



A new species of *Myiopharus* Brauer and Bergenstamm (Diptera: Tachinidae) parasitic on adults of the sunflower beetle, *Zygogramma exclamationis* (Fabricius)

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Abstract

A new species of the New World genus *Myiopharus* Brauer and Bergenstamm, *Myiopharus neilli* sp. nov., is described from the Great Plains, bringing the number of species of this genus known from America north of Mexico to 15. *Myiopharus neilli* is a parasitoid of adults of the sunflower beetle, *Zygogramma exclamationis*. It belongs to the *M. dorsalis* (Coquillett) species group, the females of which possess a strongly sclerotized and laterally flattened ovipositor and a dense tuft of blunt setae medially on the katapisternum. Both sexes of *M. neilli* are described and illustrated, the life history of the species is reviewed, and the *M. dorsalis* group is characterized.

Key words: Diptera, Tachinidae, *Myiopharus*, sunflower beetle, new species

Introduction

The sunflower beetle, *Zygogramma exclamationis* (Fabricius), is a native North American species that feeds on sunflowers during its larval and adult stages. It is present throughout the Great Plains and is the major defoliating insect pest of the cultivated sunflower, *Helianthus annuus* L. (Knodel *et al.* 2000; Brewer & Charlet 2004). Economically significant damage is mostly confined to Minnesota, North Dakota, South Dakota, and southern Manitoba (Charlet 1992; Brewer & Charlet 2004).

Three species of Tachinidae have been reared from the sunflower beetle, all in the genus *Myiopharus* Brauer and Bergenstamm. Two are exclusively parasitoids of the larvae, *M. macellus* (Reinhard) (formerly *Doryphorophaga macella*) and *M. doryphorae* (Riley) (formerly *Doryphorophaga doryphorae*). *Myiopharus macellus* is a common parasitoid of the sunflower beetle and has been reported to parasitize up to 100% of larvae (Charlet 1992; Charlet 2003). *Myiopharus doryphorae* is principally a parasitoid of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), but has been reared on rare occasions from sunflower beetle larvae in southern Manitoba (Neill 1982; Knodel *et al.* 2000). The third species is a parasitoid of adult sunflower beetles and has been reported in the literature as "*Myiopharus* sp." (Neill 1982; Charlet 1992; Charlet 1999; Knodel *et al.* 2000; Brewer & Charlet 2004). Although the life history of this species was carefully detailed over two decades ago by Neill (1982), and the species was known to be new to science at the time (specimens of it having been identified for Neill by D.M. Wood of Agriculture and Agri-Food Canada, Ottawa), it has remained undescribed. It first came to my attention when I discovered specimens of it in a shipment of tachinids reared from sunflower pests sent to me for identification by L.D. Charlet (see Materials and Methods). It is the purpose of this paper to describe this new species and to discuss its relationships within the genus *Myiopharus*.

Materials and Methods

Terms for structures of the male terminalia follow Sinclair (2000) and those for other structures follow McAlpine (1981). Methods used for dissections, measurements, and citation of specimen label data are explained in O'Hara (2002).

Images in the two color plates were taken with a Leica DC500 digital camera attached to a Leica Z16 APO microscope. From 10 to 35 images were taken of a specimen or structure at different focal planes using a Z-stepper and blended in Auto-Montage Pro version 5.02 from Syncroscopy. Blending was optimized for precision in Auto-Montage using a patch size of 30. Images were retouched and plates prepared in Adobe Photoshop CS2 version 9.0.2.

Line drawings of male terminalic structures were made with the aid of a camera lucida mounted on a Leitz Ortholux compound microscope. Male terminalia were held in place in glycerine jelly for illustration.

This study was based mainly on specimens in the Canadian National Collection of Insects, c/o Agriculture and Agri-Food Canada, Central Experimental Farm, Ottawa, Ontario, Canada (referred to herein as CNC). Several specimens of the new species were borrowed from L.D. Charlet of the Sunflower Research Unit, USDA, Agricultural Research Service, Northern Crop Science Laboratory, Fargo, North Dakota, USA, and those specimens have been deposited in the North Dakota State Insect Reference Collection, North Dakota State University, Fargo (referred to herein as NDSU).

Systematics

Myiopharus Brauer and Bergenstamm, 1889

Myiopharus Brauer and Bergenstamm, 1889: 161 (also 1890: 93). Type species: *Myiopharus metopia* Brauer and Bergenstamm, 1889, by monotypy.

The type species of *Myiopharus* is *M. metopia*, described from the Neotropical Region. Reinhard (1945) added the first North American species to *Myiopharus*, *M. dorsalis* (Coquillett, 1898), and described two additional species, *M. canadensis* and *M. securis*. This classification, recognizing three species of *Myiopharus* in America north of Mexico, was followed by Sabrosky and Arnaud (1965). An earlier synonymy of the North American genus *Adoryphorophaga* Townsend (1931) with *Myiopharus* by Mesnil (1960: 653) was either overlooked or disregarded by Sabrosky and Arnaud (1965). Aldrich (1934) described two new species of *Myiopharus* from Chile, and Guimarães (1971) grouped these and eight other species under *Myiopharus* in his catalogue of the Tachinidae of America south of the United States.

Wood (1985) re-evaluated the generic concepts of *Myiopharus* and other blondeliine genera in his revision of the Blondeliini of North and Central America. In an attempt to simplify the oversplit classification of his predecessors, and to bring related species closer together, Wood proposed a revised classification that consisted of fewer, more broadly defined, genera. His intention was to group species based on similarities and shared derived characters, and the result was 55 genera and 177 new generic synonyms for the Blondeliini of North and Central America. *Myiopharus* remained an exclusively New World genus, but swelled in size from fewer than 15 described species in the New World to 54 described species in just North and Central America (creating over 30 new generic synonyms in the process). Wood (pers. comm.) believes there are about 50 described species in South America that should also be classified in *Myiopharus* in addition to many undescribed species throughout the Neotropics, making this the largest genus in the Blondeliini. Relatively few species are known from America north of Mexico, where O'Hara and Wood (2004) listed just 14 species. It is suspected that the hosts of *Myiopharus* species are exclusively beetles in the family Chrysomelidae, with other recorded hosts probably being in error (Wood 1985). The sister group to *Myiopharus* within the

Blondeliini has not been determined, though Wood (1985) suggested that the monotypic genus *Thelyoxynops* Townsend from Trinidad might be related to, or possibly congeneric with, *Myiopharus*.

The monophyly of *Myiopharus* has not been established, and the genus could possibly be paraphyletic. It does contain species of different appearance; for example, the males of some species have a black thorax and shiny frons (Fig. 5) whereas males of other species are gray like females (Fig. 1), the eye is densely haired in most species and sparsely haired in a few, and the facial ridge is setose along most of its length in some species and on less than lower half in others (Figs. 2, 4). As well, female ovipositors vary from tubular to piercing to laterally flattened (Figs. 7–8). These sorts of differences are often used to separate genera and explain in part why the *Myiopharus* species of Wood (1985) were once dispersed among many genera. Yet there is also a continuity among species for certain characters and a continuum from one species to the next for others, such that there is no easy way to divide the genus nor any clear indication that it is not monophyletic.

Myiopharus is easily recognizable as a blondeliine tachinid by a combination of character states (Wood 1985; couplet 119 in Wood 1987): prosternum haired, first postsutural supra-alar seta smaller than first postsutural dorsocentral seta, scutellum with four setae including a pair of large and divergent subapicals, and bend of vein *M* rounded and obtuse-angled. *Myiopharus* is less easily characterized, keying out three times in Wood (1987). The genus is diagnosed in Wood (1985). The species described here, *M. neilli*, can be recognized as a member of *Myiopharus* by the following features: eye moderately to densely haired, parafacial bare, both sexes with 2 pairs of proclinate orbital setae (Fig. 4), subvibrissal ridge with row of 2–3 setae (Fig. 2), proepisternum bare, vein R_{4+5} with just a few hairs basally, middorsal depression on abdominal syntergite 1+2 not extended back to hind margin of syntergite (but close), and body black or almost so in ground color.

***Myiopharus dorsalis* (Coquillett) species group**

There are various external similarities and differences among *Myiopharus* species that will one day help in the division of the genus into species groups or subgenera. It is beyond the scope of this paper to explore the intrageneric relationships of *Myiopharus* species in such detail, but there are two small yet discrete groups of species that can be separated from the other species on the basis of modifications of the female terminalia (Wood 1985). Females of most *Myiopharus* species have a simple tubular ovipositor that is a groundplan state of the Blondeliini and presumably *Myiopharus* as well. The female of the type species of *Myiopharus*, *M. metopia*, has this type of ovipositor. A few species of *Myiopharus* have an ovipositor that has been modified into a curved and pointed piercer, and these species are thought to form a monophyletic lineage, termed here the *M. doryphorae* (Riley) species group. This species group comprises *M. americanus* (Bigot), *M. doryphorae*, and *M. macellus* (Reinhard) in America north of Mexico and includes at least several Neotropical species. A second group of *Myiopharus* species, here termed the *M. dorsalis* (Coquillett) species group, is characterized by a peculiar ovipositor in which sternite 7 is laterally flattened and apically rounded (Figs. 7–8). This unusually-shaped ovipositor may be designed to slide under an elytron of an adult beetle during oviposition (Wood 1985), thus ensuring a relatively safe delivery of a ready-to-hatch egg onto a host.

In addition to the specialized ovipositor, females of the *M. dorsalis* group possess a dense tuft of closely appressed setae on the katapisternum in front of and overlapping the mid coxae (Fig. 6) that is apparently unique to this group. The setae comprising the tuft are unusual in that they are parallel-sided and somewhat blunt-tipped, rather than evenly tapered to a point like normal setae. The purpose of this peculiar tuft of setae is not known. It is not found in males of the *M. dorsalis* group, although males of *M. neilli* have a denser group of setae in this position than males of other members of the group and most other *Myiopharus*.

The *M. dorsalis* group is clearly monophyletic based on its specialized ovipositor and katapisternal tuft of setae in females, and comprises *M. canadensis* Reinhard (Fig. 5), *M. dorsalis*, *M. securis* Reinhard, and new species *M. neilli* (Figs. 1, 3) in the Nearctic Region. Other features shared by members of the *M. dorsalis*

group but varied within the genus include: facial ridge setose on less than lower half (Figs. 2, 4), 3 katepisternal setae (illustrated for *M. dorsalis* in Fig. 173 by Wood 1987), median discal setae on abdominal tergites 3–4, and no male “sex patch” (*sensu* Wood 1985) on abdominal tergites 4 and/or 5.

***Myiopharus neilli* sp. nov.**

Figs. 1–3, 6–14.

Cited as “*Myiopharus* sp.” in Neill (1982), Charlet (1992), Charlet (1999), Knodel *et al.* (2000) and Brewer and Charlet (2004).

Holotype. Male, labelled: “Canada Manitoba/ Lowe Farm/ 49°21'N 97°35'W/ G.B. Neill”, “ex. adult of/ *Zygogramma/ exclamatonis/* [host] coll. 9.viii.1977”, “HOLOTYPE/ *Myiopharus/ neilli/* O'Hara [red label]” (CNC). Puparium pinned below specimen.

Allotype. Female, labelled: “Canada Manitoba/ Rosenfeld/ 49°12'N 97°33'W/ G.B. Neill”, “ex. adult of/ *Zygogramma/ exclamatonis/* [host] coll. viii.1977”, “ALLOTYPE/ *Myiopharus/ neilli/* O'Hara [red label]” (CNC).

Paratypes. 22♂♂, 23♀♀, all in CNC except as otherwise noted. **CANADA. Manitoba:** Lowe Farm, 49°21'N 97°35'W, G.B. Neill, ex. adult *Z. exclamatonis*, host coll. 9.viii.1977, 6♂♂ (3 with puparia), 2♀♀; same data except 12.viii.1977, 3♂♂ (all with puparia); Rosenfeld, 49°12'N 97°33'W, G.B. Neill, ex. adult *Z. exclamatonis*, host coll. viii.1975, 1♀ (with puparium and host remains); same data except 5.ix.1975, 8♂♂ (3 with puparia including 1 with host remains), 6♀♀ (2 with puparia and host remains); same data except 20.viii.1976, 1♀ (with puparium and host remains); same data except viii.1977, 1♂, 3♀♀ (1 with puparium); St. Jean, 49°16'N 97°21'W, G.B. Neill, ex. adult *Z. exclamatonis*, host coll. 22.vii.1977, 1♂ (with puparium); same data except 5.viii.1977, 3♂♂ (all with puparia, 1 with host remains), 1♀ (with puparium).

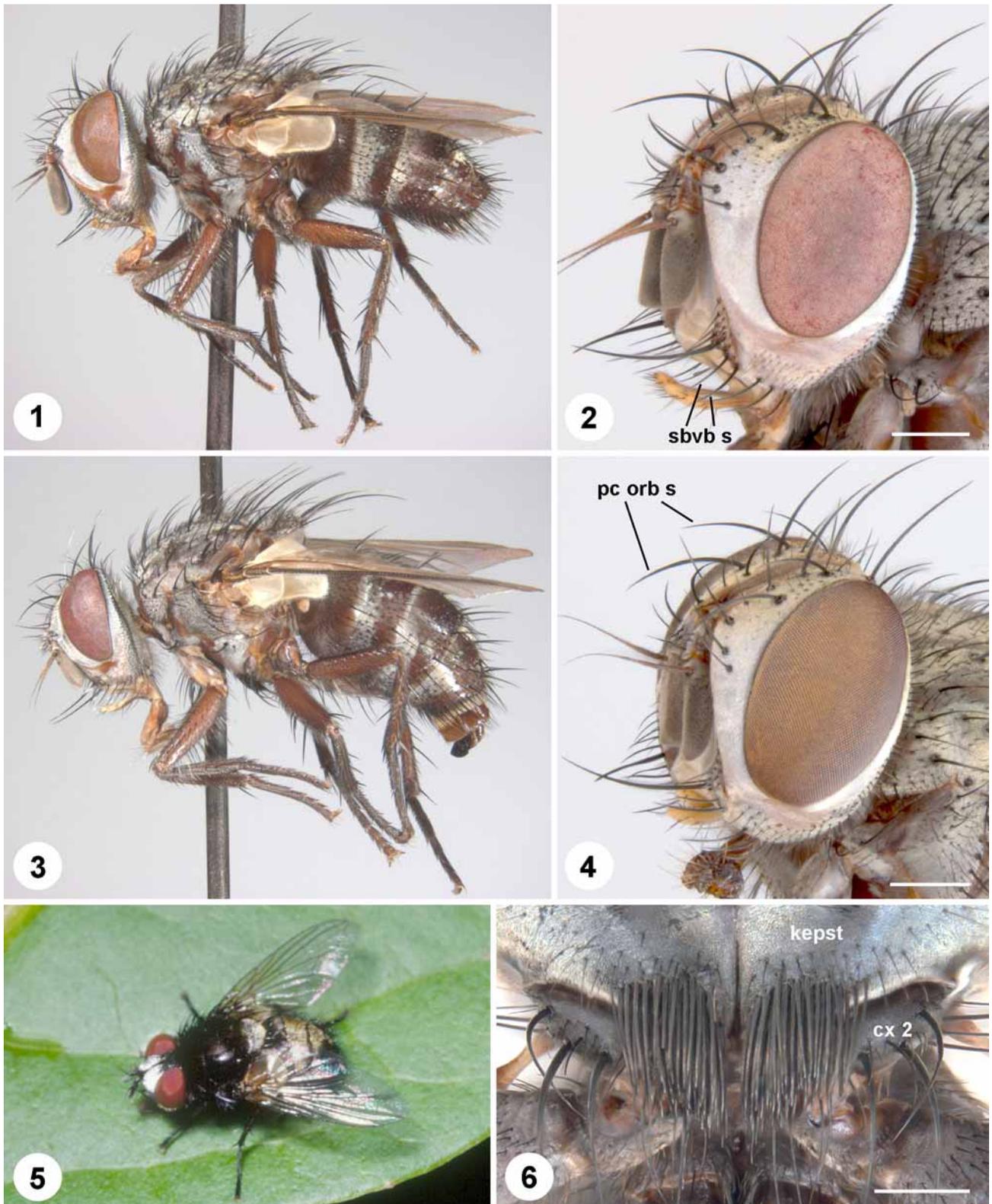
USA. Colorado: Gunnison Co., Gothie, 9500', 30.vii.1961, J.G. Chillcott, 1♀. **Minnesota:** Clay Co., Hawley Plots, 28.vii.1987, V. Beregovoy, taken from sunflower emergence trap, 1♀ (NDSU); Marshall Co., Warren, L. Charlet, T. Gross & J. Barker, ex. *Zygogramma exclamatonis* (Fabricius) on *Helianthus annuus* L., host coll. 14.vi.1985, parasitoid emerged i.1986 (in lab), 1♂, 1♀ (NDSU). **North Dakota:** Cass Co., Prosper Sunflower Plot, 27.vii.1995, L. Charlet & T. Gross, taken on head of *H. annuus*, 1♀ (NDSU); Cass Co., east of Amenia, 47°00.1'N 97°06.8'W, 20.vii.2004, J.E. O'Hara, on *H. annuus*, 1♀; same data except 21.vii.2004, 4♀♀; same data except 22.vii.2004, 2♀♀. **South Dakota:** Tripp Co., Winner, 3.vii.1924, 1♀.

Etymology

Named for Garnet B. Neill, who elucidated the biology of this species in his Ph.D. dissertation (Neill 1982) and reared many of the specimens in the type series.

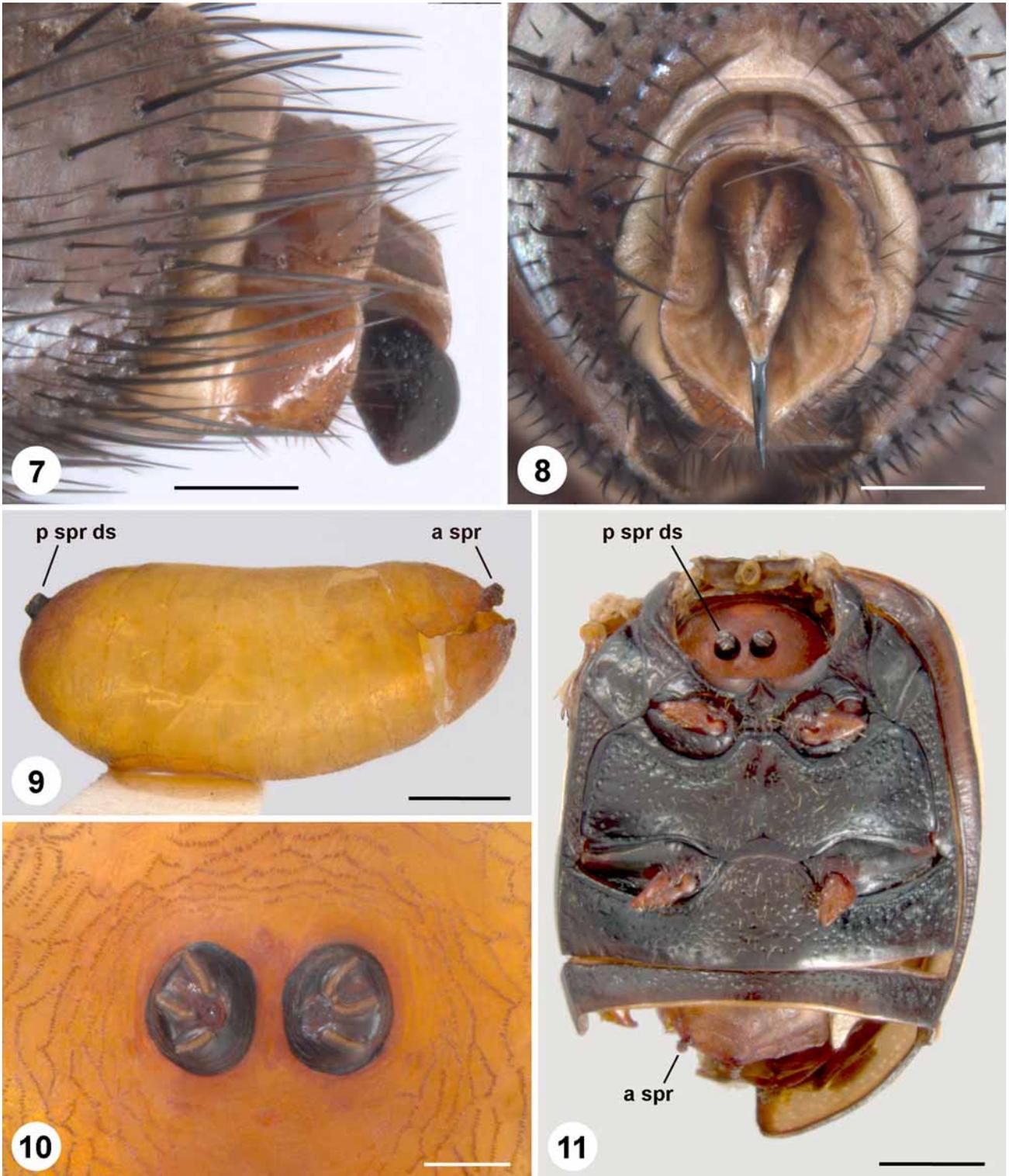
Recognition

This species is easily recognized in the female sex as a member of the *M. dorsalis* group by the presence of two distinctive features: a dense tuft of closely appressed setae on the ventral portion of the katepisternum (Fig. 6), and a laterally flattened and apically rounded ovipositor (Figs. 7–8) (see discussion under *Myiopharus dorsalis* species group). The female is readily separated from females of the other known species of the group by its broader parafacial and vertex. The widths of the parafacial and vertex are about equal in the females of *M. canadensis*, *M. dorsalis*, and *M. securis* (these comprising the other members of the *M. dorsalis* group in America north of Mexico) (Fig. 4, *M. dorsalis*), and noticeably narrower than in *M. neilli* (Fig. 2). Females of *M. neilli* and *M. dorsalis* have a black scutellum, in contrast to a more yellowish scutellum (at least apically) in the females of *M. canadensis* and *M. securis*.



FIGURES 1–6. 1. *Myiopharus neilli* sp. nov., left lateral view of male holotype. Body length = 6.9mm. 2. *M. neilli*, oblique view of head of female allotype. Scale bar = 0.5mm. 3. *M. neilli*, left lateral view of female allotype. Body length = 6.9mm. 4. *M. dorsalis*, oblique view of female head. Scale bar = 0.5mm. 5. *M. canadensis*, showing dark thorax and shiny frons that characterizes males of some *Myiopharus* species (image courtesy of S.A. Marshall). 6. *M. neilli*, ventral view of female showing tufts of setae on katapisternum in front of mid coxae. Scale bar = 0.3mm.

Abbreviations: cx 2, mid coxa; kepst, katapisternum; pc orb s, proclinate orbital setae; sbvb s, subvibrissal setae.



FIGURES 7–11. *Myiopharus neilli* sp. nov. **7.** Left lateral view of female ovipositor. Scale bar = 0.2mm. **8.** Posterior view of female ovipositor. Scale bar = 0.2mm. **9.** Puparium. Scale bar = 1.0mm. **10.** Posterior and slightly dorsal view of posterior spiracular discs of puparium. Scale bar = 0.2mm. **11.** Puparium within remains of host, *Zygogramma exclamationis*. Beetle is typically decapitated between prothorax and mesothorax. Scale bar = 1.0mm. Abbreviations: a spr, anterior spiracle; p spr ds, posterior spiracular disc.

The male of *M. neilli* is similar in coloration to the female, unlike in other members of the *M. dorsalis* group in which the parafacial and frons of males are silvery and the thorax is black (Fig. 5, *M. canadensis*). This sexual dimorphism is common among *Myiopharus* species. The *M. dorsalis* group cannot be recognized in males, although the male of *M. neilli* has a denser group of setae on the ventral portion of the katepisternum than males of most other *Myiopharus* species. The following combination of character states will serve to distinguish the male of *M. neilli* from males of all other *Myiopharus* species in America north of Mexico except for *M. aberrans* (Townsend) and *M. trifurca* (van der Wulp): thoracic dorsum viewed from above gray with four thin black vittae (dorsum not solidly black), facial ridge with setae and decumbent hairs on less than lower half (not with semi-erect setae on more than lower half), median discal setae present on abdominal tergites 3 and 4 (not lacking median discals on one or both tergites), three katepisternal setae (not two, with lower seta missing), and no sex patch on abdominal tergites 4 and/or 5. Males of *M. neilli* and the widespread *M. aberrans* do not bear much resemblance to one another despite sharing the aforementioned characteristics. The male of *M. neilli* can be separated from that of *M. aberrans* as follows: abdominal tergites 3 and 4 with white pruinosity on anterior two-thirds to three-quarters (slightly yellowish and uniformly pruinose over all of tergites 3 and 4 in *M. aberrans*), vertex broader (approximately one-third head width in *M. neilli* [see description below] and one-quarter head width in *M. aberrans* [0.24–0.28 head width, $m=0.26$, $n=10$]), and ocellar setae thin but well developed (scarcely differentiated from ocellar hairs in *M. aberrans*). The male of *M. neilli* is similar in appearance to that of *M. trifurca*, but differs from it in having a slightly broader parafacial and vertex (vertex 0.26–0.31 head width, $m=0.29$, $n=11$ in *M. trifurca*), and a denser group of setae on the ventral portion of the katepisternum (sparsely setose in *M. trifurca*). *Myiopharus trifurca* is presently known from Mexico, Arizona and New Mexico, which is south of the known range of *M. neilli*.

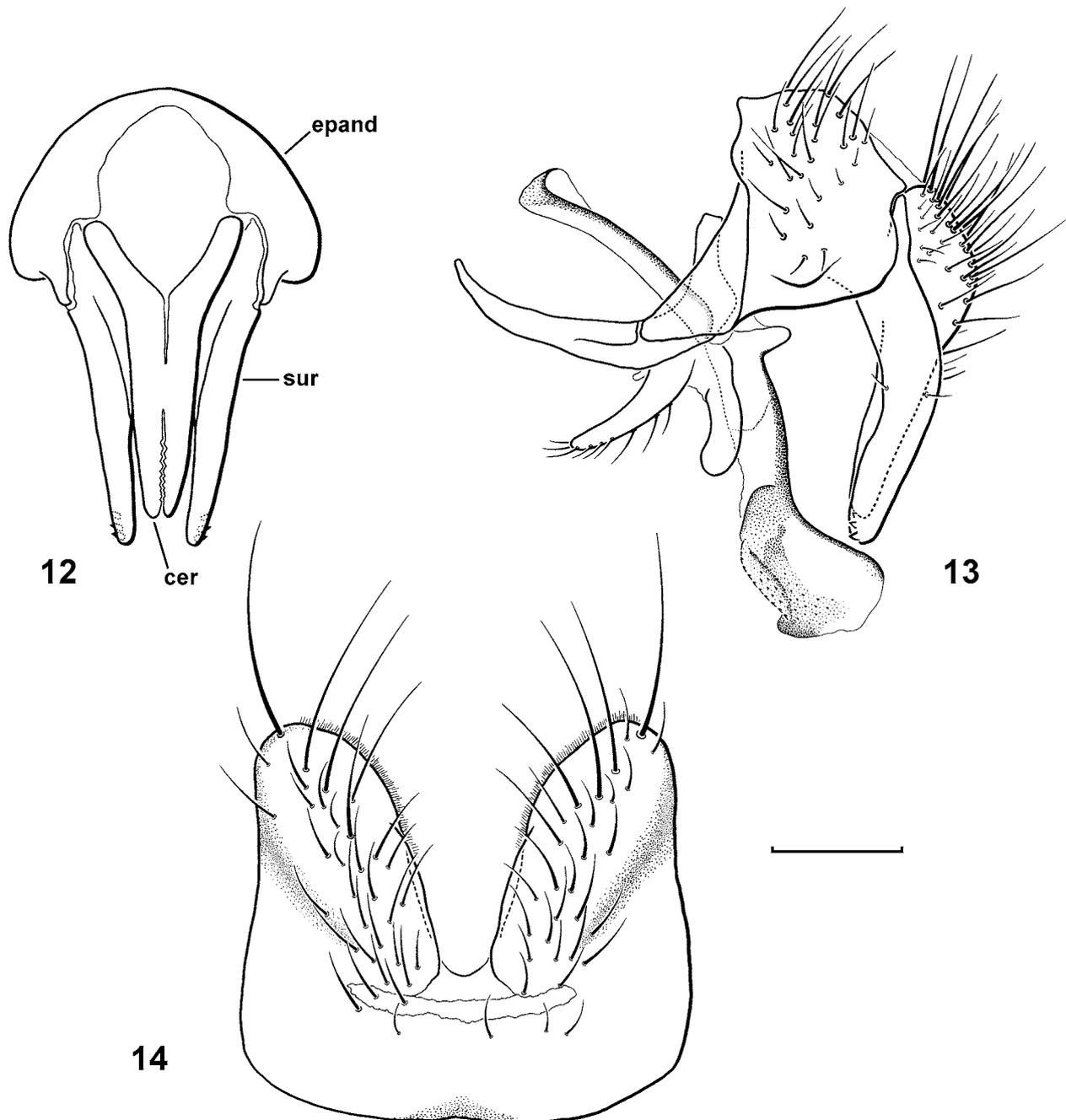
Description

Male habitus, Fig. 1. Female habitus, Fig. 3. Length 5.1–6.9mm.

Head. Not sexually dimorphic. Parafacial silvery white (male without the silvery reflective sheen found in the males of some *Myiopharus* species). Fronto-orbital plate concolorous with parafacial or with golden tinge. Genal groove yellowish orange when viewed from certain angles. Aristomere 3 mostly yellowish brown, rest of antenna mostly black. Maxillary palpus yellow apically, darker basally. Eye moderately to densely haired, 0.74–0.80 head height ($m=0.77$, $n=10$ in male; $m=0.77$, $n=10$ in female). Flagellomere 1 slender, ending well above vibrissa, 3 times longer than wide. Vertex broad in both sexes, at narrowest point 0.32–0.38 head width ($m=0.35$, $n=10$ in male; $m=0.35$, $n=10$ in female). Aristomere 1 short. Aristomere 2 scarcely longer than wide. Aristomere 3 slightly longer than flagellomere 1, evenly tapered to tip. Fronto-orbital plate with 5–8 frontal setae and 1 strong reclinate inner orbital seta that is subequal in size to outer orbital setae; lowermost frontal seta about level with apex of pedicel. Two strong proclinate outer orbital setae in both sexes. Ocellar seta somewhat thin. Outer vertical seta varied from slightly to well developed, larger than setae of postocular row. Inner vertical setae strong, parallel to one another or slightly convergent. Parafacial bare, noticeably wider than width of flagellomere 1. Facial ridge with setae and decumbent hairs decreasing in size dorsally, haired on less than half of its length. Vibrissa situated above lower margin of head. Lower facial margin not protruding beyond vibrissal angle when viewed in profile. Maxillary palpus clavate. Prementum and labella about as long as flagellomere 1.

Thorax. Black in ground color, dorsum not sexually dimorphic and with moderate white pruinosity (appearing gray against black ground color) except for 4 black vittae, inner pair of vittae thin and continuous across transverse suture, outer pair broad and interrupted anterior to suture. Legs black in fresh specimens, faded to reddish black in older museum specimens. Prosternum usually sparsely haired, rarely bare (ca. 10% of specimens). Postpronotum with 3 setae arranged in a triangle. Three postsutural acrostichal setae. Three postsutural dorsocentral setae. First postsutural supra-alar weak. Katepisternum with 2 strong setae and usually a weak third seta just below and behind anteriormost seta; in male densely setose medially in front of mid

coxa, female with an even denser tuft of closely appressed, parallel-sided, and somewhat blunt-tipped setae in this area (Fig. 6). Mid coxa without modified setae. Mid tibia with 1 strong anterodorsal seta. Hind tibia with anterodorsal setae uneven in length and not closely spaced. Tarsal claws not longer than 5th tarsomere. Upper and lower calypters white and often with slight yellowish tinge. Wing vein R_{4+5} dorsally with 1 to several hairs at base. Vein M smoothly curved at bend and ending anterior to wing tip. Scutellum with 1 pair of widely spaced discal setae, a pair each of well developed basal, lateral and divergent subapical setae (subapicals strongest followed by basals and then laterals), and a pair of crossed apical setae that are subequal to discal setae.



FIGURES 12–14. *Myiopharus neilli* sp. nov. **12.** Posterior view of male terminalia, vestiture omitted. **13.** Left lateral view of male terminalia. **14.** Male sternum 5. Scale bar for all figures = 0.2 mm. Abbreviations: cer, cercus; epand, epandrium; sur, surstylus.

Abdomen. Black in ground color, with bands of moderate and uniform white pruinosity (appearing gray against black background) on anterior two-thirds to three-quarters of tergites 3 and 4 and about anterior one-half of tergite 5. Apex deflected slightly downward in female. Middorsal depression on syntergite 1+2 almost reaching median marginal setae. Narrow black vitta medially on tergites 3–5. Syntergite 1+2 with 1 pair of median marginal setae and at least 1 pair of lateral marginal setae. Tergite 3 with 1 pair of median marginal setae, 1 pair of median discal setae (weaker than median marginals), and at least 1 pair of lateral marginal setae. Tergite 4 with row of marginal setae, 1 pair of median discal setae (weaker than median marginals), and at least 1 pair of lateral marginal setae. Tergite 5 with row of weak marginal setae and scattered discal setae. Male without sex patch of tiny appressed hairs on underside of tergite 4 or 5. Sternites 2–3 in male and sternites 2–4 in female each typically with 1 pair of strong setae; sternite 4 in male and sternite 5 in female typically with several moderately strong setae posteriorly; sternites partly overlapped by tergites.

Male terminalia (Figs. 12–14). Sternite 5 with median cleft smoothly V-shaped, inner margin with fine hairs, posterior lobe rounded apically. Epandrium with slight bulge laterally on lower portion. Pregonite smoothly curved and tapered to a rounded tip, setose along posterior margin. Epiphallus present. Distiphallus divided at base into long, thin sclerite posteriorly and broader winged and sclerotized portion anteriorly. Postgonite parallel-sided with rounded tip. Surstylus slender, gently curved at middle in lateral view, with several small spines at tip. Cerci in lateral view straight along posterior surface, shorter than surstylus, in posterior view tapered only slightly from midpoint to apex, tips separate in apical one-third.

Female terminalia (Figs. 7–8). Sternite 7 highly modified, forming a black, laterally flattened, apically rounded sclerite below the genital opening.

Puparium (Figs. 9–10). Slightly larger at posterior end than anterior end, surface nearly smooth. Anterior spiracles raised and rosette-like. Posterior spiracular discs shiny black, narrowly separated and positioned high above midline of puparium, each disc raised above puparium and bearing three nearly straight spiracular slits.

Biology

The biology of the sunflower beetle, *Z. exclamationis*, has been well documented in the literature (e.g., Westdal 1975; Neill 1982; Charlet 1992; Knodel *et al.* 2000; Brewer and Charlet 2004). The beetle has one generation per year in the northern plains of North America. The sexually immature adults overwinter in the soil, emerging as sexually mature adults the following May to early June. Mating takes place within a couple of days of emergence, and within a week the females begin laying eggs on the stems and leaves of sunflower plants. Oviposition can continue for nearly two months, during which time up to 2000 eggs can be laid. Beetle larvae appear about mid June and enter the soil to pupate when mature. Prehibernation adults of this summer generation emerge in late July to early September and feed for one to three weeks before entering the soil to overwinter.

The life history of *M. neilli*, as *Myiopharus* sp., in south-central Manitoba was detailed in the Ph.D. dissertation of Neill (1982). The following life history account is a summary from that study. Adult females of *M. neilli* oviposit on prehibernation adults of *Z. exclamationis*. The parasitoid passes the winter as a first instar free in the haemocoel of the thorax or abdomen of its host. As diapause in the beetle is ending, the first instar of *M. neilli* moves to the head and enters the supraoesophageal ganglion of the brain. Parasitized beetles do not leave the soil, and larval development of the parasitoid continues underground in its host. The parasitoid leaves the brain late in the first or early in the second instar and enters the buccal cavity, where it makes an opening to the exterior for breathing. With the posterior spiracles positioned against the opening, a respiratory funnel forms around the posterior portion of the maggot. The anterior end is kept free, and the maggot feeds on the host's tissues throughout its second and third (final) instars. Though the host is immobile during this period, it does not die until the maggot is almost fully grown and occupies most of its thorax and abdomen. Just before pupariation, the parasitoid creates two openings, one along the postero-lateral margin of the abdo-

men (through which the adult fly will later emerge) and one in the membrane between the prothorax and mesothorax (often decapitating the beetle) (Fig. 11). Larval development takes about three weeks from the time the first instar becomes active until pupariation, and the pupal stage lasts about two weeks. Adult *M. neilli* emerge from the soil in June, about one month after the emergence of non-parasitized beetles.

Neill (1982) conjectured that *M. neilli* has two generations per year. Adult flies emerge in June, when posthibernation adults of *Z. exclamationis* are available for parasitization. A generation of *M. neilli* is likely passed in these posthibernation beetles, producing a second emergence of adult flies in late summer when prehibernation adults of *Z. exclamationis* are present. Larvae of this generation of *M. neilli* overwinter as first instars in their beetle hosts.

Myiopharus neilli is a solitary endoparasitoid of adult *Z. exclamationis* and has not been recorded from other host species. Neill (1982) recorded a parasitism rate of 0.1 to 17.1% in prehibernation adults of *Z. exclamationis* at various locations in south-central Manitoba during 1975–1977. Charlet (1992) reported 1.7% parasitism in a collection of prehibernation adults of *Z. exclamationis* in North Dakota in 1987.

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