 1997). Adjacency of the antenna and maxillary palpus in eumuscomorphans probably explains the developmental results (Courtney *et al.* 2000). Hence, evidence from lower cyclorrhaphans suggests that the compromise term, 'antennomaxillary organs' is unnecessary and at best, refers only to the Eumuscomorpha.

The significance of an approximated antenna and maxillary palpus is presumably improved perceptual efficiency. If, as indicated, the basal eumuscomorphan feeding mode was predation and involved prey searching, such an improvement is understandable (Rotheray 2019a).

#### 2. Oral cavity

The cyclorrhaphan oral cavity is more diverse than generally recognised. It is a trough in lonchopterid larvae which correlates to a forward-scooping, food-gathering action (video in supplemental material of Rotheray and Lyszkowski 2015). In Platypezoidea (Platypezidae + Phoridae + allied families) it is an apical to apico-ventral opening that forms temporarily during

feeding. These larvae place the pseudocephalon against or into food and when the head skeleton retracts, a cavity is created into which food is gathered (Rotheray and Lyszkowski 2015). In most Eumuscomorpha the oral cavity is a fixed structure on the underside of the pseudocephalon (Fig. 5), and in the higher Cyclorrhapha, it is mechanically supported by the mandibles which are ensheathed by it (Fig. 2).

The oral cavity is often overlooked in morphological studies in favour of the varied and complex sculpturing of the sides and front of the oral cavity (Figs 2 & 5), the facial mask of Nye (1959), and enumeration of individual sensory structures embedded in it. Examples include Nye's (1959) study of grass-developing larvae, Meier's (1995) assessment of Sepsidae, Dempewolf's (2001) assessment of Agromyzidae and the many publications on Tephritidae from D.H. Headrick and R.D. Goeden and co-workers, see Headrick and Goeden (1986). Generalising about the nature of such fine details is difficult due to the relatively few larvae that have been examined. Their functional roles are also poorly understood although major ones are probably protection from abrasion and tactile sensitivity, while others might include specialised roles in food gathering. For example, observations of feeding in larvae of the seaweed fly *Coelopa frigida* (Fabricius) (Coelopidae), suggest that the unusual fringed scales at the front of the oral cavity function in a brush-like manner and sweep food into it (author, unpublished observations) (Fig. 2).

For poorly understood organisms, such as cyclorrhaphan larvae, observing live feeding is a neglected, but informative assessment technique (Rotheray 2020). For instance, observations and videos of feeding show that low demand, watery or soft food correlates to large, fleshy-lipped oral cavities and high demand, firm or hard food to smaller, thin-lipped oral cavities (Rotheray 2019a). These two types are most frequent among saprophagous and phytophagous larvae respectively. Specialised food-gathering functions are associated with accessory sclerites, for instance the front margin of the oral cavity in certain Calliphoridae possesses sclerites that help isolate portions of semi-solid food (Rotheray 2020).

#### Head skeleton

The head skeleton has several roles of which a major one is feeding. To feed, most cyclorrhaphan larvae use their mandibles or equivalent to gather food into the oral cavity, at the back of which is the mouth from where a pump sucks it through to the gut. The pump operates when not feeding and material is probably pumped in and out of the head skeleton more or less continuously. Based on sensilla in and around the mouth and probably, sensory neurons embedded into the body wall, this is another way that larvae assess their surroundings. The head skeleton can also assist in locomotion by anchoring the head during peristalsis using the mandibles, saliva or suction from the pump, and a larva can defend itself by striking with its mandibles and/or emitting saliva.

Variability in the size, shape and sclerotisation of head skeletons correlates to mechanical demand. For instance, small size and low sclerotisation correlate to feeding on low demand food, i.e. pumps of low power with little need for buttressing or strengthening by sclerotisation (Rotheray and Lyszkowski 2015). An example is the saproxylic larva of the Clusiidae which lacks sclerotisation in the head skeleton and sucks up watery suspensions of microbes lining and saturated into decay-softened dead wood (Rotheray and Horsfield 2013). Macrolarviparous larvae, such as those of the Hippoboscidae, develop inside the female body and feed on secretions from 'milk glands' or modified accessory glands (Ferrar 1987). Any food-gathering challenges they face are probably minimal and explain the fragile state of their head skeletons.

The higher cyclorrhaphan head skeleton comprises three sections, the borders of which are most clear in saprophagous larvae. The rearmost is the large, U- to V-shaped basal sclerite, followed by the smaller, tubular intermediate sclerite and at the front, the mandibles (Fig. 3) (Ferrar 1987, Courtney *et al.* 2000). The lower cyclorrhaphan head skeleton differs in having a

short intermediate sclerite and except for the Syrphidae and Pipunculidae, the mandibles are more or less equidistant with the labrum (upper lip) and labium (lower lip) (Rotheray and Gilbert 2008).



Fig. 3. *Silba fumosa* (Egger) (Lonchaeidae), saprophage, head skeleton extracted from puparium with torn remnant of pseudocephalon (ps); lateral view; length about 1.5mm; rear sclerite on the left is the basal sclerite (bs): dc = dorsal cornu; vc = ventral cornu; vp = vertical plate; middle sclerite is the intermediate sclerite (is): <math>p = parastomal bar; v = ventral bridge projecting below and linking the labial rods; front sclerite is the mandible (m): <math>b = mandible base; h = mandible hook.

Running along the floor of the head skeleton is a lightly sclerotised section of the gut, the cibarium-pharynx (Roberts 1971, Teskey 1981). Posteriorly, the cibarium-pharynx is continuous with the membranous foregut and, anteriorly, it ends, as it does in lower brachycerans and empidoids, just in front of the entry point of the salivary duct. In cyclorrhaphans this is more or less at the anterior edge of the basal sclerite. Beyond this point, the cyclorrhaphan cibarium-pharynx fuses with a tubular extension to the gut, the atrium of authors, which is chiefly a product of fusion and approximation between the labrum and the labium. The atrium is longer in higher than lower cyclorrhaphans and accounts for the greater development of the higher cyclorrhaphan intermediate sclerite (Teskey 1981, Rotheray 2019a).

Head skeletons are conveniently examined by extracting them from puparia. They are usually deposited sideways down on the lower, front edge of the puparium and are attached to it by the pseudocephalon which, if softened by immersion in potassium hydroxide solution, can be torn with pins to release the head skeleton (Fig. 3) (Rotheray 2019a). Head skeletons extracted from puparia are often out of symmetry because the upper side lies on top of the lower unevenly and the two sides are easy to confuse in the conventional lateral view. All-round views enable corrections and are obtained by immersing head skeletons in a watch glass or similar filled with liquid preservative and moving them with a pin. The high viscosity of materials, such as glycerol, are particularly helpful since head skeletons tend to remain in position rather than turning and sinking as occurs in watery preservatives (Rotheray 2019a).

Some parts of head skeletons are translucent and difficult to see unless head skeletons are moved round. For example, from the front of the basal sclerite and above the intermediate sclerite is a highly translucent, tapering structure that ends at the mandibles. Sinclair (1992) was the first to recognise this structure in lower cyclorrhaphan larvae as the labrum, a component whose fate

in cyclorrhaphan larvae was unclear since it seemed to be unrecognisable. By revolving head skeletons in preservative this inconspicuous structure can be seen and is present in higher cyclorrhaphans, although often depressed (Rotheray and Gilbert 2008, Rotheray 2019a). The underside of the labrum is the much more conspicuous, lightly-sclerotised, epipharyngeal plate which forms the roof of the atrium anterior to the salivary duct and has sense organs embedded in it (Roberts 1971, Courtney *et al.* 2000).



Fig. 4. *Eumerus* Meigen sp. (Syrphidae), head skeleton: phytophage/saprophage, dissected from preserved, third stage larva, about 2mm long; showing muscle bands (mb) between the cornua of the basal sclerite that operate the pump and at the end of the ventral cornu, is the upturn in the cibarial-pharynx with valve (v); specimen prepared by the late J.C. Hartley.

# Significant components

# 1. Basal sclerite

The basal sclerite is a composite structure that includes elements of the tentorial apparatus, the cibarium-pharynx and attached to it, often seamlessly, are the labrum, labium and maxillary sclerites (Teskey 1981, Roberts 1971, Rotheray 2019a). The sides of the basal sclerite are covered in bands of muscle that operate the pump. They attach to the roof of the cibarium-pharynx and the sclerotised arms of the basal sclerite, the dorsal and ventral cornua (Fig. 4). These muscles lift the roof of the cibarium-pharynx to create a partial vacuum which draws in food (Dowding 1967, Roberts 1971). With valves or sequenced relaxation along its length to prevent regurgitation, the roof lowers by natural elasticity and imbibed food is pushed through to the foregut. In the few examples where pumping has been measured it takes place at a rate of about

3-4 cycles/second (Rotheray and Lyszkowski 2015, Rotheray and Wilkinson 2015).

Dowding (1967) also discovered the role of what appears to be a groundplan or original feature of the cyclorrhaphan basal sclerite, ventral pharyngeal or cibarial ridges. Associated primarily with saprophagous larvae, a series of about nine parallel ridges run along the floor of the basal sclerite (cr in Fig. 5). In cross-section these ridges are T- or Y-shaped and their upper arms make a filter or sieve with gaps that allow liquids to pass through, but trap microbial food, such as bacteria, yeasts and algae. This occurs when the pump muscles relax and the roof of the cibarium-pharynx lowers. Critical to filtering is an upturn in the cibarium-pharynx and a valve at its end (Figs 4 & 5). These features help retain microbial suspensions over the ridges for filtering and help direct filtered liquids back out through the mouth. After several pumping cycles, the valve opens via retraction of attached muscles and a bolus of accumulated microbes passes into the foregut (video in supplemental material of Rotheray and Lyszkowski 2015).



Fig. 5. *Alipumilio femoratus* Shannon (Syrphidae), saprophage, preserved third stage larva, head skeleton in situ; length about 2mm: a = antennomaxillary organs; cr = cibarial ridges; m = mandible hook; oc = side of the oral cavity coated in cirri; v = upturn in the cibarium-pharynx leading to the valve.

Other muscles attach to the basal sclerite and include those that move the head skeleton. depress and elevate the mandibles and retract the labium etc. (Hartley 1963, Roberts 1971). Muscle attachment space and mechanical strength to support them is optimised by sclerotisation and the sheet-like form of the basal sclerite. Nonetheless, a diverse set of sizes, shapes and levels of sclerotisation exist and represent poorly investigated axes of variation, illustrations in Ferrar (1987). For instance, one axis occurring in saprophagous larvae is, relative to the dorsal cornu, loss of sclerotisation, length and upturn in the ventral cornu. These correlate to absent or vestigial cibarial filters and probably represent optimisations relative to reduced mechanical demand. Vestigial states occur, for example, in the calliphorid Calliphora vomitoria (Linnaeus) (Diptera, Calliphoridae), and absence in a growing list of saprophagous taxa, such as certain Camillidae, Chyromyiidae, Heleomyzidae, Lonchaeidae, Muscidae and Piophilidae (Rotheray 2016b). Cibarial ridges were thought to be an indicator of saprophagy, but the scale of these exceptions suggests otherwise. Their absence may be a secondary loss that enables faster feeding. It is also possible that even with cibarial ridges, larvae are able to exercise control over using them, for example, they could be by-passed by opening the valve during pumping (Ferrar 1979, Rotheray 2019a).



Fig. 6. Higher cyclorrhaphan head skeletons, not to scale, showing increasing levels of alignment and fusion between the front of the basal sclerite (bs) and the rear of the intermediate sclerite (is);  $p = parastomal bar: a = Lonchaea collini Hackman (Lonchaeidae), saprophage, no alignment or fusion; <math>b = Dasiops \ latifrons$  (Meigen) (Lonchaeidae), phytophage, some alignment and fusion;  $c = Loxocera \ sylvatica$  Meigen (Psilidae), phytophage, complete alignment and fusion.

#### 2. Intermediate sclerite

The intermediate sclerite connects to the basal sclerite and articulates with the mandibles. It is also a fusion product, chiefly between the labrum, the labium and the maxillary sclerite (= parastomal bar) (Teskey 1981, Rotheray 2019a). The most obvious components of the intermediate sclerite are the sclerotised labial rods that run along it. In dorsal and ventral views, they appear as paired structures with a cross bar, the ventral bridge, which gives the sclerite an alternative ad hoc name, the H-shaped sclerite (Fig. 2) (Ferrar 1987). The greater length of the higher than the lower cyclorrhaphan intermediate sclerite is due to the gut extension or atrium

which enhances pumping capacity by extending roof space for pump muscles and by forming a nozzle for accelerating flows of material (Rotheray 2019a).

An apparent gap is sometimes present between the basal and intermediate sclerites, but dissection shows that it is only a gap in sclerotisation. These sclerites are joined together and do not move independently of one another. In certain capitula-developing Tephritidae, however, the gap closes during feeding, presumably via pressure pushing the two sections together (Rotheray 2021).

The connection between the basal and intermediate sclerites differs in degree of fusion, i.e. how much the front of the basal sclerite and the rear of the intermediate are aligned and sclerotised (Fig. 6). Levels of fusion are associated with various axes of variation and probably others that have yet to be recognised. One is demand, in the direction that high demand correlates to high levels of fusion which helps buttress the head skeleton against the forces needed to gather hard food (Rotheray and Lyszkowski 2015, Rotheray 2020). Another is food occupying confined spaces, which appears to be associated with tube-shaped alignment. For instance, tube-shaped fusion occurs in predatory muscid larvae (Muscidae) and appears less to do with the ease or difficulty of imbibing food and more to do with reaching inside the confined space of prey bodies (Rotheray and Wilkinson 2015). Tubular alignment also occurs in the saproxylic larva of the milichiid, Neophyllomyza acyglossa (Villeneuve) (Milichiidae), which favours extracting liquid food from narrow cracks and crevices in dead wood (Rotheray 2020). Another influence is living space in the direction of confined living space correlates to foreshortened larvae. For instance, lack of space within hosts of endoparasitic larvae is probably an influence explaining the fused and relatively foreshortened basal and intermediate sclerites as occur in the Conopidae, Pipunculidae and Tachinidae, illustrations in Ferrar (1987).

#### 3. Mandible

The lower brachyceran mandible typically consists of two articulated sclerites, a base and a hook. The mandible of the Empidoidea, sister to the Cyclorrhapha, has up to six sclerites (Sinclair 1992). The cyclorrhaphan mandible is, however, a single sclerite, although a recognisable base and an apical hook are often apparent, suggesting fusion from a two sclerite state except that is, for the Lonchopteridae. In this taxon, the mandible is similar to that of lower brachycerans in having a base articulated with a hook (Rotheray and Gilbert 2008). Apart from a single sclerite the higher cyclorrhaphan mandible is unusual in its attachment points to the rest of the head skeleton, and is relatively isolated at the front of the head skeleton. These features and as noted in the introduction, developmental evidence that the mandible owes at least part of its origin to the maxilla have engendered confusion and controversy for over a 100 years.

Lower brachyceran and empidoid mandibles are closely associated with the maxilla, the mandibular-maxillary apparatus (Roberts 1969, Sinclair 1992). In empidoids this apparatus is a fleshy lobe attached to the cranium dorsally, the labium ventrally and anteriorly, to the mandible base but not the hook, which leaves the latter free (Sinclair 1992, Rotheray 2019a). It is supported by internal sclerites, has a maxillary palpus at its apex and the antenna near its base. Remarkably, these states are almost identical in lonchopterid larvae except that the maxillary lobes are relatively elongate and with an equally extensive labium, they form the sides and floor of a feeding trough (Rotheray and Gilbert 2008).

Further evidence of a mandibular-maxillary apparatus in lonchopterid larvae comes from movement analysis. Mirroring movement of the mandibular-maxillary apparatus in lower brachycerans (Roberts 1969), videos show that the mandibles and the maxillary lobes move together: the mandible base twists outwards, the hooks lift and the lobes turn inward (video in supplementary material in Rotheray and Lyszkowski 2015). In lonchopterids these coordinated movements appear due to connections within the mandibular-maxillary apparatus and initiated

by muscles that insert on to the mandible base. They help move food along the trough and guide it towards the mouth (Rotheray 2019a).

In platypezoids the mandibular-maxillary apparatus is also present and similar in connections and positions of antenna and maxillary palpus, but it differs in shape, is not as mobile and the mandible is a single sclerite. A single sclerite mandible may be an optimisation in response to high mechanical demand and/or a means of matching mandible size and shape to limited space due to the appearance of the tubular atrium (Rotheray 2019a). The two sides of the mandibular-maxillary apparatus are joined dorsally by a fleshy sheet. In eumuscomorphans these features are retained, except that the two sides of the mandibular-maxillary apparatus are approximated and as noted above, both antennae and maxillary palpi are adjacent to each other at the apex. In higher cyclorrhaphans the mandibular-maxillary apparatus is similar except that the mandibular-maxillary apparatus is similar exc

A soft pseudocephalon means that the outgroup articulation point between the mandible and the cranium is not possible in the Cyclorrhapha and the mandible articulates with the labial rods via an apodeme or extension. Lonchopterid and platypezoid mandibles are functionally simple, and often inconspicuous. During feeding they diverge from the base, to guide food towards the mouth in a movement reminiscent of a door opening. In eumuscomorphans the mandibles have greater ranges of movement and are more active in food gathering, which is indicated by relatively larger size and position at the apex of the head skeleton (Rotheray and Gilbert 2008, Rotheray and Lyszkowski 2015).

To summarise, lower cyclorrhaphan morphology suggests that a mandibular-maxillary apparatus is present in cyclorrhaphans and this is evidence that the cyclorrhaphan mandible is homologous with that of outgroups. Lower cyclorrhaphans also show that the unusual characteristics of the higher cyclorrhaphan mandible can be explained. Furthermore, Courtney *et al.* (2000) suggested that results from developmental studies indicating a maxillary origin for the mandible might be explained as misinterpretations or due to experimental difficulties involved in manipulating embryos.

In eumuscomorphans articulation between the intermediate sclerite and the mandibles is usually a hinge joint that allows the latter to raise and lower. This is possible due to elevator muscles that insert on the back of the mandible above the joint and depressor muscles that insert below it on the underside of the mandible base. Both sets of muscles originate on the ventral cornu of the basal sclerite (Roberts 1971). The hinge joint comprises a hollow or groove on each of the inflated apices of the paired labial apodemes (= the intermediate sclerite) into which fits a matching shape on the expanded, posterior end of the mandible. The angle of the joint determines the direction of mandible movement. For instance, in many larvae feeding on low demand food the joint is inclined, which means that when the mandibles lower, they move apart. This helps open the front of the oral cavity and allows food to pass into it. In contrast, in larvae feeding on high demand food the groove is horizontal and the mandibles move together which approximates the mandible hooks and is more effective for scraping and fragmenting (Rotheray and Lyszkowski 2015). Hence, from the joint alone food quality is indicated, but mandible joints are rarely investigated. They can be observed by excising the mandibles from the intermediate sclerite.

As with the basal and intermediate sclerites, the cyclorrhaphan mandible is diverse in size and shape. Mandibles with relatively long hooks scalloped or flattened on their inside margins are effective for scooping watery to oily food into the oral cavity (Fig. 2). Short, wide, thick mandibles with secondary hooks are more suitable for fragmenting harder, more demanding food, such as plant tissue (Rotheray 2020). Apart from commonalities such as these, a great range of finer differences relate to poorly investigated variables, such as the particularities of mechanical demand. Not all mandibles have sets of depressor and elevator muscles. Some have one set, such as that of the predatory *Microdon* larva (Diptera, Syrphidae) while others are fixed in the head skeleton and lack muscles, for example, predatory Syrphinae (Syrphidae), leaf-mining *Amauromyza* Hendel (Agromyzidae) and certain capitula-feeding Tephritidae (Rotheray and Lyszkowski 2015, Rotheray 2019b, 2021).

### 4. Accessory sclerites

Small accessory sclerites are often associated with the intermediate sclerite and the mandibles (Ferrar 1987, Courtney *et al.* 2000). The most widespread are the parastomal bars and the sclerites of the labial apparatus (Figs 2 & 3). The paired parastomal bars (= maxillary sclerites of outgroups) are attached to the front of the basal sclerite and extend forward over the intermediate sclerite and are connected to it by a membrane (Fig. 6a). In some larvae that feed on high demand food, the intermediate sclerite is buttressed by sclerotisation that incorporates partially or wholly the parastomal bars and the latter may appear to be absent (Figs 6b & c).

The eumuscomorphan labium has small accessory sclerites, and evidence from lower cyclorrhaphan morphology suggests they are excisions from the labial rods. In lonchopterids the paired labial rods are attached to the basal sclerite and extend forward to support the floor of the feeding trough. Except for the ventral bridge part way along, they are separate throughout their length and simple in form. In platypezoids the labial rods diverge at the ventral bridge and a pair of dorsal apodemes articulate with the mandibles. The ventral apodemes are greatly developed and extend forward and fuse apically into a hooked labial apparatus that projects freely from the lower margin of the pseudocephalon (Sinclair 1992, Rotheray and Gilbert 2008). This is the main food gathering structure in these taxa. In eumuscomorphans the dorsal apodemes retain articulation with the mandibles, but they are developed and extend forward to the front of the head skeleton where the mandibles replace the labial apparatus as the main food gathering structures. The labial apparatus is present, but excised, reduced and lies behind or under the mandibles. It comprises a central plate flanked by or just anterior to a pair of lozenge-shaped sclerites, the ligulate and subhypostomal sclerites of Ferrar (1987) (Fig. 2). In the Syrphinae and Microdontinae (Syrphidae), the labial apparatus is free and depresses during feeding to guide food into the mouth (video in supplementary material of Rotheray and Lyszkowski 2015). In higher cyclorrhaphans the labial apparatus is incorporated into the atrial floor as part of an extension (Teskey 1981). During feeding, labial muscles dilate the atrium, which helps to move food through it (Roberts 1971, Rotheray 2019a). In non-frugivorous Tephritidae the labial apparatus is secondarily free, a specialisation that probably widens the atrium even further, enabling relatively large fragments to pass through and replaces the fleshy labial lobe as a mouth covering (Headrick and Goeden 1996, Rotheray 2021). This specialisation may be a widespread feature of larvae that fragment hard food, such as many phytophagous larvae.

In higher cyclorrhaphans a pair of comma- to triangular-shaped sclerites, the dental sclerites, may be present under the mandible bases on to which some mandibular muscles insert (Roberts 1971). Dental sclerites may also represent excisions, this time from the mandible, but this is unclear. They are typically associated with low demand feeding, where their role is supporting the rear end of the oral cavity to help it contain food, prior to it being sucked up (Rotheray and Lyszkowski 2015). Dental sclerites may play more specialised roles and be fused together, fused to the mandibles or extended, such as the remarkably developed states in certain Camillidae (Rotheray 2011). Dental sclerites are usually vestigial or absent in larvae feeding on high demand food and instead, a mostly translucent and inconspicuous oral plate may be present. This plate has muscles attached to its posterior end which on retraction, flattens the rear of the oral cavity and protects it during fragmentation feeding (Rotheray 2020).

Finally, a number of sclerites, sometimes a complex, are associated with the mandibles and the front of the oral cavity, where they play specialised roles. For example, as mentioned above, sclerites of the oral cavity in certain Calliphoridae help isolate portions of food, and Rotheray and Wilkinson (2015) found that in predatory Muscidae the complex of accessory sclerites associated with the mandibles constitute a mechanism for piercing prey.

# Discussion

A barrier to understanding cyclorrhaphan larvae is the difficulty of resolving the head. The problem was summarised by Snodgrass (1953), who stated that the cyclorrhaphan larval head is so thoroughly modified that it is difficult to understand how it evolved. Teskey (1981) stated that this is because a series of groups that connect it to the heads of other Diptera are missing. These opinions are based on assessments of higher cyclorrhaphan larvae, primarily Drosophilidae and certain Calyptratae, but they are not supported by lower cyclorrhaphans.

As Hartley (1963) and Courtney *et al.* (2000) postulated, when lower cyclorrhaphans are analysed and relative to lower brachyceran and empidoid outgroups and standard criteria for making comparisons (similar position, similar shape, landmarks), proposals for resolving problematic head structures, such as the pseudocephalon, mandible, maxilla etc., can be made. Confirmation of these proposals and additional insight is likely to come from unknown larvae close to the base of the Cyclorrhapha: for example, larvae of the Opetiidae, *Microsania* (Platypezidae) and the apparent sister to the Cyclorrhapha, the Apystomyiidae (Trautwein *et al.* 2012).

The discovery of a mandibular-maxillary apparatus in cyclorrhaphans is strong evidence that the problematic cyclorrhaphan mandible is indeed homologous with that of outgroups. Nonetheless, the disparity of the cyclorrhaphan larval head is real and it explains the widespread use of ad hoc names for its components. Ad hoc names make reference to inferred homology or shape, position, function or some other characteristic; among others, Ferrar (1987) and Courtney *et al.* (2000) provide lists.

Using homology as a basis to name as opposed to recognise structures in the cyclorrhaphan larval head can be problematic, even if desirable. A particular difficulty is that components, such as the pseudocephalon, basal sclerite and intermediate sclerite, include seamless fusion with more than one structure and structures, such as the labium and maxilla, are subdivided. On the other hand, lower cyclorrhaphan morphology supports homologies that mean that the antenna, maxillary palpus and the mandible can be named as such. Lower cyclorrhaphan morphology also suggests that names, such as the ligulate and subhypostomal sclerites in Ferrar (1987) could be replaced by 'labial apparatus', which more accurately reflects the origin and relationship between these sclerites. Also, the pseudocephalon could be replaced with, 'laevicephalon' which in making reference to a soft head, reflects a key attribute.

A major feature of the cyclorrhaphan larval head is partitioning into two independently evolvable structures, the pseudocephalon and head skeleton. The pseudocephalon appears to be modified for flexibility and gathering food prior to sucking it up via an oral cavity. Major variants of the latter include an open trough (Lonchopteridae), a temporary oral cavity (Platypezoidea), a fixed, oral cavity (Eumuscomorpha) and a fixed oral cavity supported by the mandibles (higher Cyclorrhapha). The head skeleton is modified for pumping capacity and mobility. Major variations in pumping include the appearance of a tubular atrium in all cyclorrhaphans (except the Lonchopteridae), that probably enhances pumping power, and extension of the atrium in higher cyclorrhaphans by incorporating into it the labial apparatus. Major modifications in mobility include movement of the head skeleton independent of the pseudocephalon in all except the Lonchopteridae, in eumuscomorphans mandible location at the front of the head skeleton enabling movement unimpeded by other trophic structures and in higher cyclorrhaphans, by forwards and backwards movement and pivoting in the head skeleton that correlate to feeding on low and high demand food respectively (Rotheray 2020).

In higher Cyclorrhapha a close functional relationship between the oral cavity and the

mandible is more or less unaltered throughout the lineage. Nonetheless, combined with occasional innovations, a huge array of fine-grained variations in the relative size, shape, sclerotisation and mobility of components characterises the higher cyclorrhaphan larval head. Between the head and thorax further integration can occur to form trophic complexes. For instance, Rotheray (2019b) detailed how the thorax, pseudocephalon and head skeleton of leaf-mining *Amauromyza* larvae form a complex that both overcomes a range of food gathering challenges and promotes high levels of feeding efficiency. The impact of larval head traits on divergence rates within the Cyclorrhapha has yet to be assessed, but they are unlikely to be neutral. More fundamentally, accounting for variations, complexes and working out their functional roles has a long way to go and is a productive field of research (Rotheray 2019b, 2020).

In conclusion, within the lower Cyclorrhapha connecting groups sensu Teskey (1981) are present and they suggest that the higher cyclorrhaphan larval head is not as completely modified as inferred by Snodgrass (1953). Nonetheless, relative to other Diptera, the cyclorrhaphan larval head is distinct with partitioning and pumping being major contrasts. Indeed, much of the apparent disparity of the higher cyclorrhaphan larval head is explained by improvements to pumping capacity and consequential developments that include the appearance of an atrium, a fixed oral cavity, modified mandibles and capability for movement. The cyclorrhaphan larval head is highly diversified with variations, complexes and innovations underpinning diet changes and feeding specialisations, of which major influencing factors include mechanical demand, i.e. the force required to gather and pump food, and conditions of access to food, i.e. levels of confinement (Rotheray 2019a). These are significant sources of character and ecological information about which much remains to be discovered.

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# The larval habits of *Ophiomyia senecionina* Hering (Diptera, Agromyzidae) on common ragwort (*Jacobaea vulgaris*) stems

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#### Summary

The larval habits of the stem mining agromyzid *Ophiomyia senecionina* Hering, 1944 are illustrated for the first time. Puparia were observed on the stems of common ragwort (*Jacobaea vulgaris*). A description of the mine and pupariation position is provided, along with details of the species seemingly preferred biotope. Additional European records are also provided, which includes two species new to the German fauna.

#### Introduction

In November 2020, whilst examining common ragwort (*Jacobaea vulgaris*) stems for *Melanagromyza* Hendel puparia, AP observed a black puparium underneath the epidermis, just below a leaf node at Far Ings NNR, North Lincolnshire, TA0123. Images and the puparium were sent to BPW who confirmed [by examination of the posterior spiracles and subsequently, reared adults] that it belonged to *Ophiomyia senecionina* Hering, 1944, a known stem miner of *Jacobaea* sp. AP returned to the collection site and was successful in finding three additional puparia, all present on a single *J. vulgaris* stem. Searches by AP, at various other localities in North Lincolnshire, resulted in no further *O. senecionina* puparia being observed. During May 2020, BPW collected a male *O. senecionina* from a flood alleviation site in Anlaby, East Yorkshire, TA0327; examination of *Jacobaea* stems at this location [June to November] failed to produce any *O. senecionina* puparia. Detailed examination of *J. vulgaris* stems collected by BPW from several other localities [all within East Yorkshire], were found to possess *O. senecionina* puparia; two brownfield sites in Hull [TA0526 / TA0626], two areas in Hessle [TA0126 / TA0426] and Noddle Hill NR [TA1135]. As a result of these findings, the first author was able to photograph stems containing puparia (Figs. 1-3), representing the first larval illustrations of the species.

#### Discussion

*Ophiomyia senecionina* is a rare species in Britain; apart from the localities mentioned above, it is only known [confirmed records] from North Somerset [single male swept by David Gibbs in 2008, *pers. comm.*] and Surrey [four specimens reared by Spencer (in 1948, 1949, 1950 and 1960) within the British and Irish Agromyzidae collection at the Natural History Museum, London (Crowther *et al.* 2019)]. The mine created by *O. senecionina* is described by Hering (1957) as 'difficult to recognise, becomes visible after finding the puparium, the end of the mine is usually at the attachment point of a leaf. Sometimes the larva goes briefly into the petiole or midrib'. Initial examination of the stems discovered by BPW and AP agree with Hering's findings, in that the mine is difficult to recognise and the puparium is found near a leaf node. However, closer scrutiny of the stems suggests that the mine is usually invisible; only one stem (Fig. 2, left) appeared to show any trace of the mine but this may be an artefact of the epidermis being raised due to the presence of the puparium. Stems of varying age [from relatively green (Fig. 1 left) to older, slightly degrading (Fig. 2, left)] contain puparia; despite thorough investigation, no signs of the mine are detectable. The presence of the puparium, always below [or very rarely adjacent to] a leaf node, is seemingly the only indication that a plant is being utilised.



Fig. 1. *Ophiomyia senecionina* Hering, 1944 puparia in typical position, just below leaf node on *Jacobaea vulgaris* stems.



Fig. 2. *Ophiomyia senecionina* Hering, 1944 puparia on *J. vulgaris* stems; left, showing faint outline of possible mine just above and to the right of puparium.



# Fig. 3. *Ophiomyia senecionina* Hering, 1944 puparia on *J. vulgaris* stems; left, showing barely detectable puparium, its presence only highlighted due to swelling below leaf node.

Upon removal of the epidermis, above and below where the puparium is situated, frass is observed to be deposited in a few single, extremely widely spaced, discrete grains [always below the puparium indicating the larva feeds in an upward direction]. The positioning of the frass suggests that the larva mines in a relatively straight line, not spiralling around the stem.

Pupariation occurs consistently just below [or very rarely next to] a leaf node, predominantly in the upper half of the stem [only one puparium was found in the lower half], with anterior spiracles penetrating the epidermis (Fig. 4), typical for the genus *Ophiomyia*.





Depending on the colour and age of the stem, the puparium may be extremely difficult to observe, its presence only detectable owing to a slight swelling below a leaf node (Fig. 3, left). The puparium is adherent, rather weakly (Fig. 3, right)], to the epidermis and stem cortex and ranges from 0.9mm-1.2mm in width, occupying 10-38% of the width of the stem. Puparia were only found on tall, well-established plants, ranging in height from c450-870mm, with a stem diameter of 5-9mm; 200 smaller, younger plants were examined, none of which contained puparia. Over 100 old, much degraded stems were examined, resulting in no puparia found, an indication of the puparium being easily dislodged during periods of excessive weather, resulting in the puparium falling to the ground. Only the main stem possessed puparia; lateral shoots were not utilised for feeding or pupariation. Hering did not mention if more than one larva may be found mining a stem but all stems found by BPW possessed a single puparium, with AP finding two stems, one with a single puparium and one containing three puparia.

Interestingly, all puparia were found on plants in rather sheltered, isolated areas, free from human disturbance and habitat maintenance. Two brownfield sites (Fig. 5) with very little or no human disturbance, a secluded and neglected corner of a nature reserve, a disused meadow and a sheltered, unmanaged area in between a public footpath and the Humber estuary yielded puparia found by BPW. The puparia discovered by AP were on plants within an unmanaged verge of a nature reserve, in an area with no public access (Fig. 6, left). These biotopes agree well with habitats where adults have been collected; BPW swept a male from a private flood alleviation site, with no disturbance and very little management, whilst David Gibbs obtained a male from well sheltered, dry grassland (Fig. 6, right), which [at the time] was not subjected to human interactions.



Fig. 5. Typical biotope of O. senecionina; brownfield sites in Hull, East Yorkshire.



Fig. 6. Typical biotope of *O. senecionina*; left, Far Ings NNR, North Lincolnshire; right, Bristol, North Somerset.

Owing to Jacobaea vulgaris [syn. Senecio jacobaea] being one of the five injurious weeds [along with Cirsium arvense, C. vulgare, Rumex crispus and R. obtusifolius] prescribed in the Weeds Act 1959, it is consistently eradicated from most managed habitats; the extirpation of J. vulgaris is highly likely to account for the scarcity of this [and the other British Agromyzidae spp. wholly dependent on Jacobaea; Liriomyza erucifolii de Meijere, 1944 and Liriomyza latigenis (Hendel, 1920)] species and its distinct preference for undisturbed, sheltered habitats.

#### Distribution

*Ophiomyia senecionina* is a seemingly rare European species, only known from France, Germany, Slovakia and Ukraine (Guglya 2012).

Previously unpublished German records are hereby included; '1 male, *Ophiomyia* senecionina Hering, 1944, genitalia preparation no. 1118. Sample 428, 28.v.1988, leg. M. von Tschirnhaus: GERMANY, Land Nordrhein-Westfalen, Kreis Höxter, village Scherfede, 28km SE of Paderborn, 51°32'29"N, 9°01'13"E, nature reserve "Hellberg", limestone dry grassland with scattered shrubs of *Rosa canina* and *Crataegus laevigata* with flowering *Hippocrepis*, *Polygala*, and *Pilosella officinarum*; not flowering: *Sanguisorba*, *Antennaria*, *Thymus serpyllum*, *Centaurea*, *Ononis spinosa*, *Carex* spec. 89 Agromyzidae of 17 species also collected; 4Å, 11♀ *Agromyza* spec. nov (host probably *Hippocrepis*); 1♀ *Amauromyza monfalconensis* (Strobl, 1909); 1♂ 1♀ *Cerodontha* (*Xen.*) *atronitens* (Hendel, 1920); 1♂ *Cerodontha* (*Cer.*) *affinis* (Fallén, 1823); 3♂ 4♀ *Cerodontha* (*Phyt.*) *flavocingulata* (Strobl, 1909); 2♀ *Liriomyza amarellae* Hering, 1963 [males present during other visits]; 1♂ 7♀ *Liriomyza cicerina* (Rondani, 1875); 1♀ *Liriomyza* spec.; 2♂ 2♀ *Melanagromyza nibletti* Spencer, 1957; 1♂ *Metopomyza flavonotata* (Haliday, 1833); 2♀ *Ophiomyia pulicaria* (Meigen, 1830); 1♀ *Ophiomyia nasuta* (Melander, 1913);  $13^{\circ} 5^{\circ}$  Phytomyza cecidonomia Hering, 1937;  $22^{\circ} 13^{\circ}$  Phytomyza griffithsi Spencer, 1963;  $1^{\circ}$  Phytomyza plantaginis Robineau-Desvoidy, 1851;  $13^{\circ}$  Pseudonapomyza strobliana Spencer, 1973; 'F282,  $2^{\circ}$  O. senecionina, leg. Jutta Wehlitz, Malaise trap in gravel pit "Grüner Kuhweg",  $1^{\circ}$  trapped 23.v.1989–30.v.1989,  $1^{\circ}$  trapped 25.vii.1989–1.viii.1989, Germany, Land Nordhein-Westfalen, Cologne-Dünnwald,  $51^{\circ}0'25$ "N,  $7^{\circ}0'57$ "E. This biotope is a good example for a man-made habitat which houses a great insect diversity: between 1 April and 14 November 1989 in the Malaise trap, 89 agromyzid species (and 31 chloropid species) were caught, in three Malaise traps in three different gravel pits: 149 agromyzid species and 47 chloropid species, respectively (von Tschirnhaus 1992: 470-473).'

From the above lists, *Melanagromyza nibletti* Spencer, 1957 and *Phytomyza griffithsi* Spencer, 1963 are new to the German fauna.

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# The impact of cattle on the Diptera and other insect fauna of a temperate wet woodland

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#### Summary

The impact of cattle on the insect fauna of woodlands is poorly understood: here we report on a study to investigate this in a temperate wet woodland in Britain. Cattle pressure was sufficient to cause locally severe damage to soil structure and vegetation. Emergence traps were placed in small plots from which cattle, but not wild deer, had been excluded for 4 or 5 years, as well as in areas to which cattle continued to have access. Changes in abundance, species richness and diversity, and in the presence of species with restricted distributions, were assessed. For some Diptera (true fly) families, namely Tipulidae, Limoniidae, Psychodidae and Ephydridae, cattle exclusion resulted in substantial and significant decreases in individual abundance. Numbers of Plecoptera (stoneflies) and Trichoptera (caddisflies) also decreased, but not significantly so. For other Diptera families, namely Dolichopodidae, Sphaeroceridae, Lauxaniidae and Fanniidae, the converse was true: abundance increased when cattle were excluded. The total number of individual Diptera and Parasitica (Hymenoptera) increased significantly when cattle were excluded, but confidence in this result is low. Conversely, Diptera species richness decreased when cattle were excluded, although not significantly so. The diversity of Tipulidae and Dolichopodidae was significantly greater in plots to which cattle continued to have access, as measured by the Simpson index. The presence of cattle did not result in a decline in numbers of species of conservation concern: there were fewer Nationally Scarce, nationally local or locally uncommon species in plots from which cattle had been excluded. It is concluded that permitting cattle continued access to the wet woodland in question is on balance of benefit to Diptera and probably Plecoptera and Trichoptera, especially to those species with aquatic or semi-aquatic larvae, and to site nature conservation objectives. No comparative studies have been found, either on the impact of cattle on temperate woodland insect communities (wet or dry), or on the impact of any large herbivore, domestic or wild, on the insects of, specifically, wet woodland. Further research on this topic is much needed

#### Introduction

In Great Britain, about 40% of woodland area is in unfavourable condition for biodiversity as a result of herbivore browsing damage (Ditchburn *et al.* 2020). Despite this, there has as yet been little research into the impact of domestic herbivores such as cattle *Bos taurus* on woodland invertebrates, whether in Great Britain or in other temperate countries. Research has largely focused on their impact on ground flora and tree regeneration (e.g. Adams 1975, Kirby *et al.* 1994, Kirby 2003, Ramirez *et al.* 2018). More work has been done on the impact of deer on woodland invertebrates, as reviewed by Gill (2000) and Stewart (2001). They conclude that the evidence strongly points to deer being capable of having a profound impact on woodland ecosystems, including on invertebrates.

Cattle are much larger than any deer species found wild in the British Isles, the typical weight of a beef cow being about 600kg compared to 100kg for a mature red deer *Cervus elephas* hind or 25kg for a roe deer *Capreolus capreolus*. Consequently, cattle are likely to have a considerably greater ecological impact than deer, especially on soil structure (Adams 1975).

Wet woodlands in Britain are broadly defined as being those where the wetness of the ground is the overriding element in the environment and the canopy is dominated by various mixtures of alder *Alnus glutinosa*, hairy birch *Betula pubescens* and willows *Salix* spp. (Rodwell 1991). In Great Britain there is an estimated 169,000 ha of wet woodland, 11.2% of all native

woodland – it is a widespread and frequent habitat type, second in extent only to lowland mixed deciduous woodland (Ditchburn *et al.* 2020).

Various wet woodland types are listed under Annex 1 of the EU Habitats Directive, transposed into UK law through the Conservation (Natural Habitats, etc.) Regulations 1994. Two of these occur in the UK: 'Residual alluvial forests (NVC types W5, W6 and W7) and 'Bog woodland' (NVC types M18, M19, W4) (Barsoum *et al.* 2005). Annex 1 habitats are priorities for conservation action across the European Union. In the UK in 1998 wet woodland was recognised as a threatened habitat requiring conservation action under the UK Biodiversity Action Plan (JNCC 2008). The habitat is now included in statutory lists of habitats of principal importance for the conservation of biodiversity, widely known as 'priority habitats', in all four UK countries. It occupies the greatest area of all nine priority woodland habitats (Ditchburn *et al.* 2020). (Lowland mixed deciduous woodland is not a priority habitat.)

Wet woodlands frequently occur alongside and unfenced from open habitats such as grassland, heathland, moorland and fen. As a consequence, wet woodlands are often grazed and browsed, usually incidentally but sometimes purposefully, by cattle, sheep or ponies, or used by these animals for shelter. The woods are increasingly being fenced to exclude domestic herbivores on nature conservation grounds, although such action is seldom based on evidence that the livestock are having an adverse effect on wildlife. As a number of authors (Fuller and Gill 2001, Kirby *et al.* 1994, Kirby 2001, Mayle 1999) have noted, changes due to grazing or browsing, particularly by deer but also by cattle and sheep, should not be assumed to be undesirable. It is likely that maximum invertebrate diversity will occur under moderate grazing or browsing pressure, although at the species level there will always be winners and losers (Stewart 2001). There are some taxa (e.g. bryophytes and lichens and the birds pied flycatcher *Ficedula hypoleuca* and redstart *Phoenicurus phoenicurus*) of high nature conservation value that appear to thrive under fairly high levels of grazing (Fuller 2001, Kirby *et al.* 1994, Mitchell and Kirby 1990), others will respond to different grazing levels in a non-linear fashion (Fuller and Gill 2001, Mysterud *et al.* 2010).

Wet woodlands are among the richest habitats for Diptera, providing the humid, shaded or sheltered conditions that many species require for their larval development (Chandler 2010). Diptera therefore provide a good subject to test the impact of cattle on the habitat.

Here, the results of a study into the impacts of cattle presence on the abundance, speciesrichness and diversity of the Diptera (true fly) fauna within one wet woodland in South-West Britain are reported, with additional information provided on the impacts on Plecoptera (stonefly), Trichoptera (caddisfly) and Parasitica (parasitoid wasps within the order Hymenoptera) faunas. This study was conducted in part in response to concern expressed by visiting ecologists that the high levels of soil disturbance resulting from cattle trampling might be having an adverse ecological impact. It appears to be the first time the impact of domestic herbivores on the invertebrate fauna of temperate wet woodland has been investigated.

#### Methods

#### Study site

The wet woodland studied lies within Scadsbury Moor (SS518014, V.C. 4, North Devon), part of Locks Park Farm, near Hatherleigh in Devon, England. This site covers 7.23ha and, together with wet woodland, has species-rich *Molinia* grassland and dry or humid native woodland: there are no dividing fences between these habitats and the site is grazed as one unit. The estimated area of wet woodland is 1.9 ha. Further information on Scadsbury Moor may be found in Wolton *et al.* (2017). The wet woodland community conforms to National Vegetation Classification (NVC) *Alnus glutinosa – Fraxinus excelsior – Lysimachia nemorum* woodland, *Carex remota – Cirsium palustre* sub-community (W7b) (Rodwell 1991). This is closely related to the Carici-Fraxinetum

Koch, 1926 community of mainland Europe (Rodwell 1991). W7b is a widespread woodland type throughout Britain, with the exception of the English Midlands and East Anglia (Hall *et al.* 2004).

The stand within which the study was carried out was dominated by alder *Alnus glutinosa* with occasional grey willow *Salix cinerea*. The ground flora was characterised by abundant remote sedge *Carex remota*. Marsh bedstraw *Galium palustre*, creeping buttercup *Ranunculus repens* and the moss *Eurhynchium striatum* were frequent, and soft rush *Juncus effusus* and the liverwort *Pellia epiphylla* occasional. The underlying soils are mineral, derived from clay, with no peat deposits. Water originates from springs and seepages, not from fluvial flooding.

The site is grazed by cattle for a few weeks each summer, in July and August (Fig. 1). The cattle are kept on site until the open grassland is adequately grazed for nature conservation purposes. By this time, in most summers (including that of 2020), the ground in the wet woodland is heavily trampled ("poached") in places (Fig. 2), with deep wet mud requiring the human visitor to wear Wellington boots or get wet feet. Initially, when introduced to the site, the cattle typically spend most of their time in the wet woodland browsing and grazing *Carex remota*. They then shift their attention to the open grassland, all the while making frequent forays into the humid and dry woodland to browse, especially on bramble *Rubus fruticosus*.

In 2020, 14 suckler cows with calves at foot and one bull were put on the site on 29 July and removed on 17 August. This equates to 18.8 Livestock Units (LSU) for 19 days across the site, or 2.6 LSU per ha for 19 days.



Fig. 1. Beef cow in study woodland. Photo Paula Wolton.



Fig. 2. Impact of cattle on wet woodland soil and plant cover. Photo Robert Wolton.

#### Insect sampling

As part of a previous study (Wolton *et al.* 2017), two small areas of the wet woodland were fenced with two strands of barbed wire to protect Malaise traps from cattle, one in March 2015 and the other in March 2016. These served as exclosure plots for the current study. When set up they were chosen to be representative of the wet woodland habitat. The 2015 plot measured approximately  $8m \times 5m (40m^2)$ , and the 2016 plot approximately  $10m \times 10m (100m^2)$ . The plots were 35m apart, centre to centre. The fencing did not exclude either red deer or roe deer (the two deer species present in the area), trail cameras showing that both were easily able to slip under the lower strand of barbed wire. However, the fences were completely effective at excluding cattle, even calves. This study was carried out in 2020, thus cattle were excluded from one exclosure plot for five years and the other for four years beforehand.

An emergence trap was placed in each of these two exclosure plots and one within 10m of each exclosure – the "grazed" plots, so four traps in all. Within each plot, whether exclosure or grazed, the traps were carefully placed in patches that were typical of grazed or ungrazed situations as appropriate. Large mammal paths, whether caused by deer or cattle, were avoided, as were any patches of atypical hydrology and vegetation. Pieces of dead and decaying wood were also avoided other than small branches and twigs, as were any obvious large dung deposits (e.g. cow pats). No traps were placed within a metre of the exclosure fencing to avoid edge effects.

The traps were operated in 2020, the study year, between 1 May and 28 July, and again between 1 September and 2 October, cattle being present on site in August. The traps were emptied every three days. Within each plot, whether exclosure or grazed, the traps were moved every 15 days, that is after being emptied five times. Consequently, over the four months that trapping was carried out, each trap was moved seven times, so within each of the four plots eight patches were sampled (for 15 days each). Traps were moved for four reasons: (1) to minimise

any bias from non-random placement and to ensure even coverage of representative habitat; (2) to mitigate any damage to the ground surface and vegetation caused when traps were emptied; (3) to reduce any effects of changes in ground temperature and reduction in rain reaching the ground; and (4) to allow for successive generations of insects to occupy the trap areas.

Comparison of photographs taken in 2015 and 2016, when the exclosure plots were established, with the situation in 2020 revealed that the vegetation within the plots changed markedly during the four to five years that elapsed even though deer continued to have access. Ground flora cover increased and *Carex remota* was less dominant. The exclosures had firmer ground, less exposed soft mud ("squidge"), more leaf litter and more dead branches and twigs lying on the ground surface. In addition to a reduced dominance of *Carex remota*, the exclosures were more herb-rich, with more frequent *Ajuga reptans*, *Filipendula ulmaria*, *Galium palustre*, *Geranium robertianum*, *Glechoma hederacea* and *Rubus fruticosus*, plants that are readily eaten by cattle. These differences were not quantified: it would have been difficult to do so since they changed as the seasons progressed. For example, by late July much of the bare mud which was evident outside the exclosures in early May had become vegetated – to be returned to open mud once more in September after cattle had been present.



Fig. 3. Study wet woodland with adapted children's tents used as emergence traps. Photo Robert Wolton.

The exclosure traps were modified children's tents, specifically Kombat UK Lightweight Play Kids' Outdoor Dome Tents in British Terrain Pattern (i.e. camouflaged) (Fig. 3). The tents were square, covering  $1.16m \times 1.16m$ . The ground sheets were cut out, leaving an interior margin of 10cm on all four sides, so that the interior dimensions were  $0.96m \times 0.96m$ . It is assumed that half the insects emerging under the margins went inside the trap and half outside it, giving an effective capture area of  $1.06m \times 1.06m (1.12m^2)$ . The internal margins were pegged to the ground, the gap between the front margin and the ground covered with an edge of the cut-out ground sheet and any gaps around the external edge blocked with small branches, these actions together forming a reasonable seal and making ingress of adult insects capable of flight difficult even when walking. The trap contents were extracted by partially unzipping the front entrance, crawling in, and using an entomological aspirator (pooter) to catch all flies and other insects on the top and sides of the tent, the vegetation within the tents being ruffled to disturb any insects reluctant to fly. Although with a tight and strong weave, the tents remained translucent, encouraging insects to move upwards to the light where they were readily captured: others that preferred to remain in dark corners were also taken. Before trap placement, flying insects were flushed from the ground so only those developing from immature stages were likely to be sampled.

#### Identification

The insect samples were sorted and counted while still fresh and individuals identified to family level, with the exception of the Chironomidae and Ceratopogonidae which were lumped. Individuals were further identified to species level except for members of the Sciaroidea, Psychodidae, Chironomoidea, Phoridae and Sphaeroceridae (all Diptera) and Parasitica (Hymenoptera), and for females of genera where identification to species level is problematic (e.g. *Erioptera, Molophilus*, some *Platypalpus, Sarcophaga, Nemoura, Panorpa*). Species were identified using a wide range of published and unpublished keys available to members of the Dipterists Forum. For the most species-rich families encountered these were: Tipuloidea (Alan Stubbs amended by John Kramer unpublished); Rhagionidae and Stratiomyidae (Stubbs and Drake 2014); Hybotidae and Empididae (Collin 1961 supplemented respectively by Stephen Hewitt unpublished and Nigel Jones unpublished); Dolichopodidae (d'Assis-Fonseca 1978, supplemented by Martin Drake unpublished); Syrphidae (Stubbs and Falk 2002); Ephydridae (Martin Drake unpublished); Chloropidae (John Ismay unpublished); Muscidae and Fanniidae (d'Assis-Fonseca 1968 supplemented for Muscidae by James McGill unpublished); and Anthomyiidae (Michael Ackland unpublished).

#### Status assessment

Information on those Diptera species recorded which are (provisionally) Nationally Scarce was drawn from published Great Britain status assessments and reviews (Ball and Morris 2014, Chandler 2017, Drake 2017, Drake 2018, Falk 1991, Falk *et al.* 2016, Falk and Chandler 2005, Falk and Crossley 2005, Falk and Pont 2017) and from a draft Tipuloidea review (Peter Boardman *pers. comm.*). Decisions on whether or not species are local at a Great Britain level, or uncommon at a county (Devon) scale, were made in discussion with national and local experts and by reference to the Devon county Diptera database maintained by Martin Drake (now by Andrew Cunningham). There are no accepted definitions of the terms uncommon or local. Nationally Scarce species are those which have been recorded in between 16 and 100 ten km squares (moderated where appropriate by experts).

#### Statistical analysis

For abundance, the null hypothesis adopted was that there should be no difference in the number of individuals caught between the grazed plots and the exclosure plots. This approach could not be taken for species-richness because the complement of species differed between treatments (that is the total number of species caught was not the sum of the numbers caught in the two treatments). Here the null hypothesis was that the number of species recorded in the exclosure plots should be the same as that in the grazed plots, the active process being the erection of fencing to exclude cattle, not the introduction of cattle to the site.

The assumption was made that the numbers of individuals and species found within each family, suborder or order are independent of each other. This approach was considered pragmatic given the lack of knowledge about the level or direction of interaction between the great majority of the members of these taxonomic groupings, and the likely high complexity of trophic and other ecological networks present. It should be noted that sampling effort was exactly the same in all plots, allowing direct comparison.

The  $\chi^2$  test was used to determine the probability of observed differences in abundance or species-richness being significantly different from expected. For each of the two treatments (grazed plots and exclosure plots) data were pooled across the entire sampling period and for both plots. The experiment was not designed to explore variation in abundance or species-richness with time, nor patchiness of species distribution. In line with the null hypotheses, the expected frequency was either i) an equal distribution between sites when comparing individuals per family or ii) the same number of species as at the "untreated" site (grazed) when comparing species per family. The tests were performed independently – one test per family in contingency tables with the observed and expected frequencies. The Bonferroni correction was then used to reduce the chances of false positives (Type I errors) caused by multiple testing. The  $\chi^2$  test was only carried out where the expected number was 5 or more.

Simpson's diversity index and associated sample coverage estimates were calculated, using the iNEXT package (Hsieh *et al.* 2016), based on the methods given in Chao and Jost (2012), Colwell *et al.* (2012), Chao *et al.* (2014) and Chao *et al.* (2016). Since the same sampling effort was applied to both types of plot (grazed and exclosure), non-asymptotic or empirical estimates are reported based on the seamless rarefaction and extrapolation sampling curves for Hill number q = 2, equivalent to Simpson's diversity index. Similar results were also obtained using asymptotic estimates. 95% confidence intervals were calculated using a bootstrap procedure with 200 iterations. The Simpson index provides a measure of the evenness of spread of numbers recorded for each species within a community and is recommended for use by Magurran (2004) in this context in preference, for example, to the Shannon index.

#### Results

The data have been analysed to determine whether the exclusion of cattle has had any significant impact on insect abundance, on species richness, on diversity measures, or on the presence of species with a restricted distribution. An online supplementary table, available at *https://www.dipterists.org.uk/digest*, presents data on the number of individuals caught in each plot, for each identified species or, where individuals were not identified to species level, for the relevant families.

#### Abundance

A total of 4,978 individual Diptera were collected from the two exclosure plots, an increase of 21% over the 4,105 collected from the two grazed plots. This is significantly different (p<0.001) from that expected if the exclusion of cattle had no effect on abundance. However, the figures should be treated with caution because for a number of families with abundant individuals (Sciaridae, Cecidomyiidae, Ceratopogonidae + Chironomidae, Phoridae, Lonchopteridae and Agromyzidae) the two grazed plots did not consistently have higher or lower numbers than the two exclosure plots across the whole sampling period. If these families are removed from the analysis, a total of 1,429 individuals were collected from the exclosure plots and 1,344 from the grazed plots, a difference which is not statistically significant (p=0.07).

23% more individual Parasitica (Hymenoptera) were recorded from the exclosures than the grazed plots (410 v. 334, p=0.02), but the direction of change between plots was not consistent so no firm conclusion can be drawn from this increase. Consistently fewer Plecoptera (12 v. 27, p=0.07) and Trichoptera individuals (18 v. 31, p=0.25) were found in the exclosure plots than the grazed plots, but in neither case is the difference statistically significant.

Where both exclosure plots had consistently higher or lower numbers of individuals than both grazed plots, four Diptera families had significantly more individuals in the exclosures while four were more abundant in the grazed plots (Table 1). Those families that were more abundant in the grazed plots are characterised by having a high proportion of aquatic or semi-aquatic larvae. No obvious patterns in either trophic level or main types of larval food are apparent for Diptera families with respect to their relative abundance in exclosures or grazed plots.

Table 1. Number of individuals in Diptera families with a total of 10 or more individuals caught in emergence traps (so expected number in each treatment five or more), for exclosure plots and grazed plots, with details of main larval food types and micro-habitats for each family. Significance assessed using  $\chi^2$  test with Bonferroni correction; ns, not significant.

Family	Exclosure plots	Grazed plots	Significance	Main larval food types	Main larval micro-habitats present on site
A. Significantly more	individ	uals reco	orded in graz	ed plots than exclo	sures
Tipulidae	10	30	0.0375	Saprophagous, phytophagous	Semi-aquatic, mosses, liverworts, roots, decaying wood
Limoniidae	258	384	<0.0001	Saprophagous, mycophagous, predatory	Aquatic, semi- aquatic, mosses, fungi, decaying wood
Psychodidae	234	373	<0.0001	Saprophagous, coprophagous	Semi-aquatic, leaf litter, decaying wood, fungi, dung
Ephydridae	8	36	0.0006	Saprophagous Predatory	Aquatic and semi- aquatic
B. Significantly more	e individ	uals reco	orded in exclo	osures than in graz	ed plots.
Dolichopodidae	318	97	<0.0001	Predatory	Moist soil, decaying organic matter
Lauxaniidae	15	2	0.0388	Saprophagous, mycophagous	Fungi, decaying organic matter
Sphaeroceridae	259	163	< 0.0001	Saprophagous, coprophagous	Decaying organic matter including dung, fungi, leaf litter
Fanniidae	59	10	< 0.0001	Saprophagous	Decaying organic matter including general detritus, fungi and dung

C. Either no significant differences between numbers of individuals recorded in exclosures and grazed plots, or the two grazed plots did not both have higher or lower numbers than the two exclosure plots (X).

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Mycetophilidae	63	55	ns	Mycophagous	Fungi
Sciaridae	887	672	<0.0001	Saprophagous, coprophagous, mycophagous	Soil, leaf litter, deadwood, dung, fungi, semi- aquatic
Cecidomyiidae	247	155	0.0001	Phytophagous, saprophagous, mycophagous, predatory	Higher plants, decaying organic matter, fungi
Ceratopogonidae + Chironomidae	1580	1209	<0.0001	Saprophagous, Predatory	Aquatic, semi- aquatic, moist soil, leaf litter, moss, decaying organic matter, fungi
Rhagionidae	40	45	ns	Predatory	Moist soil, mosses, decaying wood
Empididae	9	9	ns X	Predatory	Organic matter, decaying wood, aquatic
Phoridae	551	452	0.0425 X	Saprophagous, predatory, parasitoids	Organic detritus, dung, carrion, fungi, living plants
Lonchopteridae	211	198	ns X	Saprophagous	Leaf litter, decaying plant matter
Syrphidae	9	7	ns	Predatory	Aphids, leaf litter, aquatic, semi- aquatic
Sciomyzidae	7	9	ns	Predatory	Slugs and snails: aquatic, semi- aquatic and terrestrial
Agromyzidae	73	75	ns X	Phytophagous	Living plants
Opomyzidae	10	7	ns	Phytophagous	Grasses
Chloropidae	9	13	ns	Phytophagous	Living plants, decaying wood, decaying plant material, fungi
Muscidae	7	8	ns	Predatory	Decaying organic matter

## Species richness

For those Diptera families where all, or nearly all (see Methods for exceptions), individuals caught were identified to species level, 112 species (with a total of 1,155 individuals) were recorded in the exclosures and 120 (1,024 individuals) in the grazed plots, a 7% increase in species density and the reverse of the pattern found for abundance. The difference is not, however, significant.

Nor indeed was there any significant difference for any family (or suborder) in the number of species found within exclosures or grazed plots. Data are presented in Table 2.

Table 2. Numbers of species in Diptera families in all plots, grazed plots and exclosure plots. Only those families with five or more species caught in the grazed plot emergence traps are considered. No significant differences exist in species richness between exclosures and grazed plots.

Diptera	All plots	Exclosure plots	Grazed plots
Tipulidae	7	3	8
Limoniidae	37	27	29
Hybotidae	7	5	5
Empididae	9	6	6
Dolichopodidae	20	18	14
Syrphidae	9	6	5
Ephydridae	6	3	6
Muscidae	7	5	6
All families where individuals identified to species	159	112	120

Three species of Plecoptera were caught in both the exclosure plots and the grazed plots, while two species of Trichoptera were caught in the exclosures compared to five species in the grazed plots (a difference that is not statistically significant).

#### Diversity

Simpson diversity index values were calculated for those families where all individuals were identified to species level (bar some females), and either 10 or more individuals were caught, with consistency in direction across grazed and exclosure plots (so those listed in sections A and B of Table 1), or five or more species were caught in the grazed plots (those given in Table 2), a total of 10 families. The index was also calculated for the superfamilies Tipuloidea (craneflies) and Empidoidea. Fig. 4 gives those families and superfamilies that showed a significant difference in diversity index values between grazed plots and exclosure plots. This figure also shows sample completeness estimates, demonstrating that very high sample coverage was achieved for the Empidoidea and Dolichopodidae, and good coverage for the Tipulidae. Similar high sample completeness values were also achieved for other families where the diversity index was not significantly different. This suggests that very few species likely to be present were not captured.

The diversity index for the families Tipulidae and Dolichopodidae was significantly greater in grazed plots than in exclosure plots. The same was true for the Empidoidea, the suborder which includes the Dolichopodidae, but not for the Tipuloidea. No significant differences between grazed and exclosure plots were found for the families Limoniidae, Hybotidae, Empididae, Syrphidae, Ephydridae, Lauxaniidae, Fanniidae and Muscidae.



Fig. 4. Families and suborders for which Simpson's diversity index between grazed and exclosure plots were significantly different at <5% level. The index and sample completeness were calculated in the iNEXT package. Estimates are shown +/- 95% confidence intervals.

## Species with restricted distribution

Thirty-four species (21% of all those identified) were caught in the emergence traps and assessed as being scarce or local at a national level or, failing that, at a county level (Table 3). 141 individuals of 18 such species were recorded from the exclosure plots and 100 individuals from 26 species from the grazed plots. The difference in numbers of individuals between the two treatments is significantly different (p<0.01) from that which would be expected should the presence of cattle have no effect. This mirrors the situation for all species regardless of status. The difference in number of species is not significant (p=0.18). Five Nationally Scarce species were found in the exclosures, and seven in the grazed plots. A summary of the numbers of restricted species caught is given in Table 4.

Table 3. Nationally Scarce and nationally local species, and others that are locally uncommon, with numbers of individuals caught. \*\*p<0.01: significantly different from that expected if the exclusion of cattle had no effect. For authors of scientific names, see online supplementary table.

Nationally Scarce (NS) species		Exclosure	Grazed	Devon
		plots	plots	status
Tipulidae	Nephrotoma dorsalis	0	2	Uncommon

Limoniidae	Paradelphomyia nielseni	0	11	Uncommon		
Limoniidae	Thaumastoptera calceata	5	3	Uncommon		
Rhagionidae	Spania nigra	0	3	Uncommon		
Dolichopodidae	Achalcus bimaculatus	4	1	Uncommon		
Dolichopodidae	Gymnopternus angustifrons	14	3	Uncommon		
Lauxaniidae	Homoneura notata	2	0	Uncommon		
Fanniidae	Fannia aequilineata	0	1	Uncommon		
Tachinidae	Eloceria delecta	1	0	Uncommon		
		26	24			
Nationally local	species	-				
Limoniidae	Lipsothrix nervosa	1	0	Common		
Limoniidae	Rhabdomastix ?edwardsi	1	0	Uncommon		
Dixidae	Dixa submaculata	0	1	Common		
Hybotidae	Bicellaria nigrita	1	0	Uncommon		
Hybotidae	Drapetis parilis	0	1	Uncommon		
Hybotidae	Trichina pallipes	22	23	Uncommon		
Dolichopodidae	Achalcus flavicollis	24	9	Uncommon		
Dolichopodidae	Medetera muralis	2	2	Uncommon		
Syrphidae	Brachyopa scutellaris	0	1	Uncommon		
Pipunculidae	Dorylomorpha maculata	0	1	Uncommon		
Ephydridae	Axysta cesta	3	1	Uncommon		
Ephydridae	Philygria picta	0	1	Uncommon		
Fanniidae	Fannia genualis	3	0	Uncommon		
Fanniidae	Fannia umbrosa	6	1	Uncommon		
Anthomyiidae	Hylemya nigrimana	0	2	Uncommon		
Anthomyiidae	Zaphne caudata	0	1	Uncommon		
		63	44			
Species that are widespread nationally but uncommon in Devon						
Tipulidae	Tipula signata	0	1	Uncommon		
Limoniidae	Dicranomyia morio	2	0	Uncommon		
Limoniidae	Euphylidorea dispar	32	16	Uncommon		
Limoniidae	Euphylidorea lineola	0	1	Uncommon		
Hybotidae	Platypalpus candicans	16	4	Uncommon		

Sphaeroceridae	Crumomyia roserii	0	3	Uncommon
Sphaeroceridae	Limosina silvatica	2	0	Uncommon
Chloropidae	Cetema elongatum/simile	0	6	Uncommon
Muscidae	Hebecnema umbratica	0	1	Uncommon
		52	32	
All species with a restricted distribution		141**	100**	

 Table 4. Numbers of Nationally Scarce and nationally local species, and of further species uncommon at the county (Devon) level.

	All plots	Exclosure plots	Grazed plots
Nationally Scarce species	9	5	7
Nationally local species	16	9	12
Other species uncommon in Devon	9	4	7
All Scarce, local or uncommon species	34	18	26

#### Discussion

Whereas in freely-draining woodlands the impact of large herbivores such as cattle on invertebrates is largely the result of the removal or trampling of herbs, saplings and undergrowth (Gill 2000, Kirby *et al.* 1994, Putman *et al.* 1989, Stewart 2001), in wet woodlands physical damage to soil structure is also a major factor. In wet woods, cattle presence may be expected to affect invertebrate communities through:

- The breakdown of soil structure leading to an increase in soft mud (sometimes referred to as "squidge" by entomologists).
- The creation of an uneven and more exposed ground surface, increasing variation in soil wetness and accessibility, including the formation of mini-pools in footprints (Fig. 5).
- The removal of living herbaceous and woody vegetation through trampling, grazing and browsing, leading to a simplification of structure and more open ground. For some taxa like craneflies this may mean access to oviposition sites is easier, while saprophagous species may find it easier to access dead and decaying organic material (Alan Stubbs *pers. comm.*).
- An increase in light intensity and temperature at ground level due to a reduction in above ground vegetation. This will increase algae and cyanobacteria, larval food for surface grazers like some ephydrids (Martin Drake *pers. comm.*).
- The reduction in cover of palatable plants and an increase in those unable to germinate under dense leaf litter.
- The incorporation of leaf litter and dead wood into the soil through trampling.
- The increase in dung, both a microhabitat in its own right and a source of soil nutrients although it may be rendered toxic by cattle being treated with wormers such as avermectins.
- Changes in seral or climax vegetation, leading either to a deceleration in the rate of succession or to succession to different plant communities than those that would develop in the absence of cattle.

These factors are likely to have either beneficial or adverse impacts, depending on the degree to which they are manifested, the interplay between them, and the biota under consideration. All are likely to affect Diptera and other invertebrate communities.

The results presented in this paper show that the abundance of individuals within some families increases with the presence of cattle, while for other families the reverse is true. The results suggest that while on one hand cattle may reduce the overall abundance of Diptera in wet woodland, including the numbers of individuals within some species of conservation concern, their presence may increase overall species richness and the number of species of conservation concern present.



# Fig. 5. Mini-pond in cattle hoof print, with grazed and trampled sedge *Carex remota*. Photo Robert Wolton.

#### Abundance

The lack of consistency for several abundant families in numbers caught between plots in relation to whether they were grazed or not calls into question the validity of the statistically significant increase in abundance found. Since eight different patches were sampled within each plot, inadvertent biases in trap placement are unlikely to explain the lack of consistency. Although the two grazed plots and the two enclosed plots appeared similar to each other to the human eye, from the perspective of members of some Diptera families they either differed markedly in their attractiveness or, alternatively, the distribution of many species was intrinsically clumped. For a few species differences in numbers of individuals recorded between the two grazed plots, or between the two exclosure plots, was pronounced. For example, 156 *Dolichopus simplex* Meigen were recorded in one exclosure plot but just 19 in the other (with 25 and 8 being caught in the two grazed plots).

Although the overall impact of cattle on Diptera abundance may be uncertain, for some Diptera families this study reveals that, as expected, cattle grazing and trampling can have a significant impact on numbers, either positive or negative. For most of those families or suborders where the majority of the larvae are aquatic or semi-aquatic, the presence of cattle had a positive effect. Craneflies (Tipulidae, Pediciidae and Limoniidae) numbers were 57% greater in grazed plots than in the exclosures. Moth flies (Psychodidae) were 58% more abundant in the grazed plots, and shore flies (Ephydridae) over four times (450%) as abundant. Likewise, numbers of Plecoptera and Trichoptera were greater in the grazed plots, although not significantly so. These results are consistent with cattle creating persistent soft wet mud suitable for aquatic or semi-aquatic larvae.

Other than their larvae not being associated with aquatic or semi-aquatic habitats, there is no obvious common factor bringing together those families that were significantly more numerous in the exclosures than in the grazed plots. Fanniidae were six times more abundant in the exclosures, Dolichopodidae over three times more abundant, and Sphaeroceridae 59% more numerous. Lauxaniidae were also significantly more abundant in exclosures, although the relatively small sample size predicates against putting a figure to this increase. Decaying organic matter is a major food source for the larvae of many of these families (as it is for many of the families where no significant differences were noted). It is possible that both the improved soil permeability and the increase in leaf litter resulting from cattle exclusion may have benefited these families, but further research is required here.

It might be expected that families with predominantly phytophagous larvae (Cecidomyiidae, Agromyzidae, Opomyzidae and Chloropidae) would be more abundant in the exclosures since these supported more living plant material at ground level, but there was no evidence of this. Likewise, it may be expected that families with larvae frequently associated with dung (Sciaridae, Phoridae, Sphaeroceridae and Scathophagidae) would be more abundant in the plots that remained open to cattle. However, only for the Scathophagidae was this true, and then not significantly so. Possible reasons are that deer continued to have access to the exclosures so providing ample faecal matter within them, or that the cattle dung was unattractive or even toxic as a result of chemical treatments for intestinal parasites.

The statistically significant 23% increase in numbers of Parasitica caught in the exclosures compared to the grazed plots is similar to the 21% increase in Diptera caught. This may be a straightforward relationship since Diptera were probably the most abundant hosts present in the soil or ground flora, although a wide range of other potential invertebrate hosts were present too, including Araneae, Lepidoptera and Hemiptera.

#### Species richness

The higher species density of Diptera and Trichoptera within plots which remained accessible to cattle, although not significant, may reflect an increase in larval habitats, notably the addition of wet mud and mini-ponds formed in hoof prints. For those families where individuals were identified to species, the direction of change in species richness between grazed and enclosed plots tended to be aligned with that in abundance, as expected, the only exception being the Chloropidae.

#### Diversity measures

Although Dolichopodidae were both more abundant and more species-rich in the exclosure plots than in the grazed ones, the reverse was true for diversity as measured by the Simpson index. This indicates that there is a more even spread in the numbers of individuals across both infrequent and common species present where cattle have access.

#### Species with restricted distribution

The results suggest that the presence of cattle may on balance favour species of conservation concern since more Nationally Scarce, nationally local or locally uncommon species were captured in the plots to which the cattle continued to have access. 26 such species were recorded from grazed plots compared to 18 from exclosures, seven of those found in the grazed plots being Nationally Scarce and five in the enclosed plots. These differences are not statistically significant from what would be expected if both types of plot had equal numbers, nevertheless the results demonstrate at the very least that in this particular wood the presence of cattle does not result in a decline in numbers of species of conservation concern. Broadly in line with this, Spitzer et al. (2008), investigating the effects of stand openness in a lowland deciduous woodland in the Czech Republic, found that a considerable proportion of epigeic woodland invertebrates, including many species of conservation concern, depended on preserving sparse canopy conditions, as achieved through coppicing or low levels of grazing by ungulates. Indeed, the rarest invertebrate species in woodlands tend to be associated with opposite ends of the successional spectrum: open clearings and areas of comparatively bare ground, and mature or senescent habitats, especially dead and decaying wood (Thomas and Morris 1994, as summarised by Stewart 2001). That the presence of cattle at moderate densities may favour scarcer species in wet woodland is therefore to be expected.

#### Previous research

Comparable studies on the impact of large herbivores other than deer on insect abundance in temperate woodland are few, and none have been found that relate specifically either to cattle or to wet woodland.

Working in the New Forest in southern England, Putman et al. (1989) used pitfall trapping to compare the invertebrate fauna in areas from which most large herbivores, mainly deer and horses, had been excluded for 25 years with that in places to which large herbivores continued to have access and grazing levels were high. They found, for all families sampled, that Diptera were more abundant in the exclosures, often considerably so. In contrast, only one Coleoptera species was more abundant in the exclosures. The authors noted that the efficiency of pitfall traps varies considerably with differences in vegetation structure, and this may have explained many of the differences observed. They also remark that impacts on insect abundance may have been different had grazing levels been lower. Allombert et al. (2005) found that introduced deer had a major impact on insects in temperate woodland in Canada. Abundance in vegetation below the browse line decreased eightfold and species density sixfold after 50 years of browsing. Likewise, deer grazing in an oak woodland in Ireland was linked to decreased ground-dwelling spider abundance and species richness, a consequence of reduced habitat structural diversity (Fuller et al. 2014). In an experiment based on simulating wild boar Sus scrofa grubbing (soil bioturbation) in an oak woodland in Germany, Mohr et al. (2005) found that grubbing substantially reduced the amount of leaf litter present and correspondingly reduced the abundance of leaf litter-inhabiting saprophagous and predatory arthropods, including Diptera larvae. Cattle trampling also reduces the amount of leaf litter present and this may account for the lower abundance of Diptera noted in areas which remained open to cattle in the current study. Looking beyond temperate woodland, in a boreal forest with Alnus tenuifolia and Salix spp. in Alaska, Suominen et al. (2010) found that the abundance of Orthoptera and Coleoptera was generally higher in plots browsed by moose Alces alces and snowshoe hares Lepus americanus, a change they attributed both to an increase in mammalian faecal matter and to browsing induced changes in microclimate, light regime, vegetation composition, litter and soil.

#### Conclusions

The concern expressed by ecologists visiting the study site that the cattle damage to soil structure and vegetation might be having an adverse impact on the wet woodland's nature conservation value appears unwarranted, at least with respect to Diptera and probably Plecoptera and Trichoptera, orders for which the habitat is widely recognised to be of high value. Indeed, permitting cattle to access the wood for grazing, browsing and shelter may have resulted in an increase in insect species richness and the number of species with national or locally restricted distributions. Overall insect abundance may, on the other hand, have been reduced, with possible adverse consequences for populations of predators such as insectivorous birds and bats. We conclude that cattle should continue to be allowed access to the wet woodland at existing levels, noting that the insect assemblages present are, as far as we know, of greater conservation significance than any other elements of the flora or fauna.

This may be the first but it is only one study of the impact of cattle on the invertebrates of temperate wet woodland. It considers one woodland community on one site, subject to moderate stocking levels for just a few weeks each year. Moreover, the results are based on just two small exclosures, cattle were excluded from these for just one time frame (four or five years), and deer retained access. Further studies are much needed!

When deciding whether to allow cattle access to wet woodland, site managers need to consider a range of factors. These include the numbers of cattle involved, whether deer or other herbivores are present, the likely long-term effects on the woodland plant communities and structure, and the impact on scarce invertebrates and on species density and abundance. Where the balance lies will depend on site conservation objectives. Often, as previous authors have noted, in general wildlife will benefit from some large herbivore access, although over-trampled wet woodland can be very poor places to find some taxa such as craneflies (Alan Stubbs *pers. comm.*). Research and guidance on optimal stocking densities is much needed.

Research is also required on the impact of longer-term exclusion of cattle. The soil structure and composition, ground flora and even tree canopy species may be expected to change radically. Latham and Blackstock (1997) found that 20 years after sheep and cattle had been excluded from an upland alder woodland in North Wales, the field layer was better developed than in parts of the wood that remain unfenced and open to grazing, with a significantly higher cover of plant litter, dead wood, bryophytes and woodland herbs, while the unfenced areas had a sparse field layer and significantly higher cover of bare soils, grasses and wet pasture species. There was prolific regeneration of ash *Fraxinus excelsior* in the fenced areas, suggesting that a fairly rapid succession to ash-dominated woodland would ensue. In the current study, if cattle are excluded from the site, the W7 alder-dominated woodland may move towards more calcifuge vegetation, with a shift away from *Alnus* dominance towards *Betula pubescens* and the appearance of sphagnum mosses and more frequent *Molinia caerulea*. This process appears to be evident in wet woodland close by from which cattle have been excluded for decades. Alternatively, as the soils deepen, it may move towards oak woodland with abundant bramble (Rodwell 1991). Either way, the impact on the invertebrate fauna is likely to be profound.

The invertebrate fauna of wet woodlands in northern Europe may perhaps be adapted to cattle grazing. Aurochs *Bos primigenius*, the extinct ancestor to domestic cattle, were present in Britain in the late Pleistocene and were widespread and perhaps abundant in the Holocene (Barnett 2019, Harris and Yalden 2008). They are believed to have been in part forest animals although their preferred habitat may have been sedge beds alongside rivers (van Vuure 2002), at least seasonally. They were as large as most present-day cattle and formed herds. Perhaps their past presence explains why the cattle-grazed wet woodland in this study was as Diptera species-rich, if not more species-rich, than the ungrazed woodland.

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Online supplementary material is available at https://www.dipterists.org.uk/digest.

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# What makes a 'good' genus? Reconsideration of *Chromatomyia* Hardy (Diptera, Agromyzidae)

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## **Summary**

The genus *Chromatomyia* Hardy was erected for a subset of species in the genus *Phytomyza* Fallén. Its status has been unstable historically and it was treated as a synonym of *Phytomyza* by many authors. It was once again supported as a synonym of *Phytomyza* by Winkler *et al.* (2009) in their molecular analysis of the *Napomyza* genus group, and while the actions proposed in that study were apparently well-supported, they were rejected by a large subset of the contemporary agromyzid research community. Because of the contradiction between the results provided in that paper (and others), and the relatively broad rejection of its findings, the evidence for both synonymy and retention of *Chromatomyia* under varied conditions were weighed. In the present analysis, *Chromatomyia* is redefined by parsing and reconsidering putative synapomorphic and homoplasious characters, and by adding new data and observations. Taxonomic outliers of *Chromatomyia* to determine fit. Reconsideration of these outliers largely confirms their phylogenetic placement, correcting previous errors in classification, and revealing more uniform morphology and life history traits within lineages than previously appreciated. Criteria are examined towards what makes a "good" genus, and the different options available for recognition of *Chromatomyia* are weighed. Based on all available evidence, it is ultimately recommended that *Chromatomyia* remain a synonym of *Phytomyza*.

#### INTRODUCTION

*Chromatomyia* Hardy is a genus of Phytomyzinae (Diptera: Agromyzidae) that belongs to the *Napomyza* genus group (Spencer 1990). The genus has received a resurgence of attention following Winkler *et al.*'s (2009) most recent inclusion of that name as a junior synonym of the diverse and speciose *Phytomyza* in their phylogenetic study. To date, that study is the most thorough quantitative analysis of *Chromatomyia, Phytomyza* and other related taxa. Earlier studies investigating broader generic relationships across the family included a more limited representation of these taxa (Scheffer *et al.* 2007; Dempewolf 2001), but they are also informative and will be examined in turn.

Consensus on the status of *Chromatomyia* has been uncommon historically, and until recently, those recognising the genus were open to the possibility of reconsidering its status. It has only been since Winkler *et al.*'s (2009) synonymy that those favouring the genus have more vigorously voiced support for its recognition as a robust and valid entity (e.g. Papp and Černý 2017, 2020; von Tschirnhaus 2021), although many have so far simply chosen to continue using the genus without comment (e.g. Kahanpää 2014; Andersen 2018).

Rejection of the synonymy seems unusual on its surface. Winkler *et al.*'s (2009) conclusions reiterated views that were already accepted in whole or in part in a number of historical publications (see below), the study itself was thorough and well-considered, and their subsequent synonymy and other nomenclatural acts were justified based on their results. Because of this contradiction between the evidence provided in that paper and the relatively broad rejection of its findings, it is worth re-examining the genus in more detail to weigh the evidence both for and against its synonymy.

The present analysis will first attempt to better clarify the definition of *Chromatomyia* by discussing character sets and providing additional data. Following re-examination of those data, the generic placement of species previously included in *Chromatomyia* will be reconsidered, paying close attention to taxa identified as phylogenetic outliers in Winkler *et al.* (2009). Secondly, criteria will be examined to evaluate their usefulness in constructing a "good" genus under varying circumstances, and these criteria will be applied to *Chromatomyia*. If the genus meets aspects of those criteria, the options available for recognition of the genus will be weighed. Lastly, recommendations will be made on how to treat this genus based on the evidence.

#### History

#### •Early years

The genus *Chromatomyia* was initially provided by Hardy (1849) for those species of *Phytomyza* that have "slipper-shaped pupae, whose transformations take place entirely within the leaf", with the remaining *Phytomyza* characterised by "pupae [that] are barrel-shaped, and whose larvae enter the ground to pass the period antecedent to their final stage".

Soon after erection of the genus, *Chromatomyia* was synonymised with *Phytomyza* by Schiner (1864), and Brazhnikov (1897) chose to treat it as a subgenus of *Phytomyza*. A number of other authors treated the genus as synonymous, including Becker (1903), Frost (1924) and Frick (1952a), and some were implicit in their acceptance of the synonymy, including Hendel (1931-6), Sasakawa (1961), Nowakowski (1962) and Hering (1967). This list of authors is of course not provided to support the synonymy of *Chromatomyia*, but to illustrate that acceptance of the synonymy was not interpreted as unusual by previous authors.

#### •Griffiths

The genus was greatly redefined and clarified by Griffiths (1972, 1974, 1980) in several important studies in his series on the boreal *Phytomyza*. It was here that *Chromatomyia* again began to be consistently treated as a valid genus. His concept of the genus was clearly stated and appears to be the most widely accepted among those still accepting *Chromatomyia* as valid today. After this series of publications, however, some authors included a wider miscellany of taxa in that genus, as discussed by Winkler *et al.* (2009). This included Spencer (1990), who found issue with Griffiths' concept, and he had an "inclination... to revert to Hardy's original concept", although he was still quite uncertain as to what the actual boundaries of the genus should be.

In his study of agromyzid miners on Saxifragaceae, Griffiths (1972) first considered resurrection of *Chromatomyia* as perhaps a subgenus or genus for *Phytomyza* species on that host family, as well as for species similarly mining on Gentianaceae and Caprifoliaceae. He noted that the morphology of the puparium and the method of pupariation, which was the basis of the original concept of the genus, occurred elsewhere in *Phytomyza* in presumably non-related lineages, but he admitted that his work was preliminary and he was unsure how many times this puparium type had evolved. Winkler *et al.* (2009) later substantiated Griffiths' suspicion in their wider analysis, illustrating frequent gain and loss of these characters throughout *Phytomyza* (including *Chromatomyia*).

Recognising that the existing characters in support of *Chromatomyia* were insufficient, Griffiths (1972) narrowed the concept of the genus to those species with a specific phallic type that he interpreted as a well-defined natural group. He detailed a characteristic "supporting sclerite" of the phallus (initially discussed by von Tschirnhaus 1969) that was borne on a dorsobasal lobe of the distal section of the phallus that was positioned above a simple (not split) terminus of the ejaculatory duct. He provided further weight to the importance of the supporting sclerite by suggesting that it did not represent the distiphallus of other Agromyzidae, but was a truly novel structure with the original distiphallus absent. While confident that those species with this phallic type defined a monophyletic group, he was quite open to the idea of the lineage being treated as a subgenus of *Phytomyza* since he was aware that he did "not have sufficient historical information on the Agromyzidae to decide such questions of the absolute rank of taxa" (Griffiths 1974). He was extremely careful about adopting *Chromatomyia* in the absence of a phylogeny, which he understood would impact his homologisation of character states. He explained support both for and against the genus, citing examples, and he was open to reinterpretations of his concept and ranking, acknowledging that *Chromatomyia* might belong within *Phytomyza*. His work defining and characterising lower groups was also thorough, and this in turn informed his higher genus-level studies. Griffiths (1974) further identified two species (*C. alpigena* (Hendel) and *C. chamaemetabola* Griffiths) related to the type species of *Chromatomyia* (*C. periclymeni* (Meijere)) that left the leaf to pupariate, further undermining that state as a useful feature for the genus.

#### •Quantitative analyses

In the period from 2001-2009, agromyzid genera and their relationships began to be conceptualised in a quantitative phylogenetic context. The first two of these studies were primarily concerned with broader generic topology within the Agromyzidae, but a number of species in the *Napomyza* genus group were included and inform the current discussion. The study of Dempewolf (2001) was a morphological analysis utilising characters from multiple life stages, and Scheffer *et al.* (2007) used a molecular approach based on DNA sequence data from three unlinked mitochondrial and nuclear genes.

In Dempewolf's (2001) study, while *Chromatomyia* was weakly supported as monophyletic under certain conditions on the basis of the slipper-shaped puparium (other homoplasious characters sometimes strengthened this support depending on the topology favoured), relationships of genera in the *Napomyza* group could not be resolved, and *Phytomyza* was not supported as monophyletic. Paralleling the findings of later studies, support was provided for monophyly of the lineage made up of *Phytomyza, Chromatomyia, Napomyza* Westwood and *Ptochomyza* Hering using external adult morphological characters. Unlike those later studies, however, applying a modified concept of *Phytomyza* to the larger group was not considered.

Scheffer *et al.*'s (2007) phylogeny provided similarly weak resolution between the genera in this group, and while the species of *Chromatomyia* were not recovered together, a lack of basal resolution did not exclude the possibility of those species being more closely associated. *Phytomyza* was strongly supported as paraphyletic with respect to *Chromatomyia*, *Ptochomyza* and *Napomyza*. It is interesting that *C. scolopendri* Goureau was recovered distantly from other congeners with a high degree of support, being the sister to *Napomyza* in their topology, as this was reflected in Winkler *et al.*'s (2009) later study, and Dempewolf (2001) noted its aberrant morphology.

The study of Winkler *et al.* (2009) is the most robust analysis of the genus group to date. This quantitative study included three unlinked mitochondrial and nuclear protein-coding genes derived from 113 species. The authors sampled across all relevant genera, with heavy sampling of *Chromatomyia* and *Phytomyza*, including approximately 16% of the known species. This density of sampling is an astonishing achievement when considering the diversity of these genera and the difficulty of accessing material useful for molecular study, with many species still known only from the original type specimen(s). Similar to previous studies, *Phytomyza* was supported as paraphyletic, recovering *Ptochomyza*, a monophyletic *Napomyza*, and species of *Chromatomyia* within it, but in this instance support for placement of all of these clades within *Phytomyza* was much more robust and additional resolution within the genus was provided (fig. 57). The position of *Napomyza* within *Phytomyza* was already well known, as seen in Hendel (1931-1963) and Nowakowski (1962), but the position of *Ptochomyza* was novel.

The single sequenced representative of the bright yellow *Aulagromyza populi* group was recovered basal to *Phytomyza* sensu stricto, which is particularly interesting because it has long been recognised that this unusual group is likely unrelated to the remainder of *Aulagromyza* (Spencer 1990). The status of the group was not addressed, however, as the results could not exclude the possibility of that group belonging outside of *Phytomyza* sensu lato, and the authors provisionally excluded it from their concept of *Phytomyza* pending further study.

With respect to the placement of *Chromatomyia* species, *C. scolopendri* was again recovered basally in *Phytomyza* s.l. alongside *Ptochomyza*, *Napomyza*, and a lineage containing *C. mimuli* Spencer and one unidentified species. The remaining sequenced species of *Chromatomyia* were recovered throughout the remainder of *Phytomyza* sensu stricto, although most species segregated into two clusters that included Griffiths' *C. syngenesiae* (Fig. 4) and *C. periclymeni* groups (Fig. 1), the latter of which includes the type species of *Chromatomyia*. For the sake of convenience, these two large clusters of *Chromatomyia* species take the names of those groups (i.e. the *C. syngenesiae* group and the *C. periclymeni* group), but this is not intended to infer actual relatedness. Support for placement of non-*Chromatomyia* species in these groups was modest to strong. Backbone support within *Phytomyza* s.s. was poor, suggesting the possibility of closer association of the larger lineages containing *Chromatomyia* species, but the possibility of a monophyletic *Chromatomyia*, at least as it was conceived of previously, appeared remote.

Following the results of this analysis, Winkler *et al.* (2009) expanded the concept of *Phytomyza* to create the much more easily characterised *Phytomyza* s.l., which uses external morphological characters for diagnosis. They also included *Ptochomyza* and *Napomyza* as subgenera, as these were both recovered near the base of the phylogeny and are each readily diagnosed and supported as monophyletic, and *Chromatomyia* was included as a junior synonym of *Phytomyza*.

# CLARIFICATIONS ON CHARACTERS PROVIDED AS EVIDENCE FOR A MONOPHYLETIC CHROMATOMYIA

#### **Immature characters**

Character states of the puparium and method of pupariation can be broken down into a number of discrete states. Behaviourally, the larva remains in the mine instead of vacating it to pupariate in the ground. With respect to the puparium, the general appearance is "slipper-shaped", but this term might be misleading. It may be better characterised as a combination of two modifications – a slight dorsoventral compression of the puparium plus ventral flexure at the anterior end. Flexure at the anterior end may be visually accentuated by elongation of the spiracles at the posterior end laterally (Fig. 8) or dorsolaterally. The anterior spiracles are also elongated (Dempewolf 2001), with the increase in length being slight to pronounced. A contemporary study of *Chromatomyia fuscula* (Zetterstedt) is available in Darvas *et al.* (2000), detailing morphology of the puparium and other stadia. Additional puparia are figured here for species in the *C. periclymeni* (Figs 2-3) and *C. syngenesiae* groups (Figs 5-9). As stated by previous authors, all of these character states occur in other *Phytomyza*, and there are exceptions or less pronounced states among species of *Chromatomyia*.

While the characters appear discrete and complex, it is possible that they are linked to method of pupariation and therefore prone to convergence, which would appear to be supported by the molecular data. Puparium shape and spiracle length both facilitate pupariation within the host leaf, and any lineage exhibiting internal rather than external pupariation should be expected to converge on this suite of characters.



Figs 1-2, Chromatomyia sempervirentis (Eiseman & Lonsdale): 1, adult; 2, puparium. Fig. 3, *P. tarnwoodensis* Eiseman & Lonsdale, puparium. Figs 4-6, *C. syngenesiae* Hardy: 4, adult; 5-6, puparium. Figs 7-9, puparia: 7, *Phytomyza spinaciae* Hendel; 8, *C. palustris* (Eiseman & Lonsdale); 9, *C. tigris* (Eiseman & Lonsdale).



Figs 10-21, puparia: 10, *Chromatomyia mimuli* Spencer; 11, *C. salviarum* (Eiseman & Lonsdale); 12, *C. verbenae* (Eiseman & Lonsdale); 13, *Phytomyza anemones* Hering; 14, *P. ilicicola* Loew; 15-16, *P. ilicis* group; 17, *P. wiggii* Lonsdale & Scheffer; 18, *P. clematiphaga* Spencer; 19-20, *P. crassiseta* Zetterstedt; 21, *P. penstemonis* Spencer.

Flattening of the body provides for better fit between the leaf layers, and longer spiracles directed towards the host epidermis allows for emergence of the spiracles through the host tissue

for anchoring and respiration. While Griffiths (1974) did not elaborate on the linkage of any elements, he did recognise that "internal ("slipper-shaped") puparia are produced by species of several different groups of *Phytomyza s.l.* Clearly any attempt to group all known species according to Hardy's criterion would produce an unacceptable artificial grouping".

#### •Similar immature states in groups putatively related to Chromatomyia

Winkler *et al.*'s *Phytomyza agromyzina* clade consists of species that internally pupariate, including the *C. periclymeni* group and species of the *P. ilicis* group (Figs 14-17). *Phytomyza ilicis* Curtis was questionably included in *Chromatomyia* by Hardy (1849), as the puparia of species in this *Ilex*-mining group are flattened and exhibit clear flexure on the anterior segments. Winkler *et al.* (2009) also placed *P. agromyzina* Meigen in this larger clade, and while puparia of this species are normally formed externally, some individuals form the puparium in the exit slit or even entirely within the mine (Eiseman and Lonsdale 2018); no flattening or flexure is evident in the puparium of this species.

Winkler *et al.* (2009) additionally recovered the *Chromatomyia syngenesiae* group as a relative of the *P. robustella* and *P. ciliata* groups, both of which similarly exhibit internal pupariation, and all of which are Asteraceae feeders. Some representatives of the *P. robustella* group have slightly flattened puparia with slight anterior flexure (such as the examined *P. continua* Hendel), but similarities to *Chromatomyia* species are more pronounced in the *P. ciliata* group. The puparia of examined species in that group (*P. arnicivora* Sehgal, *P. aurata* Griffiths, *P. campestris* Griffiths, *P. farfarae* Hendel, *P. hyperborea* Griffiths, *P. hypophylla* Griffiths, *P. lugentis* Griffiths, *P. oreas* Griffiths) exhibit slight to pronounced flexure and are sometimes slightly flattened.

#### •Similar immature states elsewhere in Phytomyza

Internal pupariation, as mentioned before, is also evident in species belonging to putatively nonrelated taxa. Griffiths (1974) already noted the presence of internal pupariation in the *P. anemones* group. The puparia of most examined species in this group (*P. aldrichi* Spencer, *P. anemones* Hering (Fig. 13), *P. fallaciosa* Brischke, *P. hellebori* Kaltenbach, *P. kaltenbachi* Hendel) reveal slight to strong flexure of the anterior segments, and all but two (*P. aldrichi*, *P. kaltenbachi*) have slightly to strongly flattened puparia. Winkler *et al.* (2009) placed the *P. anemones* group in their *P. albipennis* clade, which also houses members of the *P. atomaria* group that pupariate internally in Plantaginaceae leaves. Examined puparia of these species (*P. crassiseta* Zetterstedt (Figs 19-20), *P. penstemonis* Spencer (Fig. 21), *P. plantaginis* Robineau-Desvoidy) show their shape to be slightly flattened to fully rounded, with flexure of the anterior segments. Pupariation is also similar for *P. clematiphaga* Spencer (an unplaced species in *Phytomyza* s.s.) (Fig. 18) and the *C. mimuli* group (Figs 10-12)

In Winkler *et al.*'s (2009) *Phytomyza aquilegiae* clade, members of the *P. obscura* group also sometimes pupariate in their mines, but this is done via a pre-made exit slit, instead of having the spiracles project through the leaf epidermis. Similar states occur in *P. actaeivora* Eiseman & Lonsdale, *P. aesculi* Eiseman & Lonsdale, and the *P. petoei* group (*P. scotina* Hendel, *P. thymi* Hering, *P. petoei* Hering examined), where the puparium is rounded and with no flexure.

#### •Exceptions to immature states within Chromatomyia

Within *Chromatomyia*, complications arise when more closely examining life history and puparia where they are known, revealing more heterogeneity than previously appreciated. *Chromatomyia alpigenae* Hendel and *C. chamaemetabola* (Griffiths) are notable exceptions in that these Caprifoliaceae-miners (*C. periclymeni* group) pupariate externally (Griffiths 1974). The puparium of the latter species is barrel-shaped, with the anterior end apparently not exhibiting

ventral flexure (the operculum is missing in the examined holotype), suggesting a reversal of morphological states following loss of internal pupariation. *Chromatomyia palustris* (Eiseman & Lonsdale) mines on Saxifragaceae, and one female paratype was seen to pupariate externally (Fig. 8; Eiseman and Lonsdale 2018); the puparium of this species is slightly flattened with flexure at the anterior end. More thorough examination of species will likely contribute to the grey area between immature character states previously considered to be binary.

Examination of the puparia of internally pupariating species assigned to *Chromatomyia* reveal further deviation from "typical" states. Barrel-shaped puparia (or puparia with an almost indiscernible compression) are evident for feeders on monocots (*C. arctagrostidis* Griffiths, *C. cinnae* Griffiths, *C. cygnicollina* Griffiths), rosids (*C. leptargyreae* Griffiths), asterids (*C. autumnalis* (Griffiths), C. *ixeridopsis* Griffiths, *C. primulae* (Robineau-Desvoidy), *C. senecionella* (Sehgal), C. *syngenesiae* Hardy), Saxifragaceae (*C. tiarellae* (Griffiths)), and other Caprifoliaceae-feeders (*C. nigrilineata* Griffiths, *C. ramosa* (Hendel), *C. scabiosae* (Hendel), *C. sempervirentis* (Eiseman & Lonsdale)). Furthermore, *C. ramosa* exhibits no flexure of the anterior segments and some Caprifoliaceae-feeders exhibit very slight flexure. Broader sampling is required to determine the amount of variation in these traits both within and across species.

#### •Other considerations of homology

A final complication involves re-evaluation of the polarity of the relevant immature characters. While it has been presumed that internal pupariation has been converged upon multiple times within *Phytomyza*, it can be easily reinterpreted as being the ancestral state for *Phytomyza* s.l. Internal pupariation is seen in basal and putatively basal lineages, including *Ptochomyza*, *Napomyza*, the *Aulagromyza populi* group, *Phytomyza gymnostoma* Loew, and the *C. mimuli* and *C. scolopendri* groups, as well as in many other genera. Since directionality on character states cannot be confidently established here, caution must be used in treating either internal or external pupariation as derived states.

A character of possible phylogenetic utility is puparium colour, with white puparia typical for many *Chromatomyia* species. Implicit usage of this character can already be inferred by Spencer's (1990: 255) suggestion that *C. autumnalis* "may correctly belong in *Chromatomyia*, despite the black puparium". He continued to mention, however, that "in *Chr. pseudogentii* the puparium is also black (see Gentianaceae)". It is interesting that white puparia are seen in many species of the putatively related *P. robustella* and *P. ciliata* groups, but not the *P. ilicis* group. White puparia are also seen in some species of non-related groups. Many species within *Chromatomyia* proper have brown puparia, and while some of this may be due to seasonal effects, additional phylogenetic work may reveal patterns here and elsewhere.

An additional character of potential use was discussed by von Tschirnhaus (2021), who noted that the larvae of some species use cement-like faecal droppings during the course of internal pupariation. This hypothesis is based on extremely few observations in *Chromatomyia* and *Calycomyza* Hendel, however, so it would be useful to demonstrate the distribution of this character more widely in the genus group before applying it phylogenetically.

In considering the leaf mines themselves, no characters useful for diagnosis of *Chromatomyia* present themselves. Most species form entirely linear mines with frass in discrete grains or beaded strips, with some Caprifoliaceae feeders making primary blotch mines. There is much more diversity of mines in "non-*Chromatomyia*" *Phytomyza*, but many that pupariate internally have mines strikingly similar to those of *Chromatomyia*.

#### Male genitalic characters

The homology of the distal section of the phallus is reinterpreted here, and its complexity and importance in phylogenetic consideration is recognised. Building on Griffiths' (1972, 1974)

original characterisation, the distal section of the phallus (i.e. past the basiphallus, hypophallus and paraphalli) and its associated structures are here all considered to represent the distiphallus proper. In species treated as *Chromatomyia*, this includes both the tube-like component, which is ventral, angled away from the body and a continuation of the ejaculatory duct, and the lobe bearing the supporting sclerite, which is a dorsobasal elaboration of the distiphallus that is angled upwards, or towards the body (Figs 39-41).

The distiphallus is therefore not absent, as assumed by Griffiths and some later authors, although the ventral tubular component is narrowed and often desclerotised so that the boundary between it and the ejaculatory duct is obscured. Regarding the present interpretation of the ejaculatory pore being at the end of this flagellar structure, we are in agreement with von Tschirnhaus (2021), although he agrees with Griffiths in believing the distiphallus to be absent. Sclerotised remnants of the distiphallus are clearly evident in species of the Chromatomyia syngenesiae group such as C. horticola (Goureau) (Figs 30-34). Apparent loss is taken to an extreme in species of the C. periclymeni group such as C. sempervirentis (Figs 22-25), where the fully desclerotised tube of the distiphallus resembles a curved, membranous flagellum. A highly similar flagellate structure is often seen emerging from the anteromedial surface of the hypophallus in many other *Phytomyza*, for which it may be easily confused (see discussion of *P*. paraciliata (Godfray) below). In some species, the supporting sclerite is largely to entirely desclerotised, but it is usually more evident than the ventral tube (e.g. P. spinaciae Hendel - Figs 35-36). In these cases, and in many others where sclerotised portions are reduced or narrow and threadlike, the phallus must be observed under a high-powered microscope with increased contrast in order to detect the relevant parts.

Griffiths (1974) also noted that the terminus to the phallus (Fig. 25) is simple/unbranched in *Chromatomyia*, not bifid, but this state may not be synapomorphic and its phylogenetic value at the generic level is yet to be established. A simple terminus, as opposed to the split, bifid condition, occurs in many lineages of *Phytomyza s.l.*, including the basal *C. mimuli* and *C. scolopendri* groups, and *Ptochomyza* and *Napomyza*. It also occurs in many other genera of Agromyzidae in both subfamilies, and in the *Napomyza* genus group, it can be found in *Gymnophytomyza*, the *Aulagromyza populi* group and some other *Aulagromyza* Enderlein. With this in mind, it is possible for the bifid condition to be a secondary state (not ancestral) in *P. gymnostoma* and species of *Phytomyza* s.s., but this is in need of verification.

Given this re-evaluation, putatively synapomorphic genitalic characters defining *Chromatomyia* are as follows: distiphallus angled ventrally; distiphallus with small membranous dorsobasal lobe bearing a supporting sclerite. A short, undivided and well-sclerotised distiphallus is here considered to be the retained ancestral state, with desclerotisation of the distiphallus and its supporting sclerite occurring in many species.

#### •Taxa to be removed from Chromatomyia

Now that the parsing and homologisation of characters has been discussed, it may be informative to return to the phylogeny of Winkler *et al.* (2009) (Fig. 57) to apply these characters to the putative outliers to see if they should truly be considered *Chromatomyia*.

Starting from the base of *Phytomyza* s.l., there are the *C. mimuli* and *C. scolopendri* groups, for which the species *C. mimuli* (Figs 42-46) and *C. scolopendri* (Figs 47-50) have been examined and illustrated. For both of these species, it appears as though classification as *Chromatomyia* is inappropriate, with similarities being superficial in nature.



Figs 22-25, Chromatomyia sempervirentis (Eiseman & Lonsdale) (a member of the C. periclymeni group) male genitalia: 22, epandrium, posterior; 23, postgonite, lateral; 24, supporting sclerite of the distiphallus, detail; 25, phallus, left lateral. Figs 26-29, Phytomyza agromyzina Meigen (an outlying species of Phytomyza in the phylogeny of Winkler et al. (2009), recovered within a lineage of "Chromatomyia" species) male genitalia: 26, epandrium, posterior; 27, postgonite, lateral; 28, phallus, ventral; 29, phallus, left lateral.


Figs 30-34, *Chromatomyia horticola* (Goureau), male genitalia: 30, hypandrial complex without phallus, left lateral; 31, epandrium, posterior; 32, distiphallus (including V-shaped supporting sclerite), dorsal; 33, phallus, ventral; 34, phallus, left lateral.

For *Chromatomyia mimuli*, similarities are apparent with *C. verbenae* (Eiseman & Lonsdale) (Eiseman and Lonsdale 2018: figs 389-393) and *C. salviarum* (Eiseman & Lonsdale) (Eiseman and Lonsdale 2019: figs 110-115), which are here included in the *C. mimuli* group. The host plant is a member of the Lamiales, the phallus is long and slender and the posterior margin

of the epandrium above the surstylus bears tubercle-like setae. Although these tuberculate setae are commonly found elsewhere in the family, they are rare in the genus group and very likely to be a defining character of this particular lineage. A dorsal lobe is present on the phallus, but in light of re-evaluation, it now appears to be of a different origin – it is best interpreted as a dorsal hood produced from the basiphallus that covers the remaining distal components of the phallus. The paired sclerites of the basiphallus are seen to continue laterally along the sides of this hood. The lobe bearing the supporting sclerite in most other *Chromatomyia*, such as *C. periclymeni*, is derived from the distiphallus and confluent with the ejaculatory duct, and as such, it is narrow and more centrally positioned; the ends of the basiphallus laterally flank this smaller structure. The difference in position is obvious when compared to the analogous structure of *C. horticola* (Figs 32-34). The distiphallus of *C. mimuli* itself does appear to converge upon the state seen in *Chromatomyia*, being simple, narrow and ventrally angled, although the ventral curve occurs at a different position. In *C. verbenae* and *C. salviarum*, but not *C. mimuli*, the base of the distiphallus also splits off into a minute dorsal structure. While these analogous states are misleading, there is gross overall dissimilarity when compared to other *Chromatomyia* species.

For *Chromatomyia scolopendri*, the situation is much clearer, despite the argumentation of von Tschirnhaus (2021). There are apparently no similarities to *Chromatomyia* whatsoever aside from the extremely homoplasious and possibly even plesiomorphic larval characters discussed above. The distinct genitalia were noted by Spencer (1990), who transferred the species to *Chromatomyia* on the basis of the puparium and mode of pupariation alone. Neither a dorsal lobe nor a supporting sclerite is present, and the distiphallus is angled dorsally, not ventrally. While the dorsally angled distiphallus may have previously been interpreted as a supporting sclerite, closer examination of the structure reveals that it bears the ejaculatory pore. The ventral sclerotised portion, which may have been mistaken for the ejaculatory duct and distiphallus before, is actually a long medial sclerotised hypophallic plate that extends to the mid-ventral section of the distiphallus where it articulates with the paraphalli. As an additional note, the genitalia of the fern-feeding *C. masumiae* Sasakawa (Sasakawa 2010: figs 1-3) are highly similar to those of *C. scolopendri* and the two species should certainly be placed in the same species group.

Inside the Chromatomyia periclymeni and C. syngenesiae species groups, there are species that are traditionally considered to be "Phytomyza", and outside of these two groups, there are additional "Chromatomyia" outliers that appear to have been misplaced (P. paraciliata, C. clematoides Spencer). Beginning with the Chromatomyia outliers, exclusion of P. paraciliata from Chromatomyia seems straightforward, as already discussed by von Tschirnhaus (2021). While this species has not been examined directly, we agree with Spencer (1990) in finding the genitalia to be typical of members of the P. ciliata group (Spencer 1990), in that the distiphallus is bifid and strongly angled dorsally, immediately excluding those species based on our refined genitalic concept of Chromatomyia. The flagellate structure on the hypophallus (Godfray 1985: fig. 1), however, certainly resembles the deviated distiphallus of "true" Chromatomyia species. Similar placement of C. clematoides outside of Chromatomyia supports Winkler et al.'s (2009) suggestion that the genitalia are instead consistent with those of the P. loewii group. Examination of these structures (Figs 51-56) confirms the distiphallus to be bifid and angled dorsally; the ventral component does not represent the distiphallus, instead being a medial sclerite of the unusual hypophallus. The form of the distiphallus of C. clematoides is fascinating because the base has split into one pair of additional short processes that give the segment a striking similarity to the supporting sclerite of Caprifoliaceae-mining Chromatomyia.

#### •Phytomyza species better placed within Chromatomyia

Within the *Chromatomyia periclymeni* and *C. syngenesiae* groups, Winkler *et al.* (2009) recovered a number of species not previously considered to be *Chromatomyia: P. spinaciae* Hendel, *C. ceanothi* (Spencer) (this combination made by von Tschirnhaus 2021) and *P. agromyzina* (Fig. 57). A male of *P. spinaciae* has been examined, and the genitalia (Figs 35-36) strongly support placement in the *C. syngenesiae* group, and examination of a puparium reveals it to be "slipper-shaped". The genitalia are highly similar to those of *P. hebronensis* Spencer, which Winkler *et al.* (2009) noted was "nr. *P. spinaciae*". In both species, the distiphallus is strongly bent ventrally past a sclerotised structure readily classified as a supporting sclerite. With respect to *C. ceanothi*, and in agreement with von Tschirnhaus (2021), the male genitalia (Spencer and Steyskal 1986: fig. 1146) also suggest ventral deviation of the ejaculatory duct through and beyond a sclerotised plate that may represent a supporting sclerite.

Characterisation of *Phytomyza agromyzina* (Figs 26-29) is more difficult, as numerous dissections failed to reveal the path of the highly membranous ejaculatory duct until structures were stained. The ejaculatory duct now appears to be strongly widened to a large chamber that nearly fills both the hypophallic lobe and the space behind the base of the sclerotised distiphallic structure; the ejaculatory pore is near the base of this sclerotised structure, which does not serve to surround the ejaculatory duct at all, but is a flat dorsal extension emerging from the dorsal surface of the duct. As such, this phallic structure meets the definition of a proper "supporting sclerite" as in other *Chromatomyia*. It cannot be determined if the distiphallus is angled ventrally as in most other *Chromatomyia*, since this portion of the segment is fully atrophied. At the moment, this is an intriguing yet tentative hypothesis requiring verification, as the morphology of the adult is unusual and the puparium does not provide any supporting sclerite and its recovered phylogenetic position (Winkler *et al.* 2009) suggests that any "atypical" states are secondary conditions.

While all species of *Chromatomyia* could not be sampled by Winkler *et al.* (2009), future phylogenetic analysis will likely reveal additional outliers that on first glance, do not appear to be where they "should" be. Rejection of these revelations based on *a priori* assumptions should be carefully reconsidered. In the present case, the phylogeny of Winkler *et al.* (2009) challenged pre-existing concepts of *Chromatomyia*, and appears to have aided in delimiting a newer and more consistent concept of the genus truer to its actual evolutionary history.

#### •Other considerations of homology

As a final comment on the homology of structures, Griffiths (1972, 1974) further expanded on the genitalic terminology of species classified as *Chromatomyia* by introducing new terms such as "medial lobe", "trough-like sclerite" and "wedge-shaped sclerite". All of these terms appear to reinforce the internal consistency of species in the genus, but they are in fact misleading since there is no evidence to suggest that they arose as *de novo* structures. These terms have been used by later authors, and they do have functional descriptive value and are possibly homologous, so we do not necessarily recommend that the terms be relabeled or eliminated, only re-evaluated in an appropriately wider context.

A more parsimonious solution would be to interpret these sclerites as derivatives of a preexisting structure found in other members of the genus group. While establishing transitional series between forms is difficult and structures between any two species can appear to be dissimilar, homology should be assumed until analysis can determine homoplasy (Hennig 1966). Since these structures are located on the ventral lobe of the phallus at the junction between the basiphallus and the distiphallus, it is sensible to consider them components of the hypophallus.



Figs 35-36, *Phytomyza spinaciae* Hendel: 35, phallus, left lateral; 36, supporting sclerite of distiphallus, detail. Figs 37-41, "*Chromatomyia*" male genitalia: 37, *C. nigra* (Meigen), phallus, left lateral; 38, same, ejaculatory apodeme; 39, *C. fuscula* (Zetterstedt), phallus, left lateral; 40, same, ventral; 41, detail of supporting sclerite of distiphallus. Arrow indicates base of distiphallus, and origin point of supporting sclerite.



Figs 42-46, *Chromatomyia mimuli* Spencer, male genitalia: 42, epandrium, posterior; 43, ejaculatory apodeme; 44, postgonite, left lateral; 45, phallus, left lateral; 46, same, ventral.



Figs 47-50, *Chromatomyia scolopendri* (Goureau), male genitalia: 47, epandrium, posterior; 48, phallus, ventral; 49, same, left lateral; 50, postgonite, left lateral.



Figs 51-56, *Chromatomyia clematoides* (Spencer), male genitalia: 51, epandrium, posterior; 52, postgonite, left lateral; 53, ejaculatory apodeme; 54, phallus, ventral; 55, detail of distiphallus; 56, phallus, left lateral.

Perhaps a novel origin was assumed because these structures are sometimes slightly inset or anterior in position, but this is not unusual if taxa across the subfamily are surveyed. The form, position, or absence of the hypophallic sclerites certainly hold important phylogenetic value, but they must be revisited in a broader analysis of the genus group to aid in polarising states to confidently establish transitional series.

Papp and Černý (2020) also noted reduction of the ejaculatory apodeme as characteristic of most *Chromatomyia*. While the structure does often appear to be smaller in many species, there is much overlap in size with the same structure in other *Phytomyza* species and other Agromyzidae. Since this character state is commonly found elsewhere, especially in *Phytomyza*, and the character itself is continuous, not binary, it is of little use at the genus level. It will certainly, however, prove to be of some phylogenetic importance at lower levels in the future.

# CRITERIA FOR CONSIDERATION IN THE ERECTION OF GENERA Monophyly

Before evaluating the evidence for *Chromatomyia*, it seems relevant to consider what factors are important in the construction and recognition of a genus. While there are exceptions, it is usually considered ideal at the very minimum for a genus to represent a single monophyletic lineage that does not render other such groups non-monophyletic by its presence.

A natural conclusion stemming from the importance of monophyly is that the limits of genera and other higher groups should be developed using phylogenetic knowledge whenever possible to better recognise and evaluate natural groups in their utility as named entities. This system of naming and classification will ideally reflect evolutionary history and is theoretically recoverable through scientifically repeatable means. The branches upon a phylogenetic tree and the synapomorphous features plotted upon them can be critically evaluated. Evolutionary relationships exist, often independent of our ability to initially intuit them, and serve as an excellent verifiable standard from which to base our activities.

This system allows for "predictiveness", wherein taxa yet to be characterised or described, or specimens not easily identified (e.g. life stages or sexes not exhibiting diagnostic structures) can be located in a phylogenetic context and be more easily placed. This is not an esoteric exercise, as predictive classifications are essential in many areas, including diagnostic activities where it is important to know in a timely manner whether or not a specimen belongs to a lineage that is native or invasive to a region or is pestiferous on certain plants; in the development of pesticides by examining patterns of resistance and efficacy; and in mitigating damage from insectborne pathogens by comparison to related model taxa for which treatments have been developed, etc. The importance of this is underlined for Agromyzidae, where there are a number of devastating plant pests, many of which are polyphagous and have readily dispersed globally. Two of these are widespread species that have been classified as *Chromatomyia* and are regularly problematic: *C. horticola* and *C. syngenesiae*.

Monophyly additionally increases the stability of a classification by more confidently establishing the relationships of lineages relative to their type species, hopefully reducing the probability of future nomenclatural changes. Stability is further served by instilling confidence in relationships and classifications by transparently displaying the scientific justification and methodology used in decision-making.

#### Utility

Beyond the criterion of monophyly, the usefulness of a higher group is linked to its practical utility in diagnostics, communication and understanding. Firstly, higher groups should be ideally diagnosed by multiple complex characters that are easily observed and present in all species, aiding in recognition and memorability. The diagnostic utility of a group is often linked to its

monophyly, as characters are more likely to be homologous, and similar in detail, and are possibly reflected by parallel characters in other sexes and life stages, be they morphological, ecological or behavioural. A fuller suite of exclusively held, homologous characters allows for better understanding of taxa as living organisms, and facilitates deeper communication and debate. Understanding is further facilitated by developing taxa that are moderately sized, because "genera that are not too big or too small... are easier to handle and memorise" (Humphreys and Linder 2009).

This pragmatism in classification is a persistent idea dating at least to Linnaeus, who provided generic names that were "clear and related to things that could easily be identified and placed in a systematic context ... [that]... would, by virtue of that same system, be memorised" (Humphreys and Linder 2009).

#### Geologic age

An additional criterion suggested by Hennig (1966) for use in hierarchical ranking was the geological age of groups, as this would aid in eliminating subjectivity. Unfortunately, not enough is yet known about the age of agromyzid genera to allow for this to adequately inform the current discussion, and the uniform application of this concept across dipteran families of varying age is problematic (e.g. Agromyzidae vs Tipulidae).

#### **Conflicting benefits**

Conceptually, these rules are easy to follow, but in reality, there are difficulties and nuances in delimiting higher taxa. Firstly, and perhaps most importantly, a phylogeny may be lacking. This is unfortunately common in entomology, and perhaps especially so in dipterology, where an explosion of diversity sharply contrasts the paucity of phylogenetic knowledge available.

If phylogenies exist, there may be competing topologies based on the same or parallel character systems, and authors may be tempted to elevate a preferred data set over others. If there is consensus on topology, the naming of monophyletic groups on that tree is subjective and alternatives are open to debate.

Even in the best of cases, readily diagnosable groups may not always present themselves, and differentiation from similar taxa may not be possible unless less immediately observable character sets are examined, such as genetic sequence data or internal structures requiring dissection for exposure.

All of these challenges are present in Agromyzidae, but the goal should be to develop a system that maximises the above criteria to construct the best predictive and practical classification possible. Evaluating all elements in the delimitation of higher taxa involves the balancing of quantitative and qualitative aspects, and this can be as much art as science.

The criterion of monophyly is also not universally embraced. Firstly, the reality of biological speciation necessitates the acceptance of non-monophyly in transitory periods during the emergence of species (Hörandl and Stuessy 2010). At higher levels, the recognition of paraphyletic entities may be a pragmatic exercise, increasing the utility of named groups at the expense of monophyly. Paraphyletic groups may be more readily identified and of higher diagnostic value, as has been documented for speciose plant genera (Nordal and Stedje 2005; van Wyk 2007). Paraphyletic groups are also used to facilitate broader societal understanding of taxa with enough similarity in morphology and life history to justify their recognition. This is perhaps best known for vertebrate classes (fishes exclusive of terrestrial vertebrates; reptiles exclusive of birds and mammals), where little conceptual effort is required to recognise these groups while acknowledging that other such taxa were issued from them. Examples from insect groups are also evident, such as Symphyta (Hymenoptera) and the nematocerous Diptera. Even informally

recognising polyphyletic taxa such as lichens sometimes has strong practical utility (Gargas *et al.* 1995; Lutzoni *et al.* 2001).

#### EVALUATING THE EVIDENCE FOR CHROMATOMYIA

Given the above criteria for recognising genera, how can we apply these concepts to the debate surrounding *Chromatomyia*?

#### Monophyly

Regarding the issue of monophyly, is there enough evidence to support *Chromatomyia* as a natural group? The answer is "perhaps". After eliminating homoplasious characters and characters of highly dubious homology, morphological support is narrowed to only two characters of the distiphallus, although this composite state seems fairly convincing. Multiple phylogenetic analyses (Scheffer *et al.* 2007; Winkler *et al.* 2009) have suggested that this phallic type was derived and lost multiple times, but in the present study, homoplasy seems to be far less extensive than assumed now that outliers have been re-evaluated.

Use of these molecular phylogenies has been insightful in clarifying species group compositions by identifying species that have been incorrectly classified by previous authors. While work still needs to be done in identifying and reinterpreting atypical species, there is the possibility that most *Chromatomyia* can indeed be grouped into lineages of relatively uniform composition. That is, only those species belonging to what we are provisionally calling the *C. periclymeni* and *C. syngenesiae* species groups. Regarding the relationships of these two groups, while they were recovered as unrelated in molecular analyses, the statistical support for their division was comparatively low, allowing for the possibility of closer association or even direct relatedness.

Even if a narrowed *Chromatomyia* is supported as monophyletic, the most serious issue regarding its recognition is the fact that all phylogenetic analyses of the group have shown that *Phytomyza* cannot be considered monophyletic if one or more of *Chromatomyia*, *Napomyza* or *Ptochomyza* are recognised as full genera (Dempewolf 2001; Scheffer *et al.* 2007; Winkler *et al.* 2009). This supports assumptions based on morphological evidence by previous authors such as Nowakowski (1963) and even Griffiths (1974, in part), it was the primary reason for reducing *Ptochomyza* and *Napomyza* to subgeneric level in Winkler *et al.* (2009), and it is perhaps paramount among all arguments for synonymy of *Chromatomyia*. Even those supporting retention of *Chromatomyia* as a full genus recognise that "*Phytomyza* in its present form is a huge paraphyletic group" (Papp and Černý 2020).

If it was desired to retain *Chromatomyia* as a full genus while sustaining monophyly in all related groups, the solution would be to break up *Phytomyza* into multiple equivalent genera. This would result in a much-narrowed *Phytomyza*, a genus-level *Napomyza* and *Ptochomyza*, a dubiously monophyletic *Chromatomyia*, and numerous other exclusively monophyletic clades formerly considered *Phytomyza* that would have to be provided generic names. The difficulty with this solution is that the newly recognised genera would not be easily diagnosable, as most groups can only be identified through examination of the male genitalia, most species groups are presently ill-defined or not defined and their composition uncertain, and the internal structure of *Phytomyza* is still quite poorly understood with associations between many species and groups unknown. Most "unplaced" species listed in Winkler *et al.* (2009) would also defy generic placement, attesting to how far is left to go before we can consider our knowledge of the group comprehensive. As such, division of *Phytomyza* s.l. should be avoided until the internal structure of the genus is better known, and even species groups themselves should be used with caution.



Fig 57. Maximum likelihood phylogeny of *Phytomyza* and *Chromatomyia* species and related genera derived from analysis of three genes. Originally published in Winkler *et al.* (2009: fig. 1), with coloured text and boxes added to better illustrate the lineages discussed here. These specifically include the subgenera *Phytomyza* s.s., *Ptochomyza* and *Napomyza*; and the five recovered lineages of *Chromatomyia* (see red boxes in figure), of which the *C. mimuli* group occurs basally outside *Phytomyza* s.s., and four others occur throughout *Phytomyza* s.s. Two of the major lineages highlighted – the *C. periclymeni* and *C. syngenesiae* groups – are provisional labels based on the names of two important groups contained within.

Nimis (1998) noted that "when the taxonomy of a given group is not settled, and if there is no clear evidence that the segregates are unrelated to the old genus, the tentative segregation should preferably occur at subgeneric level; the new taxonomic information will be there, without causing unnecessary, and often provisional, name changes". With this in mind, it would not be recommended to resurrect *Chromatomyia* past the level of subgenus.

#### Utility

With regards to generic utility, the concept of *Phytomyza* s.l. is an attractive one, given that the wider group is well-supported and readily diagnosed by external, easily recognised characters in the adults of both sexes - see Dempewolf (2001), Winkler *et al.* (2009) and Lonsdale (2015). Species share proclinate orbital setulae in combination with a costa that extends to vein R<sub>4+5</sub>, M<sub>1</sub> is weak or spectral, and crossvein dm-m is absent or situated basally. The use of adult characters is also of importance, as many specimens are collected as adults, and agromyzid specimens collected as immatures must often be reared to adult characters is therefore of great use to systematists and other workers who are primarily interested in the practical pursuit of providing names for organisms.

This utility in diagnostics, combined with the monophyly of the larger genus, makes usage of *Phytomyza* s.l. the most elegant solution to the largest issue surrounding classification in the genus group.

Conversely, *Chromatomyia* is only defined by two characters of the male distiphallus, and supporting characters (puparium shape and method of pupariation) are of far lesser utility due to homoplasy, being inconsistent among species and regularly paralleled elsewhere. Even the genitalic characters, if available, are sometimes so modified that they obscure identity, becoming highly desclerotised (e.g. *Phytomyza spinaciae*) or exceptionally modified (e.g. *C. nigra* (Meigen) (Figs 37-38) and possibly *P. agromyzina*), being recognisable only to a subset of experts already familiar with these derived lineages. The regularity with which non-related species have been incorrectly dumped into either *Chromatomyia* or *Phytomyza* by numerous authors historically is a testament to the difficulty of these characters. The few case studies of phylogenetic "outliers" examined here show that convergence is a serious issue, and that misinterpretation of both homologous and parallel states is inevitable. This system is therefore impractical because the essential features are not "good", and if *Chromatomyia* is to be recognised in any capacity in the future, we reiterate that it is certainly best used below the genus level.

The impracticality of this situation is further underlined when examining identification keys including *Chromatomyia* species. Spencer and Steyskal (1986), for instance, could not differentiate *Chromatomyia* and *Phytomyza* externally and combined all species in a single key in their treatment of the United States fauna. In their key, *Chromatomyia* species came out in 18 different places! While it is expected that entities such as species groups (or other groups not regulated by the *Code of Zoological Nomenclature*) might be scattered throughout a key, lineages chosen to represent genera should ideally be more diagnosable. In another example, Papp and Černý's (2019) Hungarian species key of 169 couplets divides *Chromatomyia* and *Phytomyza* species in two places at the beginning, using exclusively male genitalic characters. Species keys must be practical above all other considerations, but in this case, the attempt to segregate *Chromatomyia* resulted in a key that that demands a dissected male for all identifications (although it is recognised that many *Phytomyza* species would still require genitalic characters for verification anyway).

Beyond diagnostics, *Chromatomyia* does not appear to be worth retaining on the basis of other utilitarian criteria that would aid in either communication or understanding of the group as whole organisms or ecological components. There is not enough exclusive homogeneity among

members in aspects of morphology, host group or life history features to allow for easy recognition, even as a paraphyletic entity. It appears to be more appropriate to recognise a heterogeneous but easily diagnosed *Phytomyza* s.l. that in turn is subdivided into species groups that are themselves better defined by more uniformity of the genitalia, host, life history, and hopefully external characters.

#### The argument made in favour of Chromatomyia

Commentary on the status of *Chromatomyia* following its most recent synonymy has thus far been provided only by von Tschirnhaus (2021). The paper was rich in detail, and we agree that among these details, three are positive contributions to the discussion: a useful historical summary; notes on the course of the ejaculatory duct and its curvature at the supporting sclerite; and preliminary observations on the use of cement-like faecal droppings by the larva that invite further study (see above).

Elsewhere, von Tschirnhaus (2021) noted that *Chromatomyia* should be retained because most Old World experts continue to recognise the genus and the genus has been used in many recent publications. This *argumentum ad populum* suggests that majority rule is a justifiable method to dismiss a scientific hypothesis, however, rather than using direct evidence. Evidence presented in support of *Chromatomyia* included unsupported genitalic homologies (see discussion of hypophallus and ejaculatory apodeme above), *argumentum ad verecundiam, argumentum ad antiquitatem,* and the use of opinion proffered in agreeable morphological papers. While those expressing these opinions may indeed be correct, this does not itself support the concept scientifically.

In rejecting the synonymy, conclusions from Winkler *et al.*'s (2009) study were dismissed as improbable without testing or demonstrating proof for dismissal. For example, while it was concluded that some specimens were misidentified based on their phylogenetic placement, those specimens were not re-examined to verify their identity. In the present study, efforts were made to demonstrate that the positions of outliers in Winkler *et al.*'s study are actually well-supported (or at least not improbable), with *C. scolopendri* and *C. mimuli* being two obvious examples based on male genitalic morphology, as well as the ecological and physiological differences listed by von Tschirnhaus (2021). Von Tschirnhaus (2021) also criticises the use of "only 18" *Chromatomyia* species in Winkler *et al.*'s analysis, and the use of too few genes. There were no comments provided, however, to suggest how many species or genes would be considered adequate, or even to point to particular species whose inclusion would have caused a different result, or genes that would provide data enough to be conclusive.

Most of the remaining points made may be valid in part, but these are largely unrelated to the issue of *Chromatomyia*'s status. One of these points is the discussion of "crown groups", which it should be noted is separate from the cladistic issue of establishing the internal structure of the *Napomyza* genus group based on synapomorphy and isolating equivalent lineages in the designation of genus groups (developed in the "monophyly" section provided above).

#### CONCLUSIONS

We have attempted to illustrate that of all of the options available in considering the status of *Chromatomyia*, recognising the group as a full genus is undesirable phylogenetically and unwarranted from a practical point of view.

*Chromatomyia* is impractical to diagnose on the basis of male genitalic characters, sometimes even when they are available under the microscope, because of problems with convergence, secondary modification, and ease of misinterpretation with similar (or sometimes quite dissimilar) structures. Diagnosis of the genus may be more convenient for taxon experts familiar with included species, being able to work upwards from initial species or species-group

recognition, but for most people engaged in specimen identification, the genus may act as an unintentional barrier.

Species also do not demonstrate an internal and exclusive homogeneity in morphology or life history to allow for recognition on the basis of other functional criteria such as communication and understanding. The use of immature character states is especially problematic, as there are exceptions, and states are readily subject to convergence because they appear to be linked to the process of internal pupariation. Winkler *et al.* (2009: 277) "estimate that [internal] pupariation must have evolved at least eight times in the *Phytomyza* group (six in *Phytomyza* sensu stricto; see Fig. 2)". Although it is yet to be determined how useful these immature characters are phylogenetically, their utility is apparently best applied at lower levels.

Even if *Chromatomyia* is eventually demonstrated to represent a natural unit, its retention is not recommended due to its limited practical utility at this time. Alternately, the option of accepting Winkler *et al.*'s (2009) concept of *Phytomyza* s.l. is much more attractive, as this genus is readily and easily identifiable, of high utility, and likely to be monophyletic. In contrast, the basal, monophyletic genus-level groups *Napomyza* and *Ptochomyza* are useful and subsequently preserved as subgenera, maintaining their diagnostic utility and associated information.

As the classification of Winkler *et al.* (2009) is sound, and counter-arguments do not include evidence to refute their findings, it is necessary here to reverse all nomenclatural acts related to the recognition of *Chromatomyia* by von Tschirnhaus (2021). This extends to recombining the remaining three *Chromatomyia* species never before placed in *Phytomyza*: *P. cepelaki* (Černý), COMB. NOV., *P. kerteszi* (Černý), COMB. NOV, and *P. masumiae* (Sasakawa) COMB. NOV. To individually reverse all the nomenclatural acts therein would be laborious and potentially unproductive by inviting an unresolvable back-and-forth of reverse actions, so it should be sufficient to state that we consider all species currently combined as *Chromatomyia* should be automatically transferred to *Phytomyza* following synonymy of the parent genus. The authors of all future studies should consider the evidence on their own volition before favouring one genus name over the other.

As a result of Griffiths' studies on boreal *Phytomyza*, immense progress has been made in understanding the diversity and evolutionary history of taxa in the *Napomyza* genus group. This has facilitated progress by later authors, including those who have reconstructed the phylogenies we now depend on to develop useful and accurate predictive classifications. The phylogenies produced by Dempewolf (2001), Scheffer *et al.* (2007) and Winkler *et al.* (2009) have been insightful in corroborating the findings of earlier authors who suspected the non-monophyly of *Phytomyza* with respect to other genus-level groups. While the first two publications had more limited representation of species in the *Napomyza* group, the third was much more robust, and while aspects of that phylogeny are ambiguous, components for which the evidence was strong have allowed for confident updates to classification.

In the present study, these phylogenies were once again useful in reassessing the placement of "problematic" species that were incorrectly classified previously, revealing more morphological and ecological consistency in their parent groups than previously appreciated. Two of these groups include most species previously considered to be *Chromatomyia*, allowing for the possibility of future recognition of a narrowed *Chromatomyia* within *Phytomyza* if it was ever deemed necessary, but at the moment there is no evidence to support this as a viable option.

*Phytomyza* is a highly speciose and morphologically diverse genus, especially with regards to the male genitalia, and the risk of convergence or loss of diagnostic characters must be assumed as a possibility. If a cladistic approach is used to develop genera in the absence of a phylogeny, we must take care in noting that synapomorphy can only be estimated. While more experienced experts may provide better estimates of relationships than others, it is an error to assume that

homoplasy is rare in evolution (Farris 1983) and that it cannot be applied to our favoured character sets. Existing and emergent data must be subject to rigorous and unbiased re-evaluation.

Future work must involve developing more thorough knowledge on the internal structure of the *Napomyza* genus group, including placement of the *Aulagromyza populi* group, ideally in the context of revisionary and phylogenetic studies, as this will better clarify species and species group definitions, quantify sister-taxon relationships, and identify homoplasious and synapomorphic characters. Harmonising species group names with those used historically, as begun by von Tschirnhaus (2021), would also be beneficial to aid in communicating the results of those quantitative analyses.

Phylogenetic analyses have not always been commonplace, and phylogenies are still not available for most taxa because of a lack of comprehensive revisionary work and/or adequate material (fresh, preserved material for molecular sequencing, for example). This is especially true for the family Agromyzidae, which is unfortunately stricken with the condition of being quite genus poor but incredibly species rich, making immediate comprehensive revisionary work difficult. In the absence of such works, it is certainly acceptable to propose genus limits and identify putative synapomorphies, with Hennig's (1966) auxiliary principle dictating homology to be presumed in the absence of contrary evidence. Indeed, there may be little alternative. This was the case for Griffiths' resurrection of Chromatomyia, where he recognised that *Chromatomyia* was a tentative concept requiring verification, but he felt justified at the time by basing his hypothesis on a complex genitalic character. This then aided him in the delineation and conceptualisation of a large and diverse group in immediate need of study. In this light, recognition of *Chromatomyia* was an important transitory step towards deeper understanding of the genus group. The senior author is sympathetic to this approach, having taken similar steps to make genera in the large *Phytoliriomyza* and *Ophiomyia* genus groups both monophyletic and of increased utility (Lonsdale 2014, 2017), while recognising that thorough quantitative analyses are still needed, and these may eventually necessitate reinterpretation of the author's findings.

#### Why was the synonymy of Chromatomyia rejected?

While consensus on the status of *Chromatomyia* is split among contemporary agromyzid workers, reanalysis of all of the data and arguments reveals that the evidence and reasoning behind the actions of Winkler *et al.* (2009) were apparently strong, well-justified, and even desirable from a practical point of view. Given this, why do some still prefer to recognise *Chromatomyia* as valid?

On a functional level, it is certainly undesirable to have additional generic synonymy in a large family that is already genus-poor. *Phytomyza* has swollen to nearly 700 species, only a small minority of which can be placed in the subgenera *Napomyza* and *Ptochomyza*. Recalling Humphreys and Linder (2009), genera that are too big or small may hinder understanding and memorability. Most *Phytomyza* species and their species groups can only be differentiated on the basis of male genitalic characters, making the group somewhat unwieldy. Removing a large subset of these to a separate genus would reduce this pressure, but as outlined above, *Chromatomyia* does not work well as a discrete entity for multiple reasons. In an examination of the limits of plant genera detected by molecular studies, Humphreys and Linder (2009) similarly found that such studies preferred large genera, contrasting the smaller, simpler ones recovered by morphological workers. Instead of explaining this as a result of the use of molecular data per se, they attributed the "current trend toward recognising larger genera [to be] a result of a return to study on a broad scale".

Perhaps synonymy of *Chromatomyia* eliminated a name that was a convenient link to species mentioned in the historical literature under that generic combination. If species are listed elsewhere under a different name, would that cause confusion or reduce stability? Many articles have been written on species combined as *Chromatomyia*, including species of economic concern

such as *P. horticola*, where there are numerous studies on agricultural impact, biocontrol agents and other control methods. In this case, any disruption would be minimised by the fact that almost all *Chromatomyia* species were previously known as *Phytomyza*, and resurrection of *Chromatomyia* would in turn result in new generic combinations for many species described as *Phytomyza* since 2009. Ultimately, however, stability is not served if classification does not reflect scientific advances. It also certainly cannot be assumed that professional scientists and the public are unable to learn new ideas resulting from these advances. To mitigate any remaining misunderstanding, widely accessible catalogues should be developed in order to aid in comprehension, with these resources providing lists of all names by which species have been known.

A last consideration might be that since Winkler *et al.*'s (2009) study was based in quantitative molecular techniques, they might have been subject to ""tree thinking", [so that] their top priority is reconstructing trees" (Wheeler 2004). This would presumably contrast more traditional techniques better designed to develop high-utility groups grounded in the practicalities of morphology and field observation. It should put one at ease to see that Winkler *et al.*'s work reveals a thoroughness in sampling and representation of diversity in a genus of high morphological variation that necessitated pragmatic diagnostics to identify taxa and classify species. Much of their work focused on life history, the recognition and understanding of details of varied morphological characters, ecology, speciation and the long and varied historical treatment of taxa. Care was taken in examining and testing putatively monophyletic groups and their definition. Changes to classification were made cautiously with consideration of justification and ramifications.

Shortcomings of Winkler *et al.*'s (2009) publication are those endemic to any study for which sampling is limited by the realities of finding access to appropriate material, and there are always technical limitations associated with deriving large volumes of sequence data for analysis. Both of these challenges can be mitigated with time as technology improves and new material is gathered, contributing to the growing library of data already stored. It has hopefully been established that contrary to working against traditional morphological systematics or rejecting its contributions, the application of molecular techniques has proven to be complementary and beneficial. Additional insight resulting from any new data should be welcomed, as this knowledge will allow for more educated decision-making, more informed and accurate diagnostics, more uniform working groups and better ecological comprehension.

As stated by Williams and Kociolek (2007), "by their very nature, classifications change as new information and ideas about relationships emerge. Classification, like all other sciences, should rest on growth and development rather than authority and convention. Thus, those new to the field, students and other users, need to be enlightened rather than indoctrinated. Information contained within the newest hypotheses will reveal new insights related to morphology and distributions over time as well as space – but not with classification by convention."

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## Phytomyza sedicola (Hering) (Diptera, Agromyzidae) new to Wales

**and a second British record** – On 25 September 2020, numerous mines were found on several patches of orpine *Sedum telephium* (Fig. 1) on the edge of Gaer Fawr Wood, an ancient woodland owned by Woodland Trust near Guilsfield in Montgomeryshire, Mid-Wales (SJ221124, V.C. 47). Subsequent visits revealed many puparia, most of which were protruding from the mines, out of slits in the leaf surface (Fig. 2). Eleven puparia were extracted to rear through over winter. Adults began to emerge on 12 April 2021, and six had emerged by 19 April. Two adult specimens were retained, and one was sent to Barry Warrington, who confirmed it as *Phytomyza sedicola* (Hering, 1924) on 16 April 2021.



Fig. 1. Orpine Sedum telephium with mines of Phytomyza sedicola.



Fig. 2. Puparium of Phytomyza sedicola protruding from a slit in the leaf surface.

This species is new to Wales, and a second British record. Its only other record is a specimen reared from *Sedum telephium* in August 1931, Keswick, Cumberland (V.C. 70), by J. C. Robbins (Spencer, K.A. 1972. Diptera, Agromyzidae. *Handbooks for the Identification of British Insects.* X, 5(g), 1-136. Royal Entomological Society, London). A single parasitoid emerged, and was identified by Professor Sir Charles Godfray as *Pediobius metallicus* (Nees, 1834) (Hymenoptera, Eulophidae). The remaining *P. sedicola* adults and puparia were released back at the orpine patches on 19 April 2021. I am very grateful to Barry Warrington for advice and confirmation – **ALASTAIR J. HOTCHKISS**, Northwood, Celyn Lane, Guilsfield, Powys, SY21 9PU

**Pandivirilia melaleuca** (Loew) (Diptera, Therevidae) recorded from Wytham Woods, Oxfordshire - On 8 July 2021, a single adult female of *Pandivirilia melaleuca* (Loew, 1847) (Fig. 1), was recorded at Wytham Woods (SP464079). This represents a new confirmed site for this therevid fly, of which adults are rarely encountered. Confirmed British records of adults were only previously known from Windsor and the surrounding area, and a second cluster in West Gloucestershire and South Worcestershire (Stubbs, A. and Drake M. 2014. *British Soldierflies and their allies: an illustrated guide to their identification and ecology.* 2<sup>nd</sup> edition, BENHS. Reading). Wytham Woods falls neatly in between these two groupings, but it remains unclear whether this species is expanding its range or has been previously overlooked.

The record is from an area of the site known as 'the dell', characterised by several mature and veteran beech trees, *Fagus sylvatica*. The specimen was observed at around 14:00 in the afternoon landing and resting on the trunk of one of these beeches, which had recently fallen (Fig. 2). The larvae develop in decaying heartwood of oak, beech and ash, and are believed to be predaceous on the larvae of saproxylic beetles.



Fig. 1. Lateral and dorsal photographs of the adult female Pandivirilia melaleuca.



Fig. 2. The fallen beech tree upon which the specimen alighted.

The individual recorded was very slow moving despite the warm weather, and easily collected into a pot by hand for photography and confirmation of identification. Field identification was confirmed later from photographs using Stubbs and Drake (*op. cit.*) – **LIAM CROWLEY**, John Krebs Field Station, University of Oxford, Wytham, Oxfordshire, OX2 8QJ; liam.crowley@zoo.ox.ac.uk

## Corrections and changes to the Diptera Checklist (46) - 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 the addition of 8 species, resulting in a total of **7224** species (of which 41 are recorded only from Ireland), and also the addition of one imported species.

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*.

**Limoniidae.** The following species was added by L.-P. KOLCSÁR *et al.* (2021. Contribution to the knowledge of Limoniidae (Diptera: Tipuloidea): first records of 244 species from various European countries. *Biodiversity Data Journal* 9: e670985): *Dicranomyia (Dicranomyia)* **radegasti** Starý, 1993

**Ceratopogonidae.** The following species is added in the present issue: *Forcipomyia tenuis* (Winnertz, 1852 – *Ceratopogon*)

Lonchaeidae. The following species are added in the present issue: *Dasiops facialis* Collin, 1953 *Lonchaea angelina* MacGowan, 2014

The following species was added by I. MACGOWAN and A. REIMANN (2021. A new species of *Protearomyia* (Diptera, Lonchaeidae) with a review of the genus in the Palearctic. *Zootaxa* **4966**(4), 487-493):

Protearomyia jonesi MacGowan & Reimann, 2021

Agromyzidae. The following species is added in the present issue: *Napomyza crepidicaulis* Warrington, 2021

**Sphaeroceridae.** The following species is added in the present issue: *Rachispoda uniseta* (Roháček, 1991 – *Leptocera*)

**Hippoboscidae.** The following species was recorded as a vagrant by A.M. HUTSON (1984. *Keds, flat-flies and bat-flies. Diptera, Hippoboscidae and Nycteribiidae*. Handbooks for the Identification of British Insects **10**(7), 1-40), so should be listed under Imported species: *Ornithophila gestroi* (Rondani, 1878 – *Ornithomyia*)

The following species is added in the present issue: *Pseudolynchia canariensis* (Macquart in Webb & Berthelot, 1839 – Olfersia)

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