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Diagnostic definitions and figures of male and female *Tetanocera punctifrons* and *T. latifibula*, new records of *T. punctifrons* in Ireland, and notes on biology (Diptera, Sciomyzidae)

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Summary

New records of *Tetanocera punctifrons* Rondani, 1868 in Ireland are presented. Distinguishing characters from the very similar *T. latifibula* Frey, 1924 are discussed. The female abdomens of both species are described for the first time. The distributions of both species are summarised. The history of type examinations and of taxonomists' conceptions of the two species is tracked, especially the relative reliability of published figures of diagnostic features. We emphasise the need for such analyses of rare and closely related species, even if apparently disjunct in distribution. Habitats of *T. punctifrons* and *T. latifibula* are described, and the biology and morphology of the immature stages are compared.

Introduction

Collection of the Palaearctic *Tetanocera punctifrons* Rondani, 1868 in Ireland has led us to analyse the features of the adults of that species and the closely related Holarctic *T. latifibula* Frey, 1924.

Considering the importance of *Tetanocera* Duméril, 1800 to the study of cladistics and behavioural evolution of Sciomyzidae (snail-killing flies), we believe it is useful to thoroughly document the range extensions and identities of such relatively poorly known and similar species. We also describe the habitats and summarise the biology and morphology of the two species in the hope of expediting further studies.

Tetanocera is one of the best-known genera of Sciomyzidae. Extensive biological information is available on 26 of the 39 species, in most cases complete life cycles (Foote 1961, 1996a, b, 1999, 2008, 2011; Knutson 1963; Knutson *et al*. 1965; Rozkošný 1965, 1967; Trelka and Berg 1977; Trelka and Foote 1970). The morphology of the immature stages has been described for 21 species and, in most cases, all stages (Knutson 1963; Foote 2013; Rozkošný 1965, 1967). Some of the information on biology and immature stages of European species, along with adult taxonomy, has been presented in regional studies by Rivosecchi (1992: Italy), Rozkošný (2002: Central Europe) and Vala (1989: Mediterranean Europe). The larvae range from overt predators of snails in open water to predators of shoreline or otherwise exposed aquatic snails to parasitoid-predators of Succineidae, slugs, or terrestrial snails. *Tetanocera ferruginea* Fallén, 1820, is one of the best-known species in the family, a result of extensive laboratory experimental studies on development, overwintering, competition, food consumption, fecundity,

survival, etc. (reviewed by Knutson and Vala 2011 and Foote 1996a). Recently Chapman *et al.* (2006) used phylogenetic methods, including molecular and larval morphological data, in exploring morphological adaptations of North American *Tetanocera* species to both aquatic and terrestrial habitats, one of the first attempts to do so within a dipteran lineage. In a subsequent publication, Chapman *et al.* (2012) built on those findings by examining feeding behaviour evolution, as feeding behaviours are dependent on both larval morphological adaptations to different environments and specific requirements related to finding and subduing different prey species. *Tetanocera latifibula*, but not *T. punctifrons*, was included in those studies.

Tetanocera is the fourth-largest genus in the family Sciomyzidae [12 Holarctic species, 8 Palearctic species (with *T. chosenica* Steyskal, 1951 ranging from Japan and Korea to Yunnan, Kwangsi, and Fukien, China in the Oriental Region); 18 Nearctic species (with *T. plumosa* Loew, 1847 extending from Alaska to Venezuela); and one strictly Oriental species, *T. nigrostriata* Li, Yang & Gu, 2001 (Yunnan)].

All species of Sciomyzidae occurring in Ireland were included in Rozkošný (1987) and Vala (1989). Stephenson and Knutson (1970) listed 26 species in 13 genera of Sciomyzidae from Ireland. They included seven species of *Tetanocera*, by counties, but without detail, based on their review of only some of the literature, some collections, and records provided by 22 colleagues in the British Isles (*T. ferruginea*, *T. fuscinervis* (Zetterstedt, 1838) [as *T. unicolor* Loew, 1847], *T. phyllophora* Melander, 1920, *T. elata* Fabricius, 1781, *T. hyalipennis* Roser, 1840, *T. punctifrons* and *T. silvatica* Meigen, 1830]. Chandler (1972) provided a much more detailed summary of the distribution of 40 species in 17 genera in Ireland, including six of the species of *Tetanocera* listed by Knutson & Stephenson (1970) but omitting *T. silvatica* and adding *T. freyi* Stackelberg, 1963 and *T. arrogans* Meigen, 1830. In Chandler (1972) a female *T. punctifrons* from Cratloe, County Clare, 1895 (Dublin Museum) served as the first detailed record of the species from Ireland; it was noted that the presence of this species in Ireland needed confirmation. The Holarctic *T. silvatica* was reinstated by Speight and Nash (1977). Speight (2001, 2004) reported collecting 1 male and 1 female of *T. punctifrons* (and 6 other *Tetanocera* species) in County Cork, but without discussion of identifying features. Speight (2007) added *T. montana* Day, 1881 to the Irish fauna with a detailed comparison of the adult to the related *T. arrogans* and including the geographical and habitat distribution of *T. montana*. Recent extensive collections of *Tetanocera* species in Ireland have been documented fully by Speight (2004: County Cork) and Williams *et al.* (2007: County Clare, County Galway, County Mayo, County Roscommon, and County Westmeath). Speight (1979) provided a list of 45 species in 19 genera, without details, and subsequently published records of six additional species. The most recent list was by McLean (1998), including 51 species. Six additional species were recorded recently (Staunton *et al*. 2008). Despite recent extensive collecting in a few areas, the Irish Sciomyzidae are still not well known; major range extensions of Sciomyzidae in the Palearctic are being reported. Currently Ireland has 60 recorded species of Sciomyzidae in 19 genera.

We report here collection of adults of *T. punctifrons* by C. Maher, C. Mulkeen, and J. Carey in Ireland (Table 1). Identifications were confirmed by LVK. The specimens, in perfect condition, were transferred from alcohol and glued to a pin; the abdomens were removed, processed in NaOH and subsequently in slightly acidic alcohol, and then placed in a microvial of glycerine pinned below the rest of the specimen. They are deposited in the Natural History Museum, Dublin.

Table 1. Date-locality and collection data for the specimens of *Tetanocera punctifrons* (Rondani, 1868) reported in the present paper.

Locality	Co-ordinates	Number/sex	Date	Collector	Collection method	Depository
Skealoghan turlough	53º36'35"N – 9º8'29"W	1♀	5/8/2005	C. Maher	Sweep-net	LVK collection, Gaeta
Annagh East	53º24'29"N – 9º2'45"W	1♀	4/9/2014	J. Carey	Malaise trap	Natural History Museum Dublin
Corgar Lough	54º3'38"N – 7º45'38"W	1♀	1/7/2014	C. Mulkeen	Malaise trap	Natural History Museum Dublin
Corgar Lough	54º3'38"N – 7º45'38"W	1♀	7/8/2014	C. Mulkeen	Malaise trap	Natural History Museum Dublin
Lough Down	53°20'57"N – 9°10'58"W	1♂	2/7/2014	C. Mulkeen	Malaise trap	Natural History Museum Dublin
Lough Meelagh	54°3'24"N – 8°9'3"W	1♂	7/8/2014	C. Mulkeen	Malaise trap	Natural History Museum Dublin

Identification and distribution

Ostensibly, with only two of the Western European species of *Tetanocera* – the central and southern *T. punctifrons* and the northern *T. latifibula* – sharing the very distinctive feature of a single strong seta on the posterior surface of the mid femur, near the apex, one might think that it should be relatively easy to confirm the identity of *T. punctifrons* in Ireland. However, some of the features traditionally used for distinguishing *T. punctifrons* from *T. latifibula* are either variable or difficult to evaluate, especially when a series of specimens of both species are not at hand for comparison, as noted below.

Rozkošný and Knutson (2011) recorded *T. punctifrons* from Ireland (based on Speight 1979), across Wales, Scotland, and England to Denmark and southern Sweden, then across central and southern Europe to Spain, Italy, Poland, Romania, Bulgaria, and Turkey and across Central European Russia, but it was absent from Norway and central and northern Sweden and Finland. They recorded *T. latifibula* from northernmost Sweden and Finland, through north-east, north-west, and Central European Russia (Kaliningrad region) and eastwards across Mongolia and Siberia, but it was absent from England to Belgium to France to Denmark and south. Foote (1999) mapped the distribution of *T. latifibula* in North America, showing it ranging from coastal and north-central Alaska just below the Arctic Circle south in mountainous areas to north-eastern California, northern Utah, central Colorado, and northern-most New Mexico as well as into the plains of southern-most Manitoba to north-western Iowa.

Tetanocera punctifrons and *T. latifibula* can be placed with about 11 other, mainly Nearctic, *Tetanocera* species in which the surstylus is quite similar in lateral view (scoop-like and more or less short) and somewhat similar in ventral view. Eight of the Nearctic species also have a pre-apical seta on the posterior surface of the mid femur, whereas all other species lack this seta. The shape of the posterior surstylus varies within some of the Nearctic species; there are few figures of them other than in Steyskal's (1959) taxonomic revision and in regional studies by Fisher and Orth (1983: California), Foote *et al.* (1999: Alaska), and Foote and Keiper (2004: Ohio). It cannot be excluded that *T. punctifrons* is the senior synonym of a species in North America.

When documenting the presence of rare species, especially in the Palaearctic, where many of the earlier described species were inadequately described and where there are often many synonyms within a genus, it can be useful, primarily for the sake of future researchers, to refer to studies of type specimens and to track the record of examination of characters and understanding of the species concepts by the leading taxonomists. We do this here for *T. punctifrons* and *T. latifibula*, the only species of this group of *Tetanocera* likely to be confused in Western Europe.

***Tetanocera punctifrons* Rondani, 1868 (Fig. 1, a-e; from Rozkošný 1984, figs 536-540)**

Rondani's type specimens of *T. punctifrons* (two males and one female from Parma, Italy) in the Florence Museum were studied by Verbeke (1964), who designated a male (No. 1512) as "type" (= lectotype). He illustrated the antenna and a posterior view of the surstyli of a cotype male (from slide preparations; these slides probably were made in Verbeke's laboratory and perhaps are in the Institut royal des Sciences naturelles de Belgique, Brussels). Verbeke (1964) also described other characters of the species and stated that Sack (1939) had correctly interpreted Rondani's concept of the species. Sack included both *T. punctifrons* and *T. latifibula* but did not mention the setae on posterior surface of the mid femur (Sack's publication was used extensively for identification of Palaearctic Sciomyzidae until Rozkošny's 1987 monograph). Under *T. punctifrons*, Verbeke (1964) synonymised *T. collarti* Verbeke, 1948 (from Belgium) and, with a question mark, *T. marginella* Robineau-Desvoidy, 1830 (from France), noting that Robineau-Desvoidy's specimens had been destroyed. Collin (1960) commented on the confused history of the name *T. marginella* (listed as a synonym of *T. elata* Fabricius by Hendel 1900) and used that

name for what we consider to be *T. punctifrons* in his key to nine British species of *Tetanocera* based in part on presence of one pre-apical seta on the posterior surface of the mid femur. For further clarification of Collin (1960), Verbeke (1968) placed *T. elegans* Collin as a synonym of *T. phyllophora* Melander, 1920. Rozkošný and Elberg (1984) listed *T. marginella* as a "doubtful species". Verbeke (1964) noted in his detailed description – based on the three syntype specimens and 29 other specimens from England, Wales, Belgium, Luxembourg, Austria, Italy, Denmark, and Bulgaria as one of the "principaux charactères" of *T. punctifrons* the presence of a posterior pre-apical seta on the mid femur, a character which "existe également chez *T. latifibula*." Subsequent authors followed this interpretation of the species and have presented figures of the male genitalia and other features.

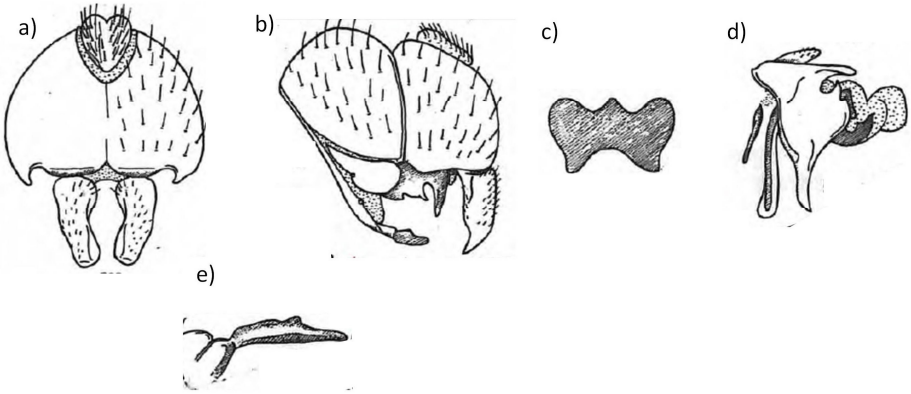

Fig. 1. Male genitalia of *Tetanocera punctifrons* (after Rozkošný 1984).

Mayer (1953), in his key to 19 species of *Tetanocera* in the Palaearctic region (in German), included *T. punctifrons* and *T. latifibula* easily separated by the length of the aristal hairs and thickness of the hind femur, and with characters of the fronto-orbital setae, frons, hind femur setae, and wing in the terminal couplets, but without figures. Rivosecchi and Santagata (1979) presented poor outline figures of the surstylus and hypandrium. Rozkošny's (1984, 1987) figures of the surstylus agree well with specimens we have seen except that in lateral view the anterior margin is more evenly and gently excavated in our specimens. Vala's (1989) figures agree with our specimens except that one of his two lateral views of the surstylus (his fig. 119 l) shows the posterior margin as slightly indented in the upper two-thirds, not straight as in our specimens. Vala (1989) and Rivosecchi (1992) presented figures of the sixth sternum of *T. punctifrons*. Vala showed two approximate protuberances on the right side, with a median protuberance; Rivosecchi showed three weak protuberances. Our specimens have a right and a left protuberance, with a weakly sclerotised median protuberance. Rozkošný's (1984) figure of *T. latifibula* and our specimens of *T. latifibula* display three equally separated, sclerotised protuberances. Rozkošný (1984, 1987) and Vala (1989) figured the "ix sternum" (epandrium) with a straight ventral margin in *T. punctifrons* and a slightly inwardly curved ventral margin in *T. latifibula*; in our specimens the margin is only slightly curved inwards in both species. Rivosecchi (1992) provided figures of the surstylus and other characters of specimens of *T. punctifrons* from Lazio, central Italy; those of the surstylus and antenna generally agree with Verbeke's (1964) figures. However, as with many of Verbeke's published figures, most of Rivosecchi's figures were made from slide preparations and thus include considerable distortion.

***Tetanocera latifibula* Frey, 1924 (Fig. 2, a-d; from Rozkošný 1984, figs. 519-522)**

Tetanocera latifibula was proposed by Frey (1924) for three males and four females from Munio and Enontekis, Finland and from "Beresow", western Siberia; he presented a few characters of *T. latifibula* in his key to 14 *Tetanocera* species and a lateral, outline view of the epandrium and surstylus of the male. His only reference to *T. punctifrons* was in a list of four species, "...not known to me but to all appearances are probably distinct." Sack (1939) gave a slightly more detailed description, without figures. Of subsequent authors, apparently only Stackelberg (1963) and Rozkošný (1984) studied the syntype specimens. Steyskal (1959) did not recognise *T. latifibula* from North America, but he described *T. hespera* from Alberta, Canada and from Alaska, Utah, and South Dakota, U.S.A. on the basis of a few characters, presented outlines of the posterior and lateral views of the postabdomen, and (1965) synonymised it under *T. latifibula*. It cannot be discounted that *T. hespera* is a valid species. Verbeke (1964) mentioned a few characters of *T. latifibula* and presented a posterior view of the epandrium and surstylus (specimen: "T4: Asie, Altai, Ularak", not part of the type series), drawn from a slide preparation that apparently has been lost. Stackelberg (1963) reproduced Frey's (1924) figure of *T. latifibula*, included it with additional characters in his key, and recorded specimens from the Kola Peninsula and from Leningrad, Russia. Fisher and Orth (1983) – an overlooked source by most European authors, of excellent figures of Holarctic species – figured the male and female postabdomens of specimens from California, U.S.A. and mentioned other characters (noted below). Apparently only Rozkošný (1984) subsequently examined Frey's (1924) type specimens; he (1984, 1987) figured the male genitalia in detail.

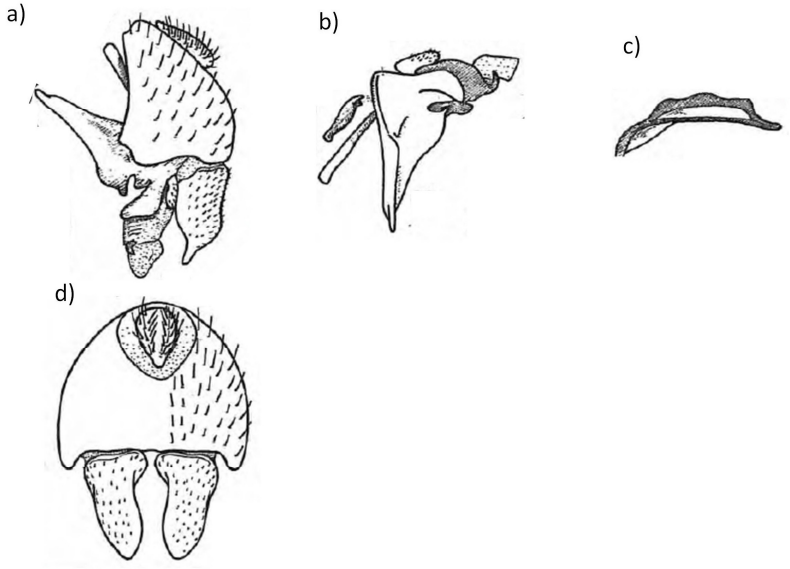

Fig. 2. Male genitalia of *Tetanocera latifibula* (after Rozkošný 1984).

Although it is difficult to reconcile some differences in the drawings (there are no photographs) of the male postabdomen in the publications noted above – the best are in Rozkošný (1964, 1987) and Verbeke (1964), the shape of the surstylus in lateral view seems to be the best feature for distinguishing males of the two species. The surstylus of *T. latifibula* seems to be shorter than that of *T. punctifrons*, is slightly curved inward in the upper half posteriorly, whereas

that of *T. punctifrons* is straight, and the anterior margin of *T. latifibula* is deeply excavated, whereas that of *T. punctifrons* is more shallowly and gently excavated towards the apex. The other characters traditionally used to separate the species, and a few other characters, seem to vary somewhat and are difficult to compare without a series of both species in hand.

We have seen the following 45 specimens:

T. punctifrons: Ireland, 2♂ 4♀; Belgium, 4♂ 2♀; France, 1♂; Spain, 1♂; Italy, 2♂; Bulgaria, 1♂; Denmark, 4♂ 4♀.

T. latifibula: Sweden, 1♂, 1♀ plus 1♀ (laboratory reared, F¹ pinned with puparium); Finland, 2 specimens; Mongolia, 1 specimen; Siberia, 1 specimen. Canada: Northwest Territories, 1♂; British Columbia, 1♂; Manitoba, 3♂ 3♀; Alberta, 1♂. U.S.A.: Alaska, 1♂; Colorado, 2♂; Nebraska, 1♂; Washington, 1♂.

We have focused above on the more recent literature of primary importance concerning these two species. However, we have also surveyed other major, older publications, e.g., by H. Loew (1841-1876), F. Hendel (1900-1938), etc. *Tetanocera punctifrons* appeared as a valid species in Hendel's (1903) key; he did not mention *T. latifibula*. Becker (1902), in his review of Meigen's collection in Paris and Vienna, did not mention *T. punctifrons.* Becker, in Becker *et al*. (1905), listed only the original description of *T. punctifrons*. Séguy (1934) did not include either species, but included *T. marginella*, which he confused with *T. elata* or *T. phyllophora*; he did not use the character of a seta on the posterior surface of the mid femur.

Additional comments on external features

a. Plumosity of arista: a fairly reliable character, well-figured for *T. punctifrons* by Verbeke (1964) and Rivosecchi (1992) from slide preparations. Recorded as broader than pedicel in *T. punctifrons*, narrower in *T. latifibula*. In addition, the plumosity is less dense and more brownish in *T. latifibula*.
b. As noted by Rozkošný (1984), in *T. latifibula* the pedicel is usually distinctly longer than half the length of the basal flagellomere (= postpedicel) but is slightly shorter in *T. punctifrons*.
c. Rozkošný (1984) also pointed out that in *T. latifibula* the second aristal segment is slightly longer than broad, whereas in *T. punctifrons* it is, at most, as long as wide.
d. We could see no differences between the species in extent of facial hairs or colour of antennae at insertion of arista, as noted by Fisher and Orth (1983) in distinguishing *T. latifibula* from other species in California.
e. Orbito-antennal spot: one of four key characters used in separating the two species by Rozkošný (1984, 1987) but apparently an unreliable character in these species. Traditionally regarded as present in *T. punctifrons* but present or absent in our Irish specimens; absent in *T. latifibula* but present or weak in our three specimens from Sweden.
f. Hind femur anterodorsal setae: traditionally recorded as two in *T. punctifrons*, and 3–4 in *T. latifibula*, as in our specimens.
g. As noted by Verbeke (1964), the antero- and posteroventral setae on the hind femur are very strong in the female of *T. punctifrons*; we noted that they are weaker and sparser in *T. latifibula*.

Female abdomen: Characters of the female abdomen have not been used extensively in taxonomic studies of Sciomyzidae; the relatively few published descriptions have been reviewed by Knutson and Vala (2011) and Murphy *et al*. (in prep). With regards to *Tetanocera*, on the

basis, in part, of study of the female terminal abdominal segments, Verbeke (1964) resolved the status of several Palaearctic names. Fisher and Orth (1983) figured the abdominal sterna of 10 species of *Tetanocera,* including *T. latifibula*, from California. Rivosecchi (1992) figured and described various features for seven species of *Tetanocera* from Italy, including, for *T. punctifrons,* the habitus, head, antenna, mid femur, abdominal terminal segments and spermathecae of the female, male postabdomen – sternite 6, ventral and lateral views, internal genitalia, and wing.

In a cladistic analysis and taxonomic revision of the related genus *Renocera* Hendel (Knutson, Mathis and Chapman, in prep.), the following characters and character states of the female abdomen have been provisionally recognised as the most important in the eight genera in the outgroup utilised by these authors:

1. Sterna 7 and 8 broadly to narrowly separated by membrane (plesiomorphic); fused (apomorphic).
2. Sternum 8 a single, transverse plate (plesiomorphic); a pair of hemispherical lobes (apomorphic).
3. Hypoproct a single, transverse, setose lobe-like plate (plesiomorphic); separated medially by membrane into two lateral lobes (apomorphic state 1); a single lobe, setose posteriorly, with anterior portion a bare concave plate with tricuspid anterior margin (apomorphic state 2).
4. Spermathecae without an apical appendage (plesiomorphic); with an apical appendage (apomorphic).

Other fine details also have been distinguished in the female abdomen. Following is a description of features common to both *T. punctifrons* and *T. latifibula* (specimens examined: *T. punctifrons*, 3♀, Ireland; *T. latifibula*, 2♀, Sweden). We note that it is important to view the sterna not only in ventral view (in which view sterna 7 and 8 may appear fused), but also with the abdomen tipped upward posteriorly (in which view any membrane separating sterna 7 and 8 can be seen more clearly).

Spiracles 6 and 7 in the extreme anterolateral corner of terga 6 and 7 – as figured for *T. plebeja* Loew by Knutson (1987). Fisher and Orth (1983) figured these spiracles in the terga for seven of the species they studied but in the membrane for *T. latifibula*. Abdomen without mid-dorsal dark stripe. Sterna 6 and 7 broadly separated by membrane. Epiproct a minute, lightly sclerotised plate, with about four setulae. Two spermathecae (viewed at 70x) hemispherical, surface smooth, base flattened, stem not sclerotised.

The following diagnoses reveal very significant differences between females of the two species, not previously described.

T. latifibula (Fig 3a, from Fisher and Orth 1983): Terga 2, 3, and 4 without a trace of mid-dorsal dark stripe. Setae near posterior margin of terga 3, 4, and 5 strongest, especially laterally (note: the posterior-most row of so-called "posterior marginal tergal setae" are <u>not</u> on the ultimate posterior margin of the terga; there is a rather broad, bare, somewhat more lightly sclerotised posterior marginal extension to terga 3-7, which is especially strong on tergum 4 [well illustrated for *T. plebeja* in Knutson 1987]). Sterna 7 and 8 broadly separated by membrane). Hypoproct a densely setose, semi-circular plate. Cerci slightly broadened apically in lateral view. Spermathecae without apical process. In Figs 3a and b, St 7 and 8 = Sterna 7 and 8.

T. punctifrons (Fig. 3b, photograph by J. Carey): Terga 2, 3, and 4 with faint to strong mid-dorsal dark stripe. Setae near posterior margin of terga 4, 5, and 6 strongest, much stronger than in *T. latifibula*. Sterna 7 and 8 appearing fused in ventral view but in posterior view barely but distinctly separated by membrane. Hypoproct a transversely rectangular plate, in some specimens very narrowly separated by median membrane on posterior margin, posterior margin only slightly

curved. Cerci not broadened apically in lateral view. Spermathecae with minute but distinct apical process (note: this apical process also is figured for *T. punctifrons* by Rivosecchi 1992).

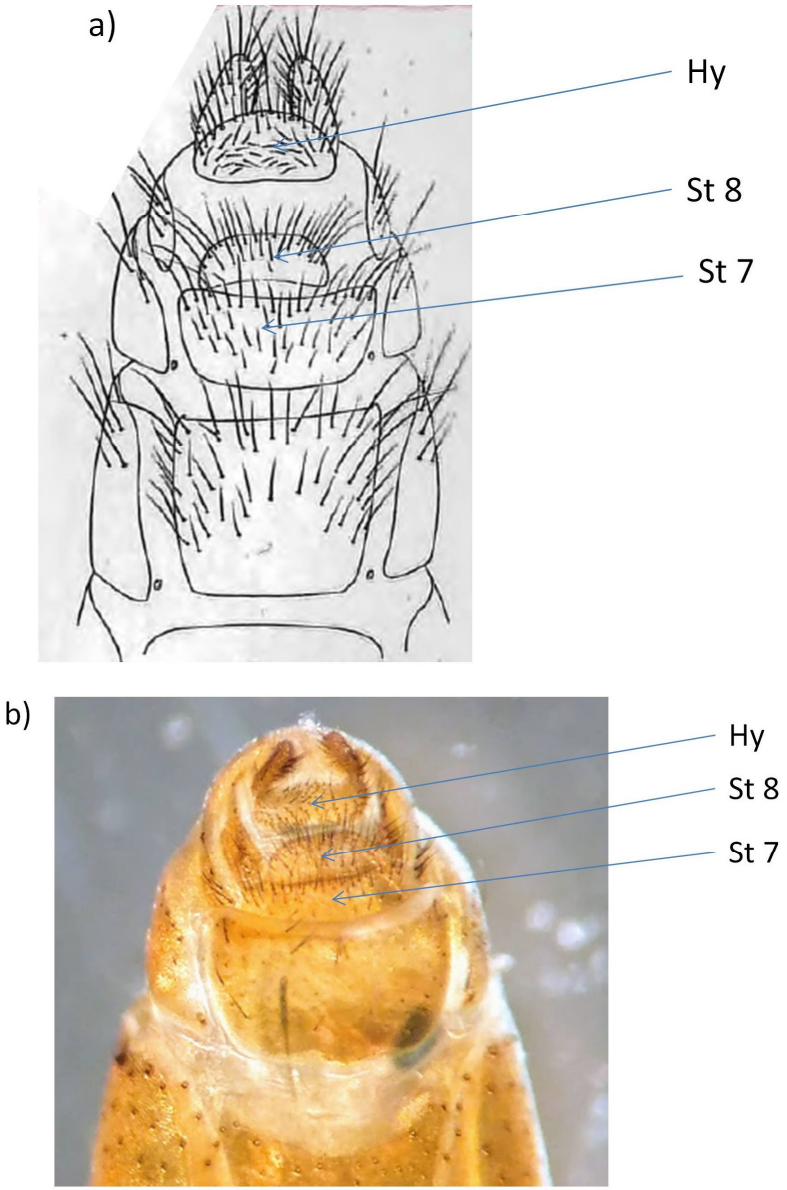

Fig. 3. Female genitalia: a, *Tetanocera latifibula* (after Fisher and Orth 1983); b, *Tetanocera punctifrons* (photograph by J. Carey).

Other characters: Other characters used by various authors in separating other species of *Tetanocera* were not found to be useful in separating our specimens of *T. punctifrons* and *T. latifibula*, but they may be worth checking further. These characters included positions of fronto-orbital setae relative to anterior margin of frons and anterior ocellus; colour of face, parafacies, and genae; width of gena relative to eye height; extent of hairs on parafacies; length of hairs on anterior margin of frons; basal flagellomere concave or straight above (but more often more deeply concave in *T. punctifrons* than in *T. latifibula*); colour of occipital spot; colour of thoracic dorsum; scutellum flat or convex; scutellum with or without an anterior ridge; colour of fore tarsus; curvature of posterior cross-vein; cross-veins infumated or not; and colour of stigma.

Key: The following key is in a format that may be of broader use than is the traditional format. That is, first we present characters that we have found to be the most reliable. Second, we include, in parentheses, characters that have been used by other students of the two species but for which there is disagreement or doubt as to their reliability. Thus we first guide the user to the so-called reliable distinctions and then provide other characters that may prove important.

1. Aristal hairs moderately dense, black, longer than width of pedicel; in lateral view pedicel at most as long as broad. Hind femur with two anterodorsal setae beyond mid length and rarely with a third, short, anterior-most seta. Surstylus long, in lateral view posterior ventral margin straight, anterior ventral margin gently and evenly excavated in apical half. (Second aristal segment at most as long as wide. Ventral margin of epandrium straight. In female, ventral setae of hind femur strong and numerous) …….. *T. punctifrons*

- Aristal hairs less dense, brownish black, shorter than width of pedicel; in lateral view pedicel slightly longer than broad. Hind femur with three or four anterodorsal setae. Surstylus shorter, in lateral view posterior ventral margin slightly excavated in basal half, anterior ventral margin more deeply and abruptly excavated in apical half. (Second aristal segment slightly longer than broad. Ventral margin of epandrium slightly excavated. In female, ventral setae of hind femur weaker and sparser) …….. *T. latifibula*

The only other *Tetanocera* species in Ireland that might be confused with *T. punctifrons* or *T. latifibula* is *T. robusta* Loew, which ranges from Ireland to Kamchatka and which is widespread in the Nearctic. Males of *T. robusta* are readily recognised by the conical projection (even in dry specimens) on the left side of the epandrium. Notably, *T. robusta* is the only species of *Tetanocera* (both males and females) with a setose prosternum (posterior portion). Furthermore, whereas *T. punctifrons* and *T. latifibula* have one strong seta before the apex on the posterior surface of the mid femur, *T. robusta* usually has one strong seta and two to three weaker setae in this area. If, as a result of collection or preparation procedure, female specimens of *T. robusta* have lost the prosternal setae and the setae on the posterior surface of the mid femur (but sockets should still be visible) or if they show unusual variation (we have seen one female *T. robusta* from Ireland with setulae on only one side of the prosternum), it might be useful to note that *T. robusta* and *T. latifibula* lack a mid-dorsal dark stripe on the abdomen (present in *T. punctifrons*). In *T. robusta*, the postpedicel is longer than wide, with the dorsal and ventral margins almost parallel, as in *T. latifibula* (not almost square as in *T. punctifrons*), and the aristal setulae are sparse but long as in *T. punctifrons* (not shorter and more dense as in *T. latifibula*).

Habitat

Many recent and on-going ecological studies of Sciomyzidae in Ireland have focused on the use of sciomyzids as ecosystem service providers and bioindicators. In a study of 10 turloughs

(temporary lakes practically unique to the west of Ireland), Williams *et al*. (2009a) showed a negative relationship between the abundance of the dominant species [*Ilione albiseta* (Scopoli)] and its prey when factors such as hydrology and vegetation structure were controlled. *Tetanocera arrogans*, *T. ferruginea,* and *T. robusta* were significant indicators of particular turloughs, but *T. punctifrons* was not collected in this study. One of the specimens of *T. punctifrons* noted in the present paper came from Skealoghan Turlough (Co. Mayo) during a separate study. Despite an intensive study of a transect at this turlough, Williams *et al*. (2009b) failed to collect *T. punctifrons*

Other recent work in Ireland has included a detailed study of the Sciomyzidae of the Shannon Callows, the largest unregulated river flood plain in Europe. Maher *et al*. (2014) delineated hydrological niches for 22 species of Sciomyzidae in Ireland, including six species of *Tetanocera*. Whereas Williams *et al*. (2009a) demonstrated a quadratic relationship between Sciomyzidae species richness and soil moisture, Maher *et al*. (2014) showed a linear relationship between species richness and hydroperiod. More recent work on Sciomyzidae in Ireland has focused on wet grasslands. In a detailed study of temporal and spatial partitioning of Sciomyzidae and Syrphidae on often ecologically overlooked wet grasslands, Carey *et al*. (2017a) found that, "Spatiotemporal analysis showed that species turnover between habitats at different times made the most significant contribution to overall Diptera diversity." Carey *et al*. (2017b) showed significant correlations between parataxonomic unit abundance and co-structure of nine families of Diptera and Sciomyzidae abundance and co-structure, making them useful bioindicators of Diptera in general. Whereas Williams *et al*. (2009a) could find no support for co-structure between Sciomyzidae communities and Mollusca, Carey (*pers. obs.*) did find a relationship between his Malaise trap collections and soil-sieved Mollusca.

Mulkeen collected four *T. punctifrons* from Malaise traps as part of an on-going study to investigate the biodiversity-supporting functions of constructed wetlands as compared to those of natural wetlands. This study has involved the use of both Malaise and emergence traps at selected sites.

Habitat of T. punctifrons

Beaver (1972) collected a few adults of "*T. punctifrons*" from marshy dune slacks and a lake margin in north-western Wales. These specimens have been destroyed, but as noted above, the distribution data would seem to support the identification. Rozkošný (1984) described the habitat of this species throughout its range as "mesic woods, alongside running water, and also in the mountains." Vala (1989) stated that adults are found at higher altitudes as well as in plains, along canals, and in dry woods. Rivosecchi (1992) recorded adults from various types of heavily vegetated habitats near water in Italy. A male collected on 14 July 1994 in France (Thoranc, Alpes Maritimes, J.P. Haenni, and C. Dufour, Mus. Neuchâtel, Switzerland) is labelled "joncs, laîches, massettes, ruisseau, partie marécageuse." In a summary of the macrohabitats of the 81 species of Sciomyzidae known from the Atlantic zone of Europe, Speight and Knutson (2012) noted, for *T. punctifrons*, "wetland / open ground; tall-herb open areas in *Alnus incana* alluvial forest; montane fen and stream-sides in seasonally-flooded, lightly grazed, humid, unimproved grassland."

Most of the extensive collecting of Sciomyzidae in Ireland has been conducted in turloughs and other seasonal or permanent, aquatic to semi-aquatic habitats. However, Speight (2001, 2004) carried out a detailed analysis of sectors (primarily infrastructure, disused, productive, plus set-aside) of a 41-ha. case-study farm in Riverstick, County Mayo. A 27-Malaise-trap survey of Syrphidae and Sciomyzidae was conducted from April through September. Of the 182 specimens of 17 species of Sciomyzidae collected by Malaise traps (23 species were collected from the farm by use of sweep-net, Malaise, and emergence traps; six other species were collected by use of

sweep-net and emergence trap), one male and one female *T. punctifrons* were collected in an acidic fen-like habitat in one of the 10 disused sectors, the male "from an acid fen/seasonally flooded, oligotrophic *Molinia* grassland" and the female "from a grassy field margin beside a permanently-flowing streamlet backed by a hedge." Speight (2004) tested the predicted occurrence of Sciomyzidae in the total of 21 different kinds of habitats in the three main sectors by intensive emergence surveys from April to September 2000-2003 inclusive (total of 1,316 trapping units where 1 unit equalled 1 sq. m trapped for 1 month). *Tetanocera punctifrons* was not recovered among the 18 species of Sciomyzidae recovered from three productive land habitats, four infrastructure habitats, and five disused habitats.

One of our female specimens was collected at Skealoghan Turlough, County Mayo, in the west of Ireland, by C. Maher. Turloughs are temporary wetlands that develop on karstified limestone; they are found primarily in the west of Ireland. The specimen was caught by sweep-net within an 8 x 8 m exclosure (Moran 2005) where no grazing had taken place for four years, in a vegetation zone dominated by the sedge *Carex nigra*. This vegetation zone is situated in one of the wetter areas of the turlough where flooding takes place for an average of six months each year (Moran *et al.* 2008). Other species of Sciomyzidae caught with this specimen of *T. punctifrons* included *Pherbina coryleti* (Scopoli, 1763), *Ilione albiseta* (Scopoli, 1763), and *Sepedon sphegea* (Fabricius, 1775).

A female specimen of *T. punctifrons* was collected by J. Carey in a Malaise trap positioned in a dense but relatively small stand of the rush species *Juncus effusus* in close proximity to a small, permanent pond in semi-improved wet grassland at Annagh East, County Galway (53°24'28.95"N – 09°02'44.90"W) approximately 350 m from the nearest large water body (Lough Corrib). The vegetation was subject to very light grazing by cattle but was generally undisturbed. Both the *Juncus* stand and the pond were located in wet grassland. This Malaise trap was part of a larger invertebrate biodiversity study being carried out in wet grassland habitats. It was operated continuously from 1 May 2014 to 4 September 2014. Other Sciomyzidae species captured with *T. punctifrons* from this location included *Colobaea bifasciella* (Fallén, 1820), *Elgiva cucularia* (Linnaeus, 1767), *Hydromya dorsalis* (Fabricius, 1775), *Ilione albiseta*, *Ilione lineata* (Fallén, 1820), *Limnia unguicornis* (Scopoli, 1763), *Pherbellia argyra (*Verbeke, 1967), *Pherbellia s. schoenherri* (Fallén, 1826), *Pherbellia ventralis* (Fallén, 1820), *Pherbina coryleti*, *Pteromicra angustipennis* (Staeger, 1845), *Pteromicra pectorosa* (Hendel, 1902), *Renocera pallida* (Fallén, 1820), *Tetanocera arrogans*, *T. elata*, *T. ferruginea*, *T. freyi*, *T. hyalipennis* and *T. robusta.*

Additional invertebrate surveys were taking place concurrently at natural and constructed wetlands in the west of Ireland between May and October 2014. During this study, two female specimens of *T. punctifrons* were captured in a south-westerly facing Malaise trap on the edge of a reed and large sedge swamp (Fossitt 2000) on the shores of Corgar Lough. The habitat was dominated by tall stands of *Phragmites australis* with occasional *Typha latifolia* and *Equisetum fluviatile*. Other habitats in the area include improved agricultural grassland and scrub (Fossitt 2000). Additional Sciomyzidae species captured at this site included *Hydromya dorsalis*, *Pherbellia ventralis*, *Renocera pallida*, *Sciomyza dryomyzina* (Zetterstedt, 1846), *T. arrogans*, *T. hyalipennis*, and *T. robusta*.

One of the male specimens of *T. punctifrons* was captured during the same study in a south-westerly facing Malaise trap on the edge of a reed and large sedge swamp (Fossitt 2000) on the shores of Lough Down. The habitat was also dominated by tall stands of *Phragmites australis* with a mixture of broadleaved herbs such as *E. fluviatile, Mentha aquatica, Filipendula ulmaria,* and *Menyanthes trifoliata*. Neighbouring habitats include wet grassland, improved agricultural grassland, and rich fen and flush (Fossitt 2000). Some other sciomyzid species captured at Lough Down included *Renocera pallida*, *T. arrogans*, and *T. hyalipennis*. The second male specimen

of *T. punctifrons* was captured in a Malaise trap on the edge of a reed and large sedge swamp at Lough Meelagh. Other habitats immediately surrounding the collection point include tall-herb swamps, hedgerows and wet grassland (Fossitt 2000).

Habitat of T. latifibula

Fisher and Orth (1983) collected an unusually large number of specimens (110 females, 226 males) (1949-1974) in north-eastern California in "open, unshaded or sparsely shaded grassy meadows and marshes," at 1334-1783 m, 7 June–21 September, primarily with a suction machine (this huge, unique resource of specimens would have been useful for further study of variation in identification features, but it was discarded by the Department of Entomology, University of California–Riverside, after Fisher had died and Orth retired). Foote (1999) collected adults, "…most commonly in Idaho and Washington by sweeping emergent and shoreline vegetation bordering open, permanent ponds and lakes" e.g. "a dense stand of *Scirpus* sp. growing in about seven centimetres of water at a small, permanent lake," but he also collected a few specimens from "unshaded vernal marshes that became dry by midsummer." Foote *et al.* (1999), in Alaska, collected adults in "open sedge and rush marshes, road-side drainage-ditches, and marshy borders of shallow lakes and ponds. Particularly common in those fresh-water situations in which standing water disappears as summer progresses." Knutson (unpublished) collected adults from a marshy area on the shore of Umeå R. in northern Sweden, on 16, 18, and 23 July 1967, where 21 other species of Sciomyzidae were found.

Biology and Immature stages

The life cycles of *T. punctifrons* and *T. latifibula* are in general similar to those of the other species of *Tetanocera* in Ireland that are typical predators of freshwater, non-operculate snails in truly aquatic situations, i.e. *T. ferruginea*, *T. hyalipennis*, *T. montana*, and *T. robusta* (Knutson and Vala 2011).

T. punctifrons: our life cycle data on *T. punctifrons* is based on a single laboratory rearing from adults collected in Belgium by J. Verbeke, reared at Cornell University by LVK, and reported in his thesis (Knutson 1963; summarised by Vala 1989). Eggs were laid end to end on leaves of substrate vegetation during August and hatched about four weeks later. During the 20-25 days of larval life the larvae killed and ate the fresh tissues of *Gyraulus parvus* (Say), *Lymnaea humilis* Say, and *Helisoma trivolvis* (Say) (none being natural prey) and *Physa* sp. About half of the tissues of each snail (12-18 snails, 2.0-8.0 mm. in length or diameter, attacked per larva) were consumed within a few hours, and then the larvae left the snail; only one larva pupariated, and the puparium did not produce an adult.

The rather extensive biological information on "*T. punctifrons*" in the papers by Beaver (1972, 1973, 1974) on studies in north Wales probably can be accepted as pertaining to that species, but the specimens upon which her studies were based, and the other Sciomyzidae she studied in Wales, were destroyed by an infestation of museum pests (O. Beaver, *pers. comm.* to C. Maher, 2008).

We summarise the main aspects of Beaver's data on life cycles as follows. A female (1 of 4 adults collected between June and August near Newborough, Anglesey, Wales) laid 69 eggs over a period of 7 days, with 41% hatching. The incubation period was 14-20 days. The total duration of larval life was 26-35 days, with the first stadium being 7-21 days (mean 13.0) and the third 11-18 days (mean 15.7). The duration of the puparial stage was 36-50 days (mean 43.3).

T. latifibula: Foote (1999) presented fragmentary results from a laboratory rearing based on a female collected on 17 August in the state of Washington, U.S.A. A few first-instar larvae dissected from eggs (37 laid on the cheese-cloth cover of the breeding jar during late August) fed on *Physella* snails 1.4-10.0 mm in length. Only one larva pupariated, having killed and consumed

38 snails during the 35 days of larval life. The puparium, formed on 20 March on the lid of the rearing dish, produced a male on 29 March. The author concluded that *T. latifibula* has only one generation per year, with overwintering as eggs or young larvae.

Knutson (unpublished) had similar difficulties rearing *T. latifibula*. A female collected on 18 July 1967 near Umeå in northern Sweden (by LVK) laid 46 eggs between 24 July and 24 August. Several eggs hatched (some having been held in a refrigerator at 7°C for 3 months), but most larvae emerged only partially from the egg membranes, as Foote (1999) also noted during his rearings. Several larvae killed and ate *Lymnaea peregra* (Müller) and *Planorbis* (Linnaeus) but refused *Bathyomphalus contortus* (Linnaeus). Only one larva pupariated (23 November) after about 70 days passing through the three larval stadia; it produced a female on 11 December. Knutson concluded (as did Foote 1999) that *T. latifibula* has only one generation per year, with overwintering as first-instar larvae within the egg membrane.

The morphology of the immature stages of *T. latifibula* and *T. punctifrons* is similar to those of other aquatic, predaceous species of *Tetanocera*. The integument of first-instar larvae is unpigmented, whereas that of older larvae is rather darkly pigmented, with a dark mid-dorsal stripe; integumentary papillae are lacking in both species; the body segments are tuberculate, especially laterally; the posterior end is uplifted dorsally, the posterior spiracular disc bears short, subequal dorsal and lateral lobes and much longer ventrolateral and ventral lobes, and the ventrolateral lobes have a short, broad basal portion and a narrower, longer apical portion. The ventrolateral lobes of first-instar *T. latifibula* are exceptionally long and not bipartite, similar only to the Nearctic *T. soror* Melander. Both species have well-developed float hairs between the spiracular openings on spiracular plates of the spiracular tubes, and the projecting anal proleg bears long, recurved spines. The anterior spiracles have 13-16 papillae in *T. punctifrons* and 16 in *T. latifibula*.

The puparia of both species are very similar, with the posterior end uplifted dorsally and an evident anal proleg, except that *T. latifibula* differs from *T. punctifrons* in having weaker posterior spiracular disc lobe vestiges, and a weaker mid-dorsal stripe, without lighter-coloured borders. Finally, the integument of *T. latifibula* has a bronze cast, not present in *T. punctifrons*.

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