

# The importance of antennal mechanosensilla of *Sepedon fuscipennis* (Diptera: Sciomyzidae)

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**Abstract**—The styli, often called the arista, of the antennae of adult *Sepedon fuscipennis* Loew (Diptera: Sciomyzidae) are shown to possess mechanosensilla, the number and arrangement of which differ between the sexes. It is suggested that the mechanosensilla provide sensory input to the female regarding the touching, or appositioning, of her styli by the male with his forelegs during copulation. Among the Sciomyzidae, *S. fuscipennis* males are unique in appositioning the antennae of the female during mating. Large clusters of pollen found on the styli of both sexes suggest that mechanosensilla and chemosensilla also provide sensory information about potential sources of food such as nectar (*i.e.*, carbohydrates).

**Résumé**—Nous démontrons que les styles, souvent appelés aristas, des antennes des *Sepedon fuscipennis* Loew (Diptera: Sciomyzidae) adultes possèdent des sensilles mécanoréceptrices, dont le nombre et la disposition varient selon le sexe. Nous croyons que ces sensilles mécanoréceptrices fournissent des signaux sensoriels à la femelle durant l'accouplement lorsque le mâle touche les styles de la femelle en y apposant ses pattes antérieures. Chez les Sciomyzidae, les mâles de *Sepedon* sont les seuls à pratiquer cette apposition des pattes sur les antennes de la femelle durant l'accouplement. La présence d'importants amas de pollen sur les styles des deux sexes laisse croire que les sensilles mécanoréceptrices et chémoréceptrices procurent aussi des renseignements sur les sources potentielles de nourriture, telles que le nectar et donc les hydrates de carbone.

## Introduction

Very few studies have been conducted on the sensilla of the antenna of Sciomyzidae (Knutson and Vala 2011). Having seen photographs (Figs. 1A, 1B) of mating in two *Sepedon* Latreille (Diptera: Sciomyzidae) species, it occurred to J.G.S. that the female might be receiving sensory input regarding the male via her antennae during copulation because the male appositions her antennae with his forelegs. It also seemed possible that any sensilla present, their number and/or their location might differ between the sexes because males receive no corresponding input during copulation. On the basis of these observations, it was decided to examine the antennae for mechanosensilla to determine if they differed between the sexes.

## Materials and methods

### Collecting and maintaining flies

This study was conducted during the summers of 2009 and 2010. In 2009, live *Sepedon fuscipennis* Loew were collected in a cattail (*Typha latifolia* Linnaeus) marsh adjacent to the running track at the University of Massachusetts in Amherst, Massachusetts, United States of America (42°37.849'N, 72°5.403'W). In 2010, W.L.M. collected live *S. fuscipennis* in a broadleaf cattail (*T. latifolia*) marsh in Fishers, Indiana, United States of America (39°55.981'N, 86°3.022'W) and shipped them in 80% ethanol to J.G.S. (see the section "Taxonomy"). Specimens of *Sepedon testacea* Loew examined during the summer of 2010 were collected in South Africa with Ray Miller (KwaZulu-Natal, South Africa).

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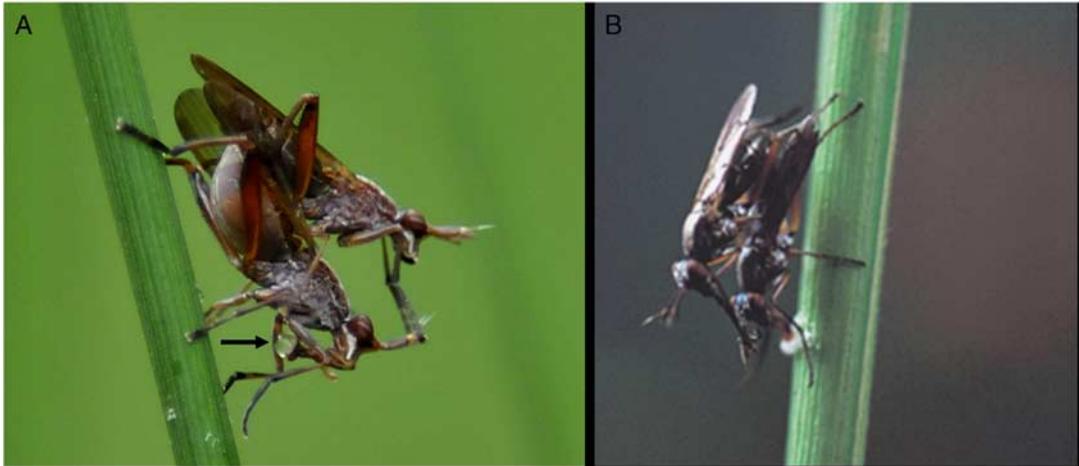
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**Fig. 1.** (A) Mating pair of *Sepedon fuscipennis* collected at Clay Pond (Great Falls), Maryland, United States of America, by Karolyn Darrow (Smithsonian Institution). Note the male is appositioning his forelegs to the female's styli. The female is seen in the process of bubbling (see arrow); (B) Male of *Sepedon* sp., possibly *Sepedon aenescens* Wiedemann (Berg and Valley 1985a), in Taiwan appositioning his forelegs to the stylus of the female while she feeds on the nuptial gift (photographed by S.-Y. Lee, Taiwan Agricultural Research Institute; available from <http://taipei.tzuchi.org.tw/tzquart/2006su/qs2.htm> [accessed 28 November 2012]).



Flies were captured either by use of a sweep net or with a clear plastic cup (473 cc) used in conjunction with a 30.5 cm square of plastic nylon mesh. The cup and mesh were positioned on either side of a cattail leaf, trapping the fly inside. A plastic lid, in which a 7.6 cm hole had been cut and over which mesh had been glued, was affixed to the cup. Until taken to the laboratory, flies were kept in screened fly cages (20.3 cm per side) with one side covered with a clear plastic sheet. Droplets of a mixture of yeast and honey were placed on the inner sides of the cage. Water was available to the flies from plastic cups (266 cc) containing dental wicks (Absorbal<sup>®</sup>, Wheatridge, Colorado, United States of America).

In the laboratory, flies were kept in a metal cage (30.5 cm per side) with clear plastic sides to allow better observation. The cage floor was lined with cotton that was moistened daily to replicate the natural environment of the flies. Wooden applicator sticks were positioned in the cage to provide resting and oviposition sites. Flies isolated for observation were held in a clear plastic cup (473 cc) with a mesh top, similar to the container in which they had been caught. They were supplied with droplets of a mixture of

yeast, powdered milk, honey, and water that was coloured with red food dye dabbed on the cage wall. Cages were cleaned weekly to prevent mould infestation. After several days of observations, flies were killed by freezing, placed in 80% ethanol, and prepared for the scanning electron microscope (SEM).

### Taxonomy

The nominative *S. fuscipennis* is widespread throughout the United States of America and Canada (Knutson *et al.* 1986). Three forms of the *S. fuscipennis* group are known: *S. f. fuscipennis* (from just west of 100° longitude in southern Texas to just north of 40° latitude in Illinois and Indiana, east to southern New England, south to Florida, United States of America); *S. f. nobilis* Orth (Alaska and Northwest Territory east to Newfoundland, south to New York, west to New Mexico and California in the United States of America and Canada); and *S. f.* “intermediate” (narrow distribution band from Kansas northeast through Illinois, Indiana, south Ohio, Pennsylvania, New York, to Massachusetts, United States of America) (Orth 1986). Two forms are known from Massachusetts (*S. f. fuscipennis* and *S. f.* “intermediate”). To ensure

collection and subsequent study of a single form, on 6 June 2010, W.L.M. collected 6 ♂ and 4 ♀ *S. f. fuscipennis* directly into 80% ethanol at an isolated stand of broadleaf cattail (*T. latifolia*) in Fishers, Indiana, a site from which only *S. f. fuscipennis* is known to occur. He shipped them to J.G.S. on 8 June. As expected, all 10 specimens exhibited characters diagnostic for *S. f. fuscipennis* – distinct velvety black parafacial spots and, in the males, the anterior process of the aedeagus relatively large and long relative to the posterior process.

### Observing the mating behaviour

Flies collected during the summer of 2009 were kept in small screened cages as described above. Flies were observed periodically for mating behaviour. Flies collected during the summer of 2010 were killed immediately in the field.

### Preparation for SEM

Using SEM to observe any type of sensilla on the antennae, especially the styli, of flies collected in 2009 was difficult because the antennae were completely covered by compacted masses of adhering pollen. Therefore, the procedures of Cuperus (1985) and Albert (2003) to clean and remove any debris on the antennae were followed. Specimens received from W.L.M. in 80% ethanol (summer 2010) were removed from the 80% ethanol and blotted dry, with care being taken not to break any parts. Once dry, they were placed in a beaker of boiling carbon tetrachloride for one minute. The specimens were then run through three changes of fresh, boiling carbon tetrachloride for one minute each, air dried, and placed onto stubs for SEM.

### SEM

During the summer of 2009 some of the flies were examined in low vacuum SEM requiring only mounting the fixed flies on stubs. Later in 2009 and in 2010 flies were prepared for high vacuum conventional SEM. Flies were placed in 80% ethanol until critical point dried by use of liquid CO<sub>2</sub>. Specimens were blotted dry using Kimwipes<sup>®</sup> (Roswell, Georgia, United States of America), mounted on stubs, sputter coated with ~15 nm gold, and examined in an FEI Quanta 200 SEM (FEI Company, Hillsboro, Oregon, United States of America), at 10 kV.

## Results

### Mating behaviour and bubbling

The main focus of the behavioural studies was to determine if the male always appositioned his forelegs to the styli of the female during copulation (Figs. 1A, 1B). In all of our observations (2009) ( $n = 10$ ), males always appositioned their forelegs to the styli of the females during copulation. Once flies of both sexes had fed on a honey–yeast-powdered milk mixture coloured red using food dye, they immediately began to “bubble” (Fig. 1A). The colour of the bubble produced by bubbling flies always took on the colour of the red food dye and was produced from food previously ingested into the crop (conclusion supported by dissections).

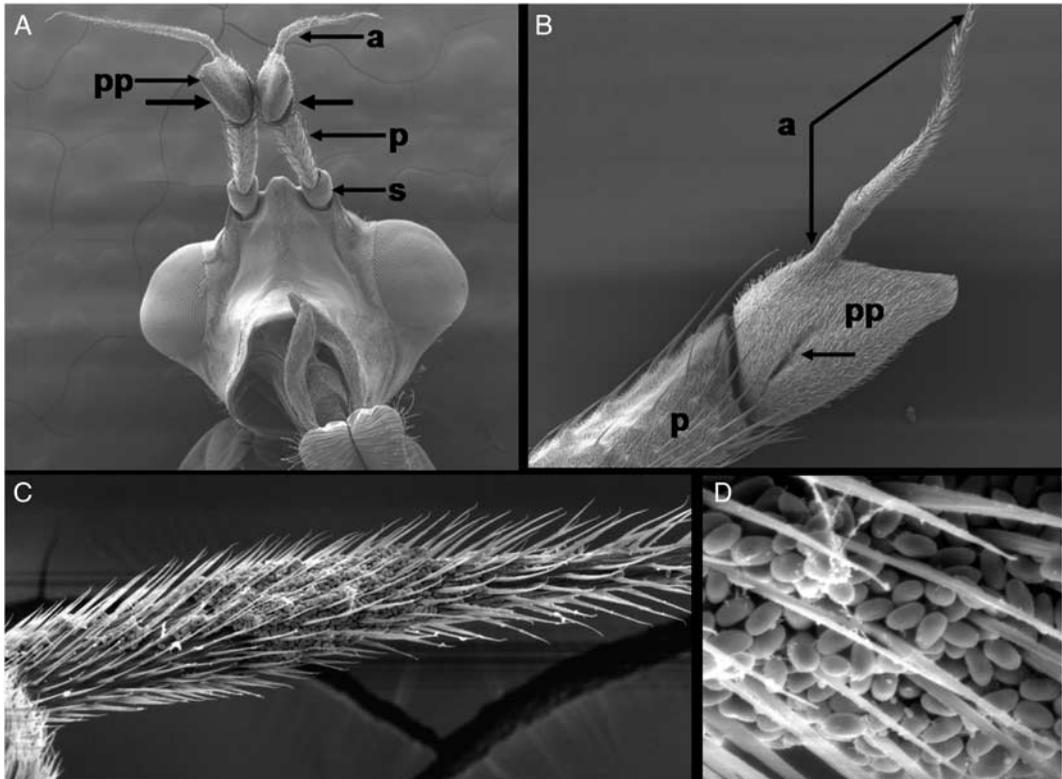
### SEM preparation

During the first summer of research (2009), it was impossible to observe the sensilla on the antennal styli of most specimens because of two factors: (1) the orientation of the specimen and the antennae on the stubs (Figs. 2A, 2B) and (2) the large clusters of pollen adhering to and between the spinelike setae of the styli (Figs. 2C, 2D).

### Styli mechanosensilla

After cleaning the antennae with boiling carbon tetrachloride (2010), it was possible to observe the sensilla on the styli of every specimen. SEM clearly showed a groove (Fig. 2B) on the postpedicel of the antenna. However, the main interest of the study was the mechanosensilla, thus SEM results focussed on them. The number and arrangement of the mechanosensilla differed between the sexes. In both sexes they were always located on the medial surface of the stylus. Females had more sensilla than did males, singly arranged in a linear fashion of four or more campaniform sensilla (Fig. 3A), situated on the 3rd segment of the styli on the “elongate, acuminate apical” portion (Stuckenberg 1999) and about halfway between the base and the tip of the stylus (Fig. 2B). In contrast, males had two patches of mechanosensilla, with two campaniform sensilla for each patch (Fig. 3B). As in females, mechanosensilla in males were located about halfway between the base and the tip of the stylus.

**Fig. 2.** (A) Head of male *Sepedon fuscipennis* showing position of the antennae. The unlabelled arrows point to the outer portion of the antennae, and the same orientation applies to the styli (a). The scape (s), pedicel (p), postpedicel (pp), and styli (a) are present (bar = 500  $\mu\text{m}$ ); (B) Portion of the antenna showing the pedicel (p), postpedicel (pp), and stylus (a). Note the arrow pointing to the postpedicular groove (bar = 200  $\mu\text{m}$ ); (C) Antenna of male showing masses of pollen stuck between the spinelike chaetae or setae of the stylus and obscuring underlying sensilla (bar = 50  $\mu\text{m}$ ); (D) Higher magnification of C showing the masses of adhering pollen stuck between the spinelike setae (bar = 10  $\mu\text{m}$ ). Specimens from 2009 and were not cleaned as in “Materials and methods”.



## Discussion

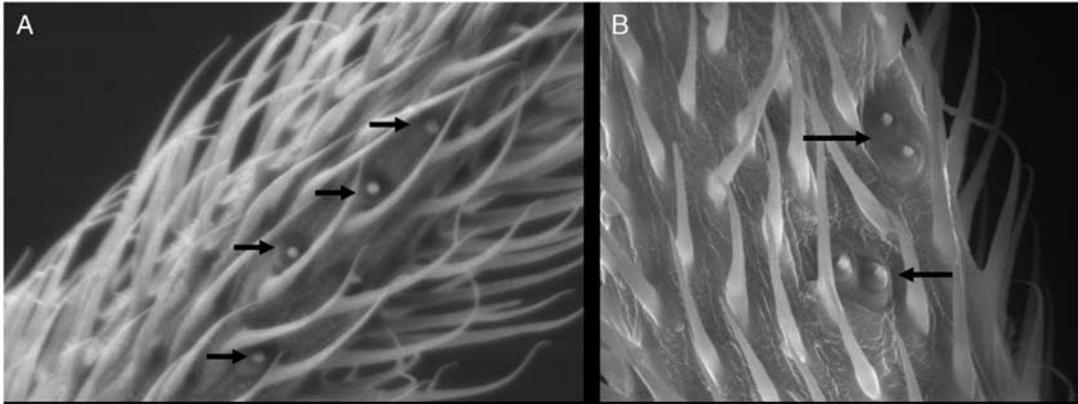
### Suggestions for specimen preparation

It is imperative that future studies of antennal sensilla or of any other cuticular structure of adult species of *Sepedon* follow the cleaning procedure reported by either Cuperus (1985) or Albert (2003) and used in the summer 2010 study prior to placement of specimens on stubs. This procedure is essential in removing debris such as pollen from the structures being examined. It is also imperative to mount the head so as to allow observation of the medial surface of the stylus of the antenna, where the mechanosensilla are located.

### Mechanosensilla on the antennal styli and their function

The suggestions of Stuckenberg (1999) have been followed here. He stated, “It is proposed that the term arista be reserved for the cyclorhaphous antennal mechanoreceptor”. Knutson and Vala (2011) recommend using stylus for the Sciomyzidae. The only known study of sensilla on the antenna of a species of *Sepedon* is by Gaponov *et al.* (2006), who made no mention of mechanosensilla on the stylus of any of the Sciomyzidae species examined; they reported only olfactory sensilla. Mechanosensilla are classified as Type I mechanoreceptors because they are associated with the cuticle and, based on

**Fig. 3.** (A) Inner portion, about halfway between the base and the tip, of the stylus of a female *Sepedon fuscipennis* showing the arrangement of the mechanosensilla (four are visible here – see arrows) tucked between the numerous spinelike chaetae or setae (bar = 10  $\mu\text{m}$ ); (B) In contrast to the female, the male has two groups of mechanosensilla arranged in pairs and in a nonlinear arrangement (bar = 10  $\mu\text{m}$ ). Specimens from 2010 and cleaned as stated in the “Materials and methods”.



function, respond to cuticular distortion or compression (*i.e.*, they are strain sensors) (McIver 1985). The mechanosensilla caps of insects can be level with the cuticle or elevated above the cuticle. In *S. fuscipennis*, the campaniform sensilla (Figs. 3A, 3B) are associated with the cuticle, the sensilla are dome shaped and raised above the cuticle. On the basis of their structure, it is hypothesised that these sensilla should respond to cuticular distortion or compression as the stylus is bent medially during mating.

Knutson and Vala (2002) noted that, “Except for the morphology of the postabdomen, body size, and development of setae on the ventral surface of the hind femur in many genera, there is little sexual dimorphism amongst Sciomyzidae”. The presence of sexually dimorphic mechanosensilla on the styli of *S. fuscipennis* adds to this list of sexually dimorphic characters. The fact that the mechanosensilla show sexual dimorphism (*i.e.*, differences in number and arrangement) (Figs. 3A, 3B) suggests that they serve different functions for each sex. It was difficult for us to count the numbers of mechanosensilla because the antennal styli of the Sciomyzidae are heavily covered with chaetae or setae (*e.g.*, *Sepedon*) (Figs. 3A, 3B) or long dense setae (*e.g.*, *Coremacera* Rondani) (Gaponov *et al.* 2006). Berg and Valley (1985a) provided a detailed account of mating in *Sepedon* species; however, their focus was on production

and importance of the nuptial gift produced by the male. They made no mention in their paper concerning the position of the male during copulation and the apposition of his forelegs to the styli of the female. A photograph taken by entomologist Ernie Bay of Washington State, United States of America of a pair of *Sepedomerus macropus* (Walker) mating also shows the male appositioning his forelegs to the styli of the female (photograph in the possession of W.L.M.). According to Lloyd Knutson, Gaeta, Italy (personal communication), this behaviour among the Sciomyzidae is unique to the genus *Sepedon*, but based on the photograph of *S. macropus*, this behaviour may apply to other members of the genus. In a brief study of copulatory behaviour of *Sepedon neavei* Steyskal, *S. testacea* Loew, and *Sepedon pleuritica* Loew, Barraclough (1983) did not report the male tarsi contacting the female’s antennae. We did not examine the styli of those species of Sciomyzidae, such as *Tetanocera* Duméril species, where the male mates with their tarsi over the female eye. Also, we have no information on whether males of other members of *Sepedon*, besides *S. fuscipennis* and *S. macropus*, also apposition the female antennae during mating. Unless one specifically and carefully examines mating behaviour, as done by Tobin and Stoffolano (1973), minute details such as where the foretarsi are placed can be missed. Interesting, however, is the report of

Barnes (1979) for several species of *Neolimnia* Tonnoir and Malloch: "During copulation the male's fore tarsi rest on the female's frons, and frequently his claws are hooked over her anterior frontal margin between the antennae and eyes". No mention, however, is made of the male touching the female's styli or antennae.

Based on observations in this study, personal communication with Knutson, and Figures 1A, 1B, it is suggested that the mechanosensilla on the antennal styli of female *Sepedon* provide feedback to the female regarding the males appositioning his forelegs to her styli. This may be an inherent, behavioural component of the mating ritual that the female uses as an important signal of the correct species and, if not present, will not accept the male's copulatory attempt. The position of the sensilla on the medial surface of the styli and their linear arrangement correlates with the bending of her antennae medially as the male appositions his forelegs to the lateral surface. This agrees with the idea of Johnson *et al.* (2009), who also noted that arrangement and location of mechanosensilla influence the stress placed upon them, which in this case would be from the lateral surface medially. This also agrees with Johnson *et al.* (2009), who further noted that, "The oval shape of a campaniform sensillum means that it can be deformed more readily in one direction than the other, providing a level of directional sensitivity to the strain".

Another suggested function of these sensilla in both sexes is monitoring any contact the adult has while obtaining nectar from flowers. This hypothesis is based on the large packs of pollen found adhering to the antennal styli (Figs. 2C, 2D) and on the "bubbling" behaviour observed in our laboratory during the summer of 2009 (*i.e.*, flies took nutrients, presumably nectar, into the crop, but later used these fluids to produce bubbles) as shown in Figure 1A. Stuckenberg (1999) also suggested that "...the emergence of the Brachycera from nematoceros ancestors involved coevolution of antennal transformation and pseudotracheate labella, linked to a new feeding mode appropriate in new floras that appeared in the Triassic and Jurassic".

Even though bubbling behaviour has been reported in some Diptera (Stoffolano *et al.* 2008), no specific reference in the literature for

the Sciomyzidae was found. Mating trophallaxis, however, has been reported for several sciomyzids (Barraclough 1983; Knutson and Vala 2011) and this behaviour involves regurgitation of liquids and, possibly salivary gland secretions from the crop (Stoffolano and Haselton, 2013) (*S. testacea* is mentioned in the paper by Barraclough 1983). Bubbling behaviour in the Sciomyzidae, unlike that shown in other Diptera for getting rid of excess water in the diet (Stoffolano *et al.* 2008), may also be involved in the production of the froth "nuptial gift" presented to the female during courtship and mating (Green 1977; Berg and Valley 1985a, 1985b). Prasad *et al.* (2010) mentioned trophallaxis in the India species of *Sepedon* they studied, but did not mention bubbling.

During SEM examination of male *S. testacea* in Cape Town, South Africa (their summer 2010), with Ray Miller, large packs of pollen on the styli were found. Thus, both our study of *S. fuscipennis* and observations in South Africa with *S. testacea* suggest that adult *Sepedon* obtain carbohydrates from flowers. In fact, Berg and Knutson (1978) reported that adults have been collected while feeding on flowers. A study on honey bees (*Apis mellifera* Linnaeus; Hymenoptera: Apidae) by Scheiner *et al.* (2005) demonstrated that antennal mechanosensilla are mainly involved in surface discrimination and not in shape discrimination of flowers. The mechanosensilla on the antennal styli of both sexes of *Sepedon* may serve a similar function.

### Future studies and questions

The Sciomyzidae are of considerable interest in regard to biological control programs to halt or lessen the impact of schistosomiasis (Berg 1973; Appleton *et al.* 1994) and fascioliasis (McDonnell 2004), plus gastropod pests of agriculture and horticulture (Barker *et al.* 2004), yet very little research has been conducted on either adult sensory physiology or on their selection of flowers from which they obtain carbohydrates. Both areas should be explored further.

Judd (1964) reported three species of Sciomyzidae feeding on marsh marigold (*Caltha palustris* Linnaeus; Ranunculaceae); one of the species was *S. fuscipennis*, which confirms that this species feeds on floral resources in the vicinity of marshes and which helps explain the numerous pollen grains observed on the antennal

styli of *S. fuscipennis* during the 2009 study and the South African research by J.G.S. Studies describing the manner and/or type of flowers on which *S. fuscipennis* feeds are needed. Examination of the literature for the presence and use of chemoreceptors on the antennae of anthophilous flies failed to produce any results. Thus, finding chemoreceptors responsive to sugars on the antennae of *Chrysops fuliginosa* Wiedemann (Diptera: Tabanidae) (Liscia *et al.* 1982) supports the suggestion that many flies use their antennae in perceiving nectar sugars. A closer look at the Sciomyzidae is needed. Feeding on flowers should account for the large quantities of pollen found on the styli in this study. Histological and ultrastructural studies also should be made of the entire antennal sensilla with a focus on the postpedicel groove. According to Stuckenberg (1999), the Sciomyzidae fit into the category of antennal evolution that he called individuals having a “compound flagellar base” or postpedicel; the segment that should possess most of the olfactory sensilla, which in *Sepedon* may be inside the postpedicular groove (Fig. 2B). In a cleared postpedicel of *Sepedon sp.* and, using a compound light microscope, David McAlpine, Australian Museum, Sydney, Australia (personal communication) found a major sacculus opening into the groove and up to seven smaller secondary sacculi or pits. In this study, we did not examine the sacculus. Stuckenberg (1999) also noted that the enlargement of the postpedicel segment permitted for an increase and diversification of sensilla with invaginated pits (here the postpedicular groove) and that this adaptation related to life history feeding strategies such as anthophily, nectarivory, saprophagy, and coprophagy. For the Sciomyzidae, it probably was driven by adults feeding on snails and various types of eggs for protein and nectar for carbohydrates. Both are essential in their diet as shown by McDonnell *et al.* (2005). Finally, more studies need to be conducted on sensory inputs between the sexes during mating and what effect, if any, ablation of the female’s antennal styli might have on mating.

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### References

- Albert, P.J. 2003. Electrophysiological responses to sucrose from a gustatory sensillum on the larval maxillary palp of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Journal of Insect Physiology*, **49**: 733–738.
- Appleton, C.C., Miller, R.M., and Maharaj, R. 1994. Control of schistosomiasis host snails in South Africa – the case for biocontrol by predator augmentation using sciomyzid flies. *Journal of Medical and Applied Malacology*, **5**: 107–116.
- Barker, G.M., Knutson, L., Vala, J.-C., Coupland, J.B., and Barnes, J.K. 2004. Overview of the biology of marsh flies (Diptera: Sciomyzidae), with special reference to predators and parasitoids of terrestrial gastropods. *In* Natural enemies of terrestrial molluscs. *Edited by* G.M. Barker. CABI, Wallingford, United Kingdom. pp. 159–219.
- Barnes, J.K. 1979. Biology of the New Zealand genus *Neolimnia* (Diptera: Sciomyzidae). *New Zealand Journal of Zoology*, **6**: 561–576.
- Barraclough, D.A. 1983. The biology and immature stages of some *Sepedon* snail-killing flies in Natal (Diptera: Sciomyzidae). *Annals of the Natal Museum*, **25**: 293–317.
- Berg, C.O. 1973. Biological control of snail-borne diseases: a review. *Experimental Parasitology*, **33**: 318–330.
- Berg, C.O. and Knutson, L.V. 1978. Biology and systematics of the Sciomyzidae. *Annual Review of Entomology*, **23**: 239–258.
- Berg, C.O. and Valley, K. 1985a. Nuptial feeding in *Sepedon* spp. (Diptera: Sciomyzidae). *Proceedings of the Entomological Society of Washington*, **87**: 622–633.
- Berg, C.O. and Valley, K. 1985b. Further evidence of nuptial feeding in *Sepedon* (Diptera: Sciomyzidae). *Proceedings of the Entomological Society of Washington*, **87**: 769.

- Cuperus, P.L. 1985. Inventory of pores in antennal sensilla of *Yponomeuta* spp. (Lepidoptera: Yponomeutidae) and *Adoxophyes orana* F.v.R. (Lepidoptera: Tortricidae). *International Journal of Insect Morphology and Embryology*, **14**: 347–359.
- Gaponov, S.P., Khitzova, L.N., and Sergeev, A.S. 2006. Fine morphology of Sciomyzidae (Diptera) female head sensory system. *In* Abstracts from the 6th International Congress of Dipterology, 23–28 September, Fukuoka, Japan [online]. pp. 84–85. Available from <http://www.nadsdiptera.org/ICD/AbstractsICD6.pdf> [accessed 26 October 2012].
- Green, T. 1977. A man's obsession reveals the riches of a hidden world. *Smithsonian*, **8**: 81–87.
- Johnson, E.A.C., Bonser, R.H.C., and Jeronimidis, G. 2009. Recent advances in biomimetic sensing technologies. *Philosophical Transactions of the Royal Society A*, **367**: 1559–1569.
- Judd, W.W. 1964. Insects associated with flowering marsh marigold *Caltha palustris* L., at London, Ontario. *The Canadian Entomologist*, **96**: 1472–1476.
- Knutson, L., Orth, R.E., Fisher, T.W., and Murphy, W.L. 1986. Catalog of Sciomyzidae (Diptera) of America north of Mexico. *Entomography*, **4**: 1–53.
- Knutson, L. and Vala, J.-C. 2002. Morphodiversity and biodiversity in *Sepedon* Latreille and related genera: a lineage, a tribe, or a subfamily? (Diptera: Sciomyzidae). *In* 5th International Congress of Dipterology, 29 September–4 October, Brisbane, Australia. Abstracts, International Congress of Dipterology, Brisbane, Australia. p. 119.
- Knutson, L.V. and Vala, J.-C. 2011. *Biology of snail-killing sciomyzid flies*. Cambridge University Press, Cambridge, United Kingdom.
- Liscia, A., Angioy, A.M., Crnjar, R., Pietra, P., and Stoffolano, J.G. Jr. 1982. Chemocettori sui labelli, tarsi ed antenne di *Chrysops fuliginosus* Wied.: uno studio elettrofisiologico preliminare. *Bollettino della Soc. Italiana di Biol. Sperimentale*, **58**: 673–677.
- McDonnell, R.J. 2004. The biology and behaviour of selected marsh fly species (Diptera: Sciomyzidae), potential biological control agents of liver fluke disease in Ireland. Ph.D. thesis. National University of Ireland, Galway, Ireland.
- McDonnell, R.J., Mulkeen, C.J., and Gormally, M.J. 2005. Sexual dimorphism and the impact of temperature on the pupal and adult stages of *Sepedon spinipes spinipes*, a potential biological control agent of fascioliasis. *Entomologia Experimentalis et Applicata*, **115**: 291–301.
- McIver, S.B. 1985. Mechanoreception. *In* *Comprehensive insect physiology, biochemistry and pharmacology*. Vol. 6. *Edited by* G.A. Kerkut and L.I. Gilbert. Pergamon Press, Oxford, United Kingdom. pp. 71–132.
- Orth, R.E. 1986. Taxonomy of the *Sepedon fuscipennis* group (Diptera: Sciomyzidae). *Proceedings of the Entomological Society of Washington*, **88**: 63–76.
- Prasad, K.D., Knutson, L., and Ghorpadé, K. 2010. Notes on the biology of India *Sepedon* species (Diptera-Sciomyzidae): larval development on snail eggs, labellar hooks of adult flies, and trophallaxis. *Colemania*, **22**: 3–12.
- Scheiner, R., Schnitt, S., and Erber, J. 2005. The functions of antennal mechanoreceptors and antennal joints in tactile discrimination of the honeybee (*Apis mellifera* L.). *Journal of Comparative Physiology A*, **191**: 857–864.
- Stoffolano, J.G. Jr., Acaron, A., and Conway, M. 2008. “Bubbling” or droplet regurgitation in both sexes of adult *Phormia regina* (Diptera: Calliphoridae) fed various concentrations of sugar and protein solutions. *Annals of the Entomological Society of America*, **101**: 964–970.
- Stoffolano, J.G. Jr. and Haselton, A.T. 2013. The adult Dipteran crop: a unique and overlooked organ. *Annual Review of Entomology*, **58**: 205–225.
- Stuckenberg, B.R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. *Studia Dipterologica*, **6**: 33–48.
- Tobin, E. and Stoffolano, J.G. Jr. 1973. The courtship of *Musca* species found in North America (Diptera: Muscidae). I. The house fly, *Musca domestica* L. *Annals of the Entomological Society of America*, **66**: 1249–1257.