



A new species of *Dasineura* Rondani (Diptera: Cecidomyiidae) in flower galls of *Camassia* (Asparagaceae: Agavoideae) in the Pacific Northwest, USA

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Abstract

A new species, *Dasineura camassiae* Gagné (Diptera: Cecidomyiidae), is described, illustrated and compared to some of its congeners from related hosts and western North America. The new species causes flower galls on *Camassia* (Agavoideae; Asparagaceae) in the Pacific Northwest. Its current known distribution is Oregon and Washington, USA. Larvae develop in spring in flowers of *Camassia* spp., causing the young ovaries to enlarge prematurely and eventually abort, without forming seeds or mature fruit. Full-grown larvae crawl out of the gall in rapid succession and drop to the soil where they pupate; they remain there until spring of the following year when the adults emerge and lay eggs. The galls they induce in camas lily buds represent the first known association of the cosmopolitan genus *Dasineura* with the group of plants that includes *Agave* and its relatives.

Key words: Agavoideae, *Camassia*, Cecidomyiidae, Dasineurini, flower gall midges, Lasiopteridi, Nearctic

Introduction

A previously unknown gall midge was recently discovered in flower galls of western camas “lilies” (*Camassia* Lindh; Fig. 1), both in Oregon and at a Washington site overlooking the Columbia River Gorge, USA. Although related to xeric dwelling yuccas and agaves, plants of the North American genus *Camassia* (Asparagaceae: Agavoideae) proliferate in wet, spring-fed prairies and oak savannahs, where they form a dominant component (Sultany *et al.* 2007; Fishbein *et al.* 2010). These cecidomyiid galls were first discovered in 2009, when we noticed unusual buds with precociously enlarged ovaries (Fig. 2) that were presumed at first to be cleistogamously self-pollinated flowers. Interestingly, larvae of the cecidomyiid induce developmental changes that result in multiple floral gall forms. In sympatric populations of *Camassia* the gall midges appear to be selective, feeding only on one species, a topic currently under further investigation (Barosh *et al.* in prep.).

The camas gall midge, described here as *Dasineura camassiae* Gagné, belongs to a large cosmopolitan genus of 476 species (Gagné & Jaschhof 2014), but the discovery of this new species is the first record of gall induction by *Dasineura* across the large Agavoideae subfamily. *Dasineura* Rondani belongs to the supertribe Lasiopteridi and is distinguished from other genera of gall midges by the following combination of characters: The antennae have an uneven number of flagellomeres within a species, not restricted to 12; male flagellomeres have a single basal node and distinct apical neck, while those of the female have almost no neck beyond the node; the costal wing vein is broken just posteriad of its juncture with the R₅ vein, which terminates anterior to the wing apex; the tarsal claws are robust, curved beyond midlength, and have a basal tooth; the empodia are approximately as long as the tarsal claws and the pulvilli are about 1/3 the length of the claws; the gonocoxite has a mediobasal lobe that is closely juxtaposed to the side of the aedeagus; the female eighth tergite is longitudinally divided into two sclerites; the ovipositor is elongate-protrusible and its cerci are fused to form a single lobe. Larvae of *Dasineura* spp. (see Gagné 1989: Fig. 19) are generally uniform morphologically, with a full basic cecidomyiine complement of papillae and a

clove-shaped spatula. Larvae of most species are gregarious, active and occur in galls of ephemeral tissue such as leaves and flower parts. Full-grown larvae of species from the temperate regions typically drop to the soil and emerge as adults in the current or following year depending on their specific life history.

Many *Dasineura* species are still only sketchily known and no modern keys exist to separate them. The purpose of this paper is to formally describe the species on *Camassia* and show how it differs from its congeners. In addition, we document the insect's distribution, gall formation, and larval behavior (Figs. 1-5) based on research at multiple sites on two different host species of *Camassia* and several subspecies. Comparisons were made as far as possible with the eight *Dasineura* species known in the world from the previously broadly defined Liliaceae, which once included *Camassia*, as well as with the ten species of *Dasineura* known from various hosts in western United States and Canada. This first study of the gall midge-*Camassia* interaction will provide greater resolution of the affinities of the numerous, yet poorly known, members of *Dasineura* and has ecological implications for populations of *Camassia* that are increasingly being used in restoration and conservation efforts.

Material and methods

Initial attempts to rear larvae from galls began in 2009-2010, when these were first discovered in the Willamette Valley of Oregon. Regular surveys and transects in *Camassia* populations at diverse sites in the Pacific Northwest and elsewhere have extended that distribution as noted below. Larval biology of this species was observed through the 2011-2013 seasons in Oregon and Washington and continues as a work in progress. Stems with galls were collected or observed intact in *Camassia* populations. Some stems and galls were studied or reserved for rearing at both Willamette University and in Washington DC. Mature larvae were either dissected from galls or collected as they exited the flower galls to drop to the soil. Some larvae were preserved in 70-100% ETOH for further morphological or molecular study, but most were kept alive in an effort to rear adults. Once separated from a gall, the larvae were placed immediately in pots filled with damp peat moss as explained in detail in Gagné and Moser (2013); sometimes the peat was mixed with an equal amount of sand. As this new species showed a single generation per year, pots were maintained through the winter. Adults that emerged in late winter to early spring were preserved in alcohol and subsequently mounted in Canada balsam using the technique outlined in Gagné (1989). Anatomical terminology in the description follows McAlpine *et al.* (1981) whereas that of the larval stage follows Gagné (1989). The holotype and most paratypes are in the insect collection of the National Museum of Natural History in Washington, DC (NMNH). A few paratypes will be deposited at Willamette University, Salem, Oregon (WILLU), as well as vouchers of plant hosts from each site. TB and SK observed this species in the field and lab, collecting it in both Oregon and Washington; the taxonomy and description are the responsibility of RJG.

Dasineura camassiae Gagné, new species

Camas gall midge

Figs. 6-14

Description. *Adult.* Head: Eye facets circular, contiguous on ventral half of eye, farther apart dorsally, eye bridge 4-5 facets long, but facets between the eyes at the bridge are 1-3 diameters apart. Antenna: scape and pedicel with many setae ventrally and medially; male flagellomeres, 13-15 (n=4); female flagellomeres, 13-14 (n=6); all but last flagellomere with long necks in male (Fig. 7), about two-thirds length of node, without necks in female. Frons with 10-21 setae and scales. Labella hemispherical, with several stout setae laterally. Palpus 4-segmented, the first two segments short, stout, not twice as long as broad, the last two narrower, at least 3-4 times as long as broad.

Thorax: Wing (Fig. 6): length in males, 1.4-1.7 mm (n=4); in females, 1.7-1.8 (n=6). Anepisternum with several scales on dorsal third; anepimeron with 8-12 setae; remaining pleura bare.

Male abdomen: First through sixth tergites rectangular, each with anterior pair of trichoid sensilla, single row of setae along posterior margin, without lateral setae and elsewhere mostly covered with scales; seventh tergite unsclerotized posteromedially, with pair of anterior trichoid sensilla, a few setae posterolaterally, and sparse scales; eighth tergite pigmented only anteriorly, its only vestiture the pair of anterior trichoid sensilla. Second through seventh sternites rectangular, with mostly single horizontal row of posterior setae, 2-3 rows of setae mixed with

scales in transverse group near midlength, and pair of closely adjacent trichoid sensilla anteriorly. Eighth sternite as for seventh but with 2 rows of posterior setae. Terminalia (Figs. 8-9): cercus ellipsoid, with a few setae apically; hypoproct narrow, parallel-sided, deeply notched apically, the resulting narrow lobes each with a single long seta; gonocoxite cylindrical laterally, its mediobasal lobe broad, subdivided, the dorsal part of the lobe short, hemispherical, setulose, the ventral part closely sheathing one side of the aedeagus nearly as long as aedeagus, narrow, mostly setulose but glabrous ventroapically, tipped with two short setae; gonostylus slightly tapering and narrowest just before the blunt apical tooth, setulose basally, more so on venter than on dorsum, glabrous and lined with ridges beyond, the whole with sparse, scattered short setae; aedeagus elongate, tapered to narrow apex.

Female abdomen (Figs. 10-12): First through sixth tergites rectangular, fifth and sixth each narrower than the previous tergites, sixth about twice as wide as long; all with two anterior trichoid sensilla, single row of posterior setae, without lateral setae, elsewhere mostly covered with scales; seventh tergite slightly longer than broad, concave laterally, with two anterior trichoid sensilla, two rows of posterior setae, and otherwise with a few scattered scales; eighth tergite divided into two separate, narrow longitudinal sclerites, each with trichoid sensillum anteriorly, and just beyond posterior end with several short setae. Second to seventh sternites as for male; eighth sternite not apparent. Ovipositor elongate, protrusible, ninth segment to end of fused cerci approximately 6 times length of sixth tergite, with wide, lightly pigmented dorsolateral sclerite present along length of ninth segment, each subdivided by closely placed, oblique, parallel lines; cerci fused, cylindrical, tapering, with several thick setae near apex and only a few thin setae elsewhere; hypoproct narrow, with 2 distal setae.

Pupa. Unknown.

Larva. Third instar: Cylindrical, pointed anteriorly, blunt posteriorly. Integument covered with pebbled verrucae. Head capsule hemispherical, cephalic apodemes about as long as head capsule, antennae about twice as long as wide. Spatula (Fig. 13) with two triangular anterior teeth, slightly extended laterally just posterior to teeth. Terminal segment (Fig. 14) with four setae of equal length on each side. Papillae of the usual makeup for *Dasineura* (see Fig. 19 in Gagné 1989).

Material examined. HOLOTYPE: male, reared from larva ex fruit-like ovary of *Camassia leichtlinii* subsp. *suksdorfii*, Mountain Dawn Farm, Linn Co., Salem, Oregon (44.755183° N, 122.639417° W), V-28-2012, T. Barosh, emerged III-2013, deposited in USNM. PARATYPES (all from *Camassia leichtlinii* subsp. *suksdorfii* unless otherwise noted): 3 males, same data as holotype; 2 males, same data except V-28-2013, S. Kephart *et al.*, emerged III-26-2014; 5 larvae, male, Fruitland Creek, Marion Co., Salem, Oregon (44.914334° N, 122.938023° W), V-23-2012, T. Barosh, emerged III-4-2013; 5 larvae, 6 females, same pertinent data, V-18-2013, S. Kephart *et al.*, the females emerged III-7 to 15-2014; 5 larvae, Oregon, Marion Co., near Stayton, Kingston Prairie (44.777308° N, 122.7453583° W), VI-4-2010, S. Kephart; 5 larvae, same data except V-24-2013, S. Kephart *et al.*; 1 female, same data, emerged II-27-2014; 1 male and 1 female, same data, emerged III-6-2014; 5 larvae, *Camassia quamash* subsp. *breviflora*, Oregon, Wasco Co., near Mosier, Columbia River Gorge (45.68727° N, 121.32855° W), IV-23-2014, K. Theiss; and 1 female, *C. quamash* subsp. *breviflora*, Washington, Klickitat Co., Catherine Creek Trail (45.709816° N, 121.3619° W), collected IV-28-2013, S. Kephart, emerged II-19-2014.

Etymology. The name *camassiae* is the genitive form of *Camassia*, the generic name of the host.

Remarks. As far as can be determined, *D. camassiae* is distinct from other known species of *Dasineura*. Of the species of *Dasineura* from the old “Liliaceae,” two are from eastern North America and six from Europe and western Asia. The North American species are *D. smilacinae* Bishop (1911) and *D. torontoensis* Felt (1915). The first was reared from root galls of *Maianthemum* (formerly *Smilacina*) *racemosum* (L.) Link. (Asparagaceae) in New York, USA, but its original description is insufficiently detailed for accurate species delimitation. The location of any type or other specimens is unknown. The second species was reared from root galls on *Maianthemum canadense* Desf., from Ontario, Canada. The type female of *D. torontoensis* is demonstrably different from the species on *Camassia*. Its ovipositor is much shorter, with the length of the ninth segment to the cerci (inclusive) only three times as long as the length of the sixth tergite, as opposed to six times as long in the new species. It is possible that the root gall maker on *M. racemosum* will eventually be found to be similar to that on *M. canadense*.

Of the six *Dasineura* species from the Palearctic Region, four have been reared from *Asparagus* (Asparagaceae), the same family in which *Camassia* is currently placed (APG 2009). The original descriptions of three of these Palearctic insects, all from bud or stem galls on their hosts in the Mediterranean Region, are inadequate for present discrimination and they have not been critically examined since they were originally described. These species are: *D. asparagi* (Tavares 1902) from *A. aphyllus* L. from Portugal; *D. turionum* (Kieffer

and Trotter 1904) from *A. officinalis* L. from southern continental Italy; and *D. minardii* (De Stefani 1913) on *Asparagus* spp. from Sicily. The fourth species from *Asparagus*, *D. asparagiiflora* Fedotova (1993a), was found in flowers of *A. persicus* Baker from Kazakhstan. Fedotova's illustrations show the gonostylus to be appreciably more linear and longer than that of *D. camassiae*. The R_5 wing vein of *D. asparagiiflora* is shown as much shorter than the species from *Camassia*, not reaching beyond the extent of CuA_1 . The two remaining Palearctic species appear also to be distinct from the species on *Camassia*. *Dasineura severzovi* Fedotova (1996) was reared from flower galls of *Polygonatum "severzovii"* (Asparagaceae) in Kazakhstan. The original illustrations show a species very similar to *D. asparagiiflora* with a long, linear gonostylus and an extremely short R_5 wing vein not reaching beyond the extent of CuA_1 . Original illustrations of the sixth species, *D. alliicola* Fedotova (1993b), reared from flowers of *Allium galanthum* Kar. & Kir. (Amaryllidaceae) in Kazakhstan show a much more bulbous gonostylus than does *D. camassiae*. Another difference is that the female postabdomen is described as "short" and with very setose fused cerci. The female postabdomen of *D. camassiae* would not pass for short and its fused cerci have sparse setae (Fig. 11).

The ten North American species of *Dasineura* known from west of the Great Plains are a diverse group, all from non-liliaceous hosts, i.e. conifers or dicots that are phylogenetically and morphologically distant from *Camassia*. Their names and hosts are as follows: *D. abiesemia* Foote from *Abies* spp. (firs, Pinaceae); *D. californica* Felt and *D. gemmae* Felt from *Salix* spp. (willows, Salicaceae); *D. cercocarpi* Felt from *Cercocarpus* sp. (mountain mahogany, Rosaceae); *D. gentneri* Pritchard from *Trifolium* spp., (clovers, Fabaceae); *D. gibsoni* Felt from *Cirsium arvense* (L.) Scop. (thistle, Asteraceae); *D. gleditchiae* (Osten Sacken) from *Gleditsia triacanthos* L. (honey locust, Fabaceae); *D. hildebrandi* (Felt) from *Arctostaphylos* sp. (manzanita, Ericaceae); *D. lupini* Felt and *D. lupinorum* Gagné from *Lupinus* spp. (lupines, Fabaceae). Another species from western North America, *D. pergandei* Felt from *Prunus* sp. (cherry, Rosaceae), carried to date in *Dasineura*, does not properly belong in the genus. Its proper position will be dealt with elsewhere. Original references for these species can be found in Gagné & Jaschhof (2014) and information about their particular plant damage can be found in Gagné 1989. Males of each of the ten *Dasineura* are present in the USNM and all have gonostyli that are distinctly different in shape from the species on *Camassia*, either more bulbous basally or linear-elongate, instead of slightly tapering and narrowest just before the apex as in *D. camassiae*.

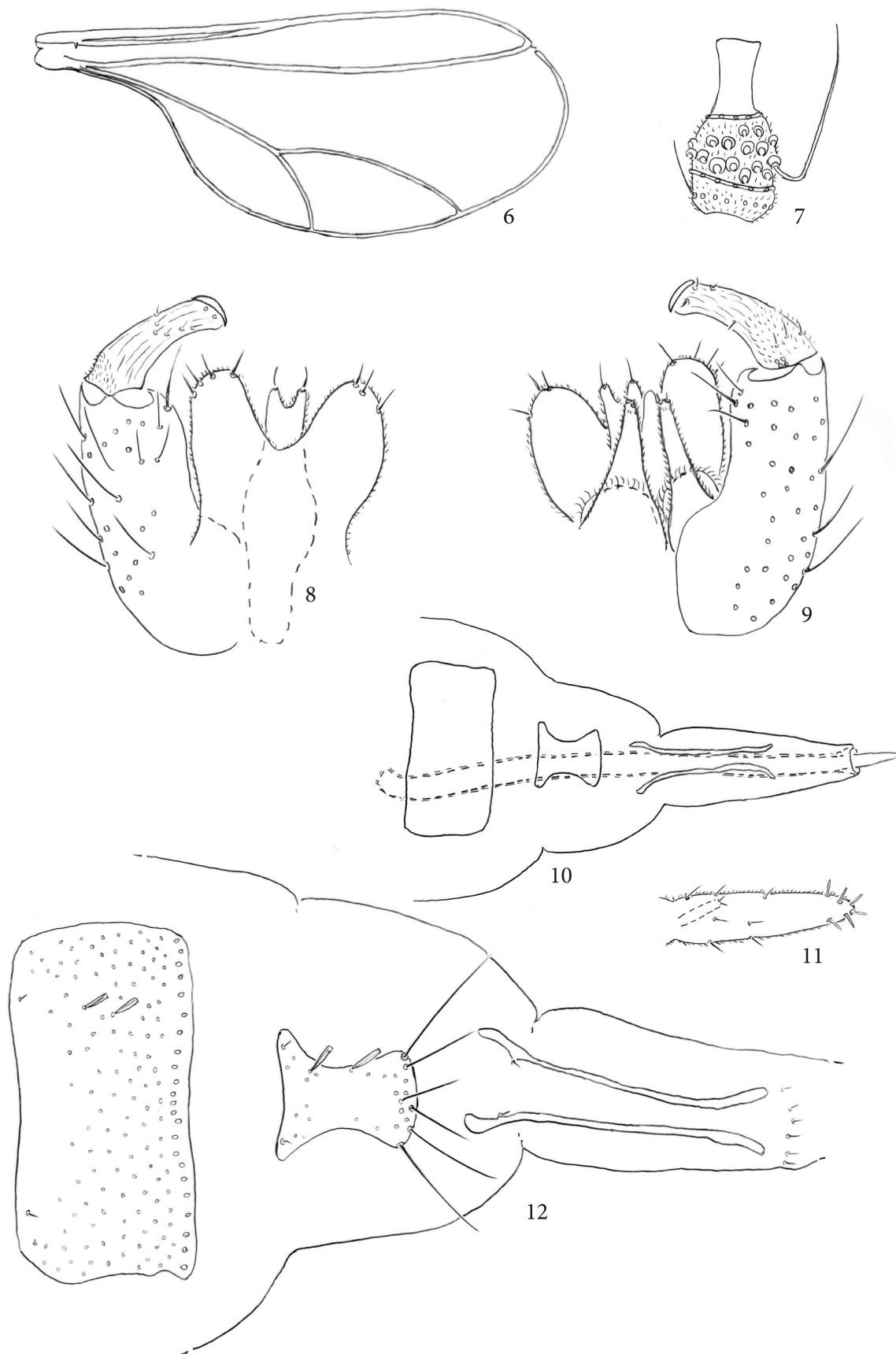
Habitat and distribution. Of six species of *Camassia*, all from North America, four are native to the Pacific Northwest and include 10 subspecific taxa (Gould 1942; Ranker & Hogan 2002). *Dasineura camassiae* has been found in association with only two species of *Camassia* including those noted above, *C. leichtlinii* (Baker) S. Watson subsp. *suksdorfii* (Greenm.) Gould (great camas) and *C. quamash* (Pursh) Greene subsp. *breviflora* Gould (small-flowered camas). By far, this insect is most prevalent on *C. leichtlinii* in seasonally wet habitats ranging from woods to open prairie. For example, *C. leichtlinii suksdorfii* grows along Fruitland Creek near Salem, Oregon in a riparian woods, with ash (*Fraxinus latifolia* Benth.) and white oak (*Quercus garryana* Douglas ex Hook.). Interestingly, *D. camassiae* is absent from *C. quamash* subsp. *maxima* (common camas) even when growing sympatrically with the *C. leichtlinii-Dasineura* association, as at Mountain Dawn Farm and Kingston Prairie, two sites in Oregon's Willamette Valley that include a mosaic of meadow, oak savanna, and forest. In contrast, *D. camassiae* galls are found on a different subspecies of *C. quamash*, i.e. subsp. *breviflora*, in the Columbia River Gorge, in moist swales with oak savanna near ash, maple (*Acer macrophyllum* Pursh) and pine (*Pinus ponderosa* Dougl.). This subspecies shows some morphological features intermediate between *C. quamash* and *C. leichtlinii* in this transition zone between western and eastern Oregon (Kephart et al. unpubl.).

Life history and behavior. This insect emerges from the soil in late winter to early spring, likely when *Camassia* spp. form buds but before they flower, based on emergence times from our rearing pots. Females presumably lay their eggs among the developing flower parts, potentially before these are fully formed or fused as larvae develop inside the three-loculed ovary. Alternatively, the newly hatched larvae may arise from eggs laid outside the young ovary while parts are still soft, and then enter the developing ovaries that subsequently enlarge to form galls. In either case, in ovaries that have been occupied by *D. camassiae* larvae, the ovules abort, and parts of the locule liquefy. Galled flowers produce no seeds and develop differently from uninfested buds and flowers (Figs. 1, 2), sometimes keeping their tepals completely or partially closed while the ovary enlarges. In rare cases, all six sepals and petals open, exposing the engorged, fruit-sized ovary. Larvae may be present in all three locules of an ovary; each *Camassia* plant can present upwards of nearly 70 buds. The 1-40 larvae per gall are gregarious and can be found crawling freely among the ovules (Fig. 3). When full-grown the larvae leave the flower gall via a hole in the enlarged

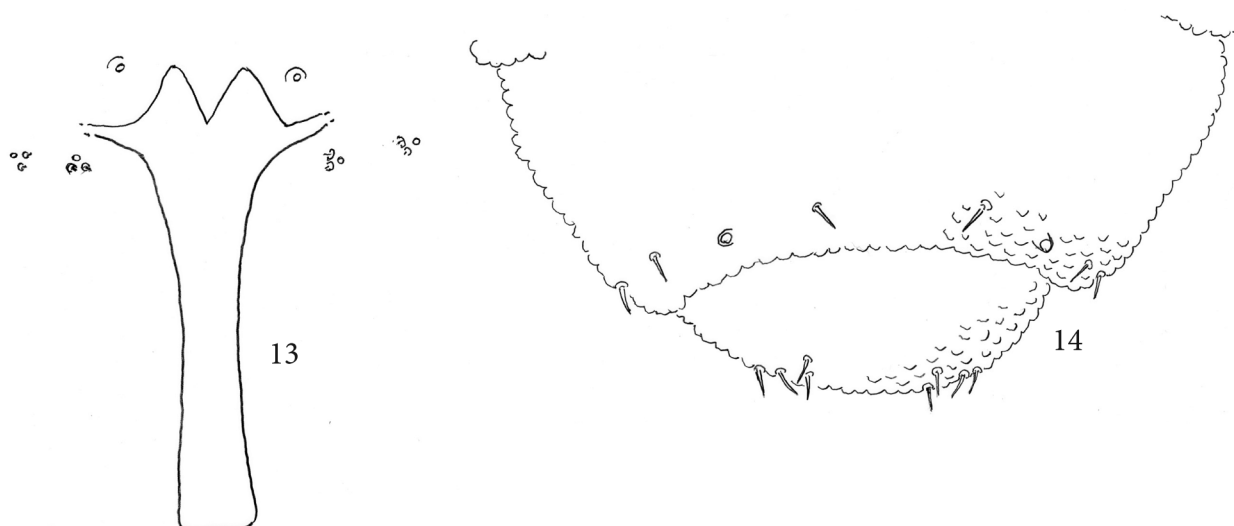
fruit-like ovary (Fig. 4), which later softens and shrivels. The larvae drop to the soil (Fig. 5) in which they quickly burrow and then enter diapause until the following spring when they pupate. This species is univoltine and is presumably specific to *Camassia* spp. inasmuch as the life cycle of the insect and host are closely timed.



FIGURES 1–5. *Camassia leichtlinii* flowers and galls. **1**, Normal open flower and closed bud gall (arrow) beginning to enlarge. **2**, Rarer, tri-form galled flower. **3**, *Dasineura* larvae on inside surface of newly dissected locule. **4**, Mature gall with exit hole formed by *Dasineura* larva. **5**, One of several larvae observed escaping from this gall in succession. Note the orbicular shape and translucent coloration of the softened tissue around the exiting insect.



FIGURES 6–12. *Dasineura camassiae*. **6**, Wing. **7**, Male third flagellomere (ventral). **8**, Male terminalia (one gonopod removed; dorsal). **9**, Same (ventral). **10**, Female postabdomen, 6th tergite to cerci (dorsal). **11**, Detail of female fused cerci (dorsal). **12**, Detail of female sixth through eighth tergites (dorsal).



FIGURES 13–14. *Dasineura camassiae*, larva. **13**, Sternal spatula and associated papillae. **14**, Eighth and terminal abdominal segments (dorsal).

Discussion

Dasineura camassiae is a new species described from two species of *Camassia* that grow in geographically disjunct regions of Oregon and Washington. *Dasineura camassiae* is clearly distinct from its congeners on related hosts worldwide or on unrelated hosts in western North America. All have the specific antennal, wing, tarsal, and abdominal features of *Dasineura*. This genus is a fairly homogeneous group, but certain characters are useful for discrimination among species. These mainly include details of the female and male postabdomens, specifically, the vestiture of the abdominal sclerites, the length of the ovipositor relative to that of the sixth tergite, and the shape and vestiture of the female cerci, the male hypoproct and the gonostylus. Compared with other species, *D. camassiae* differs in the length, shape and vestiture of the female postabdomen, including the paucity of setae on the cerci, and in differences of the male terminalia, mainly the weakly bulbous gonostylus that narrows near its apex. As these features become more commonly and accurately described for additional species of *Dasineura*, new taxonomic insights will allow a better understanding of the systematics of this diverse genus.

The diversity of sites sampled for the new species defines the present geographic range and host specificity of *Dasineura* on *Camassia*. *Dasineura camassiae* was most prevalent on *C. leichtlinii* subsp. *suksdorfii*, including the three sites sampled, as well as at least three other localities in Oregon's Willamette Valley. The two galled populations of *C. quamash* subsp. *breviflora* occur in the Columbia River Gorge, just east of the Cascade mountains, in a climate considerably drier than the Willamette Valley; both populations are geographically isolated from valley populations of *C. leichtlinii* and could represent cryptic host races or species. An intriguing pattern also emerged in the distribution of *Dasineura* galls where *C. leichtlinii* *suksdorfii* grows in close sympatry with *C. quamash* subsp. *maxima* at Kingston Prairie and Mountain Dawn Farm. Plants of both species occur within a few meters of each other, yet our searches in multiple years revealed no galls whatsoever on this subspecies of *C. quamash* at either sympatric or allopatric sites. Although gall midges are often species or genus specific, this putative host differentiation by *Dasineura* is worth exploring for these two *Camassia* species, which differ morphologically and are phylogenetically distinct (Uyeda & Kephart 2006, Fishbein *et al.* 2010, Archibald *et al.*, accepted for publication).

The discovery of *D. camassiae* on multiple *Camassia* species extends our knowledge of the taxonomy of this diverse genus of gall midges and the phenotypic effects of gall induction on its host plants. *Camassia* reaches its greatest diversity in the Pacific Northwest, where it is a prominent native flower in wet prairie and oak-savanna habitats that are undergoing considerable fragmentation and loss (Sultany *et al.* 2007). Further studies of the taxonomy, geographic range, and host plant preferences of *D. camassiae* will help characterize it, while potentially facilitating the conservation and restoration of these important habitats.

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