

**LIFE HISTORY AND DESCRIPTION OF ADULTS AND IMMATURE STAGES
OF *GOEDENIA STEYSKALI*, N. SP. (DIPTERA: TEPHRITIDAE) ON
GRINDELIA HIRSUTULA HOOKER AND ARNOTT VAR. *HALLI*
(STEYERMARK) M. A. LANE (ASTERACEAE) IN SOUTHERN CALIFORNIA**

RICHARD D. GOEDEN

Department of Entomology, University of California, Riverside, CA 92521, U.S.A. (e-mail: richard.goeden@ucr.edu)

Abstract.—*Goedenia steyskali*, n. sp., is a nearly monophagous, univoltine fruit fly (Diptera: Tephritidae) reared from and studied in the flower heads of *Grindelia hirsutula* Hooker and Arnott var. *halli* (Steyermark) M. A. Lane belonging to the family Asteraceae, tribe Astereae, and subtribe Solidagininae, like all other known hosts of *Goedenia* spp. This tephritid also has been reared from *Grindelia camporum* E. Greene. A key to *Goedenia* spp. in North America North of Mexico is provided that incorporates this new species. This new species is distinguished from all other North American congeners by the combination of its extensively darkened legs, an uninterrupted discal wing band that rarely attains the posterior wing margin, and the prominent, central, tawny or yellow area on the scutellum. The second- and third-instar larvae and puparium also are partially described and figured, and selected characteristics of these stages are compared with the same stages of other species of *Goedenia*. The anterior thoracic spiracle bears four papillae in the second instar and three papillae in the third instar. The third instar of *G. steyskali* lacks oral ridges, as do the third instars of four other congeners studied to date. Among these same congeners, the third instar of *G. steyskali* has the fewest minute acanthae and pores in the center of the truncated, posteriorly sclerotized, caudal segment. In turn, these structures and a pair of posterior spiracular plates are ringed by two to three, concentric, incomplete series of shallow, elliptical depressions. The life cycle is of the aggregative type. The first and second instars feed on ovules and soft achenes, but the latter instar after or near final molt begins to feed like the third instar in the receptacle, which may be mined extensively, and on sap. Overwintering occurs as sexually immature adults, or mainly as prepupal third instars and puparia in flower heads on dead plants in apically open, thin-walled, vasiform cells consisting of floret and achene fragments glued together with dried liquid feces and sticky sap. The flattened, dark, sclerotized caudal segment of the third instar serves as a plug that tightly closes the mouth of the cell, yet allows respiration, and thus apparently also may serve to shield the larva from arthropod predators during overwintering. Overwintered puparia of *G. steyskali* were parasitized by chalcidoid Hymenoptera in the genera *Eurytoma* (Eurytomidae), *Pteromalus* (Pteromalidae), and *Torymus* (Torymidae) as probable, primary, solitary, larval-pupal endoparasitoids.

Key Words: Insecta, *Goedenia*, *Grindelia*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of adults and immature stages, flower-head feeding, aggregative life cycle, phragmosis, seed predation, parasitoids

Most indigenous, western North American Myopitini (Diptera: Tephritidae: Tephritinae) formerly assigned to the Palearctic genus *Urophora* Robineau-Desvoidy were transferred to *Goedenia* by Freidberg and Norrbom (1999). To date, the life history and immature stages of four of the eight known species of *Goedenia* have been described in detail, i.e., *G. timberlakei* (Blanc and Foote) by Goeden et al. (1995), *G. rufipes* (Curran) by Goeden (2002a), *G. setosa* (Foote) by Goeden (2002b), and *G. stenoparia* Steyskal by Goeden (2002c). This paper describes the life history and selected immature stages of a fifth, heretofore undescribed species, *G. steyskali*.

MATERIALS AND METHODS

The present study utilized specimens of adults reared from flower heads of *Grindelia hirsutula* Hooker and Arnott var. *halli* (Steyermark) M. A. Lane collected in the vicinity of Lake Cuyamaca, Cleveland National Forest at about 1370 m elevation in northeastern San Diego County, California. The life history study and description of the immature stages of *Goedenia steyskali* were based in large part on dissections of samples of live mature and dead overwintered flower heads collected during 1992–1999. One or two-liter samples of the large, resinous, flower heads containing the larvae and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Two second-instar and 19 third-instar larvae and 10 puparia dissected from flower heads of *Grindelia hirsutula* were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an in-

creasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$ and 14/10 (L/D) photoperiod. Six pairs of virgin males and females obtained from *G. hirsutula* in emergence cages were held in separate, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names follow Foote et al. (1993). Format used to describe the adults follows Steyskal (1979), Foote et al. (1993), and Goeden and Norrbom (2001). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c; 2002a, b, c), Goeden et al. (1993), Goeden and Headrick (1992), Goeden and Norrbom (2001), Goeden and Teerink (1997), Headrick et al. (1996), Teerink and Goeden (1999), and our earlier works cited therein. Means \pm SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 6. The holotype, allotype and 18 paratypes of each sex of *Goedenia steyskali* are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); the remaining eight paratypes reside in my research collection.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—In accordance with revisionary changes made by Freidberg and Norrbom (1999), the following key to *Goedenia* based on Foote et al. (1993) incorporates the new species described below as well as the single species of *Neomyopites* known from America north of Mexico. It thus includes the only other indigenous, U.S. or Canadian species of Myopitini likely to be confused with *Goedenia*, but not *Rhyencina* nor introduced, Palearctic *Urophora* spp. now present in North America [three-digit figure numbers refer to figures in Foote et al. (1993), not to the present publication].

KEY TO SPECIES OF GOEDENIA

- 1. Wing without dark bands or spots except sometimes in pterostigma or, very rarely, in cell r_1 (figs. 488, 489) 2
 - Wing with dark bands or spots in addition to that in pterostigma 3
- 2. At least basal $\frac{3}{4}$ of all femora black; pleuron and scutellum shining black, scutellum sometimes with yellow apex; wing pattern as in fig. 488 *timberlakei* (Blanc and Foote)
 - Legs entirely yellow; pleuron and scutellum black but distinctly tomentose; wing pattern as in fig. 489 *Neomyopites claripennis* Foote
- 3. Scutellum wholly black 4
 - Scutellum yellowish, at least in center (fig. 503, a) 5
- 4. Dark marks on wing consisting largely of isolated spots (fig. 490); frons entirely yellow or orange; scutal setulae all small, brownish, none strongly projecting *grindeliae* (Coquillett)
 - Dark marks on wing consisting of transverse bands as well as spots (Fig. 491); posterior half of frons dark brown (fig. 504); scutal setulae sparse, black, erect, some distinctly projecting *setosa* (Foote)
- 5. Thorax partly shining reddish yellow, including anterior pleura and part of scutum; wing pattern as in fig. 492 *rufipes* (Curran)
 - Thorax largely black, including entire scutum 6
- 6. Legs with femora at least basal third black 7
 - Legs with femora mostly or entirely yellow, with at most basal fourth black 8
- 7. Wing pattern reduced and usually fragmented (fig. 495) *caurina* (Doane)
 - Wing pattern with discal and subapical bands

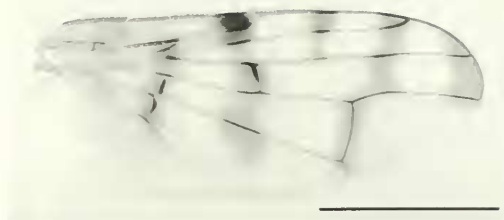


Fig. 1. Right wing of female *Goedenia steyskali*. Line = 1 mm.

- of wing usually largely intact; discal band usually does not attain hind margin of wing, or if so, faint and narrow posteriorly (Fig. 1) *steyskali* Goeden, n. sp.
- 8. Discal and subapical bands of wing narrow, i.e., half or less as wide as adjacent hyaline areas between them in cells r_1 and r_{2+3} ; discal band usually failing to attain hind margin of wing, or faint and narrow posteriorly when does; discal band commonly broken in cell dm, less so also in cell R_{2+3} ; notopleuron usually yellow or tawny at base of posterior notopleural seta (fig. 507, a); wing pattern as in fig. 493 *stenoparia* (Steyskal)
- Discal and subapical bands usually entire and wider, i.e., about as wide as adjacent hyaline areas between them in cells r_1 and r_{2+3} ; discal band usually attains hind margin of wing (fig. 494); scutellum entirely or mostly microtrichose *formosa* (Coquillett)

***Goedenia steyskali* Goeden, new species**
(Figs. 1, 6D, E, F)

Female (Holotype).—*Head*: Generally tawny, sometimes reddish brown or with dark brown areas on frons, except occiput and often ocellar tubercle black. In profile, 1.0–1.3 times as high as long, face distinctly protruding below antenna, face and frons meeting at an angle of ca. 120°; parafacial 0.6–1.0 as wide as first flagellomere; face white or paler than frons, strongly concave, facial ridges distinct; eye 0.7–1.0 times as wide as high; gena below eye 0.2–0.4 times eye height; frons 0.5 to 0.7-mm wide at vertex, narrowing very slightly at antennal bases; antenna short, tawny, microtrichose, arista black; two frontal setae, one orbital seta, one ocellar seta, one inner and one outer vertical setae, all shiny black, like

most microtricha on head; proboscis geniculate, labella length 0.6–0.9 times as long as head height, 0.7–1.0 times as long as head length.

Thorax: Scutum microtrichose over shiny black ground-color, except for one bare, narrow, shiny, medial stripe and pair of shiny, stripes aligned with dorsocentral setae, with intra-alar setae between them; many, short, black, upright setulae investing scutum; central third to half of scutellum generally tawny, rarely yellow; thoracic setae all black; dorsocentral seta distinctly posterior to supra-alar seta, one-third the distance from supra-alar to acrostichal seta; anepisternum, anepimeron, and katepisternum mostly shiny and bare, tawny or yellow stripe from postpronotal lobe across dorsal part of anepisternum; scutellum strongly convex, free of setulae and microtrichia centrally, scutellar setulae sparse and lateral, two pairs of scutellar setae; halter tawny or yellow. Legs tawny with basal thirds to entire femora black, middle femur usually least darkened, posteroventral setae prominent on front femur, hind femur without outstanding anteroventral seta, leg setulae dark brown or black. Wing 2.0–2.9 mm long, wing pattern *Myopites*-type as in Fig. 1, with well-developed discal and subapical bands, the latter usually not attaining the posterior wing margin, these bands two-thirds to just as wide as adjacent hyaline areas between them in cells r_1 and r_{2+3} ; discal band rarely broken in cell dm; subapical band sometimes nearly interrupted along vein M.

Abdomen: Tergum microtrichose, except anterior and posterior ends shiny black, covered with brown or black, upright setulae inserted much closer to each other than their average length, becoming longer laterally and posteriorly; single row of long, black setae along posterior margin of last abdominal tergite; ov scape funnel-shaped, 0.75–1.35 mm long ventrally, black, covered with black setulae which are shortest posteriorly.

Male (allotype).—*Thorax:* Like ♀, but ♂

with head in profile, 1.0–1.4 times as high as long, parafacial 0.6–0.9 as wide as first flagellomere, eye 0.8–0.9 times as wide as high, gena below eye 0.3–0.5 times eye height, frons 0.5 to 0.8 mm wide at vertex, narrowing to 0.4 to 0.5 mm at antennal bases, labella length 0.6–0.8 times as long as head height, 0.7–0.9 times as long as head length. Wing 2.0 to 2.6 mm long. Subapical band usually narrowed or interrupted along vein M.

Variation.—In only one ♀ paratype (4%) among the holotype and 25 ♀ paratypes of *G. steyskali* are none of the femora darkened; i.e., entirely tawny. In nine (35%) of these 26 ♀ types, the discal wing band very faintly and narrowly attained the posterior wing margin. Similarly, the subapical band was narrowed along vein M in 10 (38%) of these 26 ♀ types.

Likewise, in only one (5%) of 22 ♂ types, the discal wing band distinctly attained the posterior wing margin; whereas, in an additional six (27%) of these 22 ♂ types, the discal wing band only faintly and narrowly attained the posterior wing margin. The subapical band was narrowed along vein M in 16 (73%) of these 22 ♂ types.

Diagnosis.—The main morphological characters distinguishing the adults of *G. steyskali* from most other species of *Goedenia* are the combination of the usually extensively dark legs, the discal wing band that rarely attains the posterior wing margin, and the prominent centrally tawny or yellow scutellum. This species is readily distinguished from *G. caurina* (Doane) with its reduced and fragmented wing pattern, and from *G. stenoparia* which usually has legs mostly yellow (Goeden 2002c). *Goedenia formosa* (Coquillett) has a discal wing band that always attains, often broadly, the posterior wing margin, and is the only species that sometimes has a hyaline spot in the apical wing band in cell r_{4+5} (Goeden 2002c).

As discussed below, *G. steyskali* apparently is nearly monophagous. So far as

known, it breeds in only two *Grindelia* spp., one or more species of which have also been reported (for *Urophora* spp.) as host plants for *Goedenia caurina* (Wasbauer 1972, Steyskal 1979, Foote et al. 1993), *G. formosa* (Wasbauer 1972, Goeden 1987, Steyskal 1979, Foote et al. 1993), and *G. grindeliae* (Coquillett) [fly spp. reported as *Urophora* spp. by Wasbauer (1972) and Foote et al. (1993)]. Since my discussion of the host relations of North American *Goedenia* (as *Urophora*) (Goeden 1987), I have identified a single ♀ reared from a mature flower head of *Grindelia camporum* E. Greene collected 1.6 km east of Tehachapi, Kern County, 16.ix.1988, as *G. formosa*, which confirms the record for this host in Wasbauer (1972). However, my recent analysis (Goeden 2002c), questions the records for *Grindelia* as a host plant for *Goedenia caurina* in Steyskal (1979) and Foote et al. (1993). I also never have recorded *Goedenia grindeliae* from *Grindelia*, only a single ♂ reared from a flower head of *Heterotheca villosa* (Pursh) Shinnery collected by D. H. Headrick in Whitewater Canyon, Riverside County, on 15.x.1987. Future taxonomy and life history studies of *Goedenia caurina*, *G. formosa*, and *G. grindeliae*, which my associates and I had not found time to research in detail, may further clarify the host-plant relations of these species relative to *Grindelia*.

Types.—Holotype, ♀; Cuyamaca Rancho State Park along State Highway 74 at 1,180 m (3,830 ft); Cleveland National Forest, San Diego County, CA; 3.iii.1995; R. D. Goeden, coll. (hereafter RDG, coll.)/J. A. Teerink, coll. (hereafter JAT, coll.)(all dates are flower head collection dates); reared from flower head of *Grindelia hirsutula* var. *halli*; allotype, ♂, along State Highway 79 on north shore of Lake Cuyamaca at 1,356 m (4,450 ft), Cleveland National Forest, San Diego County, CA; 25.ii.1997; RDG/JAT, coll. (USNM). Paratypes: CALIFORNIA: 7 ♂, 8 ♀ (6 ♂, 3 ♀ to USNM); same data as holotype (USNM).

5 ♂, 7 ♀ (5 ♂, 6 ♀ to USNM); same data as allotype (USNM). 1 ♂; same data as holotype, except 24.viii.1995. 1 ♀; southwest of Lake Cuyamaca at 1350 m (4,430 ft), 7.ix.1995, otherwise same data as holotype and allotype. 1 ♂, 6 ♀; same data as holotype, except 20.iii.1996 (USNM). 7 ♂, 3 ♀ (6 ♂, 3 ♀ to USNM); same data as allotype, except 20.iii.1996 (USNM). 1 ♀; Mulholland Drive just west of San Diego Freeway at 466 m (1,530 ft), Santa Monica Mountains, Los Angeles Co., CA; 28.ix.1990; reared from flower head of *Grindelia camporum* E. Greene (USNM).

Etymology.—This tephritid is named for George C. Steyskal, who first identified my specimens as a new species of *Urophora* (Goeden 1987), a genus that he had earlier revised (Steyskal 1979), and who contributed much to the taxonomy of Diptera.

Immature stages.—The second- and third-instar larvae and puparium are partially described to the best extent that specimen preparation allowed for use of scanning electron microscopy.

Second instar larva: White, cylindrical, tapered anteriorly, bluntly rounded posteriorly (Fig. 2A); gnathocephalon conical (Fig. 2B-1, C), smooth, with few minute acanthae ventrally (Fig. 2B-2); dorsal sensory organ well-defined, round, flattened (Figs. 2C-1, D-1, E-1), pore above each dorsal sensory organ (Fig. 2C-2); anterior sensory lobes (Figs. 2C-3, D-2), separated by vertical medial cleft, each bear terminal sensory organ (Figs. 2D-3, E-2), lateral sensory organ (Fig. 2E-3), supralateral sensory organ (Fig. 2E-4), and pit sensory organ (Fig. 2E-5); stomal sense organ (Figs. 2C-4, D-4, E-6) ventrolaterad of anterior sensory lobe and fused with lateral-most (Figs. 2C-5, D-5, E-7) of five, foliose, protrudent, lateral integumental petals (Figs. 2C-6, E-8) dorsad of each mouthhook, three vertical pairs of medial integumental petals between anterior sensory lobes (Fig. 2C-7); mouthhook (Figs. 2B-2, C-8, D-6) bidentate; median oral lobe laterally compressed, apically tapered (Figs. 2C-9, D-7); verruciform sen-

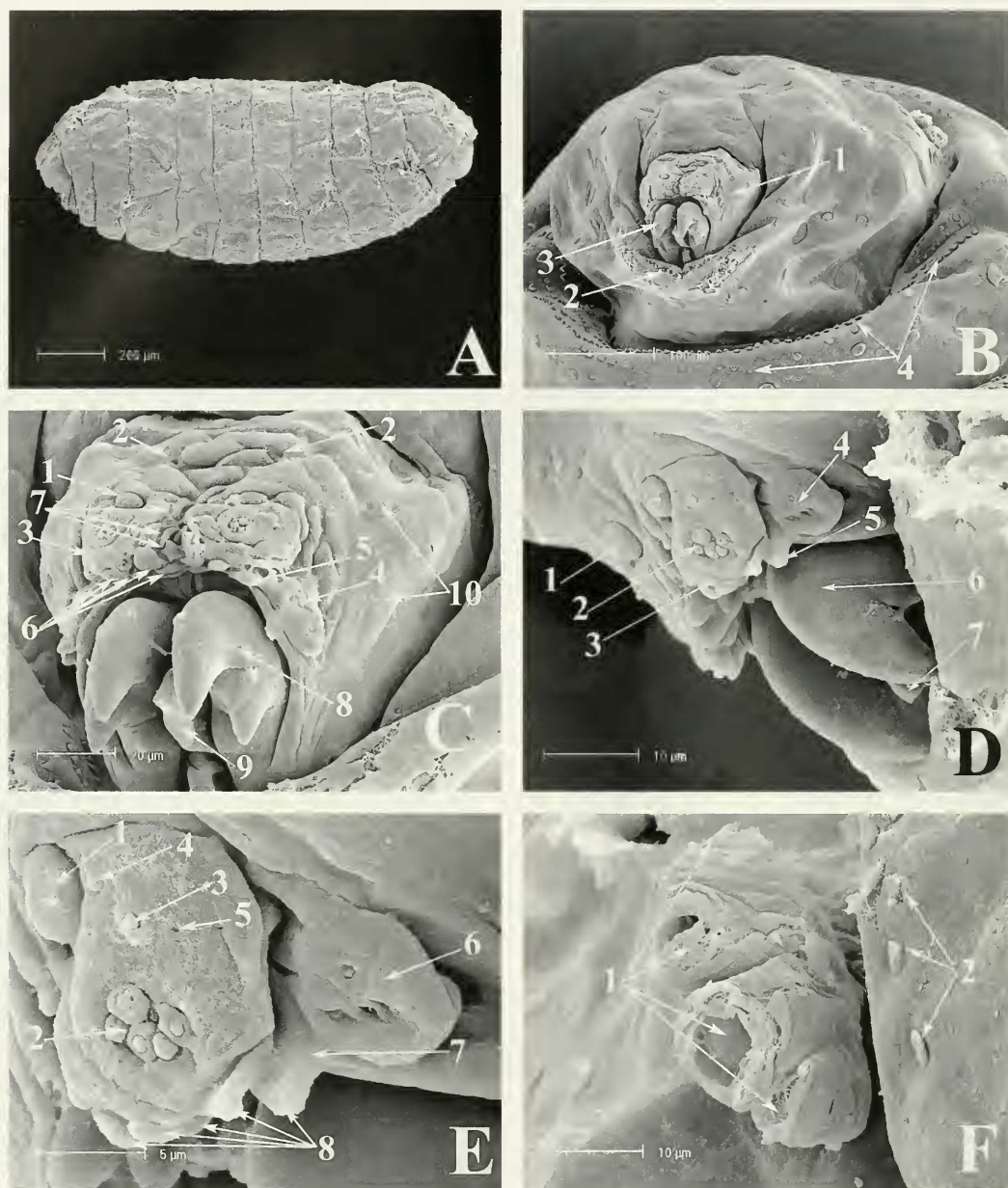


Fig. 2. Second instar of *Goedenia steyskali*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, frontoventral view, 1—gnathocephalon, 2—mouthhook, 3—minute acanthae; (C) gnathocephalon, frontolateral view, 1—dorsal sensory organ, 2—pores, 3—anterior sensory lobe, 4—stomal sense organ, 5—lateralmost lateral integumental petal, 6—lateral integumental petals, 7—medial integumental petals, 8—mouthhook, 9—median oral lobe; (D) gnathocephalon, lateral view, 1—dorsal sensory organ, 2—terminal sensory organ, 3—anterior sensory lobe, 4—stomal sense organ, 5—lateralmost lateral integumental petal, 6—mouthhook, 7—median oral lobe; (E) 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ, 5—pit sensory organ, 6—latermost lateral integumental petal, 8—lateral integumental petals; (F) 1—three-papillae of anterior spiracle, 2—minute acanthae.

silla circumscribe posterior third of gnathocephalon dorsolaterally and laterally (Fig. 2C-10); anterior spiracle with four, subglobose papillae (Fig. 2F-1); posteriorly directed, spatulate, apically rounded, minute acanthae (Figs. 2B-3, F-2) circumscribe anterior fourth of mesothorax (Fig. 2B-4) and metathorax, anterior and posterior fourth of first abdominal segment (A-1), anterior and posterior third of A-2, most of A-3 to A-6, all but middle third of A-7, and anterior third of A-8. Posterior surface of caudal segment not examined.

The habitus of the second instar of *G. Steyskali* (Fig. 2A) approximates those of *G. timberlakei* (Goeden et al. 1995) and *G. rufipes* (Goeden 2002a). Differences noted include five lateral integumental petals in *G. steyskali* (Figs. 2C-5, E-8), like *G. rufipes* (Goeden 2002a), not four, as pictured for *G. timberlakei* (Goeden et al. 1995). Moreover, the latter species appears to have only a single pair of medial integumental petals (Goeden et al. 1995), not two pairs, like *G. rufipes* (Goeden 2002a), or three pairs like *G. steyskali* (Fig. 2C-6). The numbers of these integumental petals were not quantified for *G. timberlakei* by Goeden et al. (1995), but their presence and general positions were noted and illustrated. Another difference is that the anterior spiracle of the second instars of *G. steyskali* and *G. rufipes* bear four papillae (Fig. 2E), not two papillae, like *G. timberlakei* (Goeden et al. 1995), or three papillae like *G. rufipes* (Goeden 2002a).

Third instar larva: Elongate-ellipsoidal, roundly tapered anteriorly, bluntly truncated posteriorly (Fig. 3A), integument white, ventral aspect of metathorax, and abdominal segments A1 and A2 with dark brown to black infuscation; caudal segment dark brown or black (Fig. 6B); minute acanthae, apically pointed or rounded, conical and posteriorly directed (Figs. 3B, 4B-1) or hemispheroidal (Fig. 4C-1), circumscribe anterior fourth of meso- and metathorax, and abdominal segment A1, all but middle third of A2, anterior half of A3, posterior

four-fifths of abdominal segments A4 to A6, and posterior half of A7; prothorax smooth (Fig. 4A-1); gnathocephalon (Figs. 3C, 4A-2) conical and medially divided by vertical cleft (Fig. 3C-1), dorsal sensory organ well-defined, hemispherical (Fig. 3C-2); anterior sensory lobe (Fig. 3C-3) bears terminal sensory organ (Fig. 3C-4); lateral sensory organ (Fig. 3C-5), supralateral sensory organ (Fig. 3C-6), and pit sensory organ (Fig. 3C-7); two medial, integumental petals (Fig. 3C-8); four, papilliform, lateral integumental petals (Figs. 3C-9, D-1) above each mouthhook (Figs. 3C-10, D-2), stomal sense organ (Figs. 3C-11, D-3) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Figs. 3C-10, D-2), anterior tooth concave posteriorly (Fig. 3D-4); median oral lobe laterally compressed, apically pointed (Figs. 3C-12, D-5), separated from labial lobe (Fig. 3D-6) with two ventral pores (Fig. 3D-7); anterior thoracic spiracle on posterior margin of prothorax (Fig. 4A-3) bears three doliform papillae (Fig. 3E); mesothoracic, lateral spiracular complex with at least four, verruciform sensilla in vertical series (Fig. 4A-4), mesothoracic spiracle not seen; metathoracic, lateral spiracular complex with nearly closed, lateral spiracle (Figs. 4A-5, B-2) and five, verruciform sensilla in vertical series (Figs. 4A-6, B-3); lateral spiracular complex of first abdominal segment consists of nearly closed spiracle (Figs. 4A-7, C-2) and four, verruciform sensilla in vertical series (Figs. 4A-8, C-3); caudal segment with paired posterior spiracular plates (Figs. 4D-1, E) separated by bare area with interspersed hemispherical minute acanthae medially (Fig. 4D-2) and open pores dorsally (Fig. 4D-3), these structures in turn ringed by two to three incomplete, concentric series of shallow, elliptical depressions (Fig. 4D-4), with three, tapered, stelex sensilla (Fig. 4F) dorsal and dorsolateral to each posterior spiracular plate; posterior spiracular plate (Fig. 4E) bears three rimae (Fig. 4E-1), ca. 0.003 mm in length, and four, spinose, in-

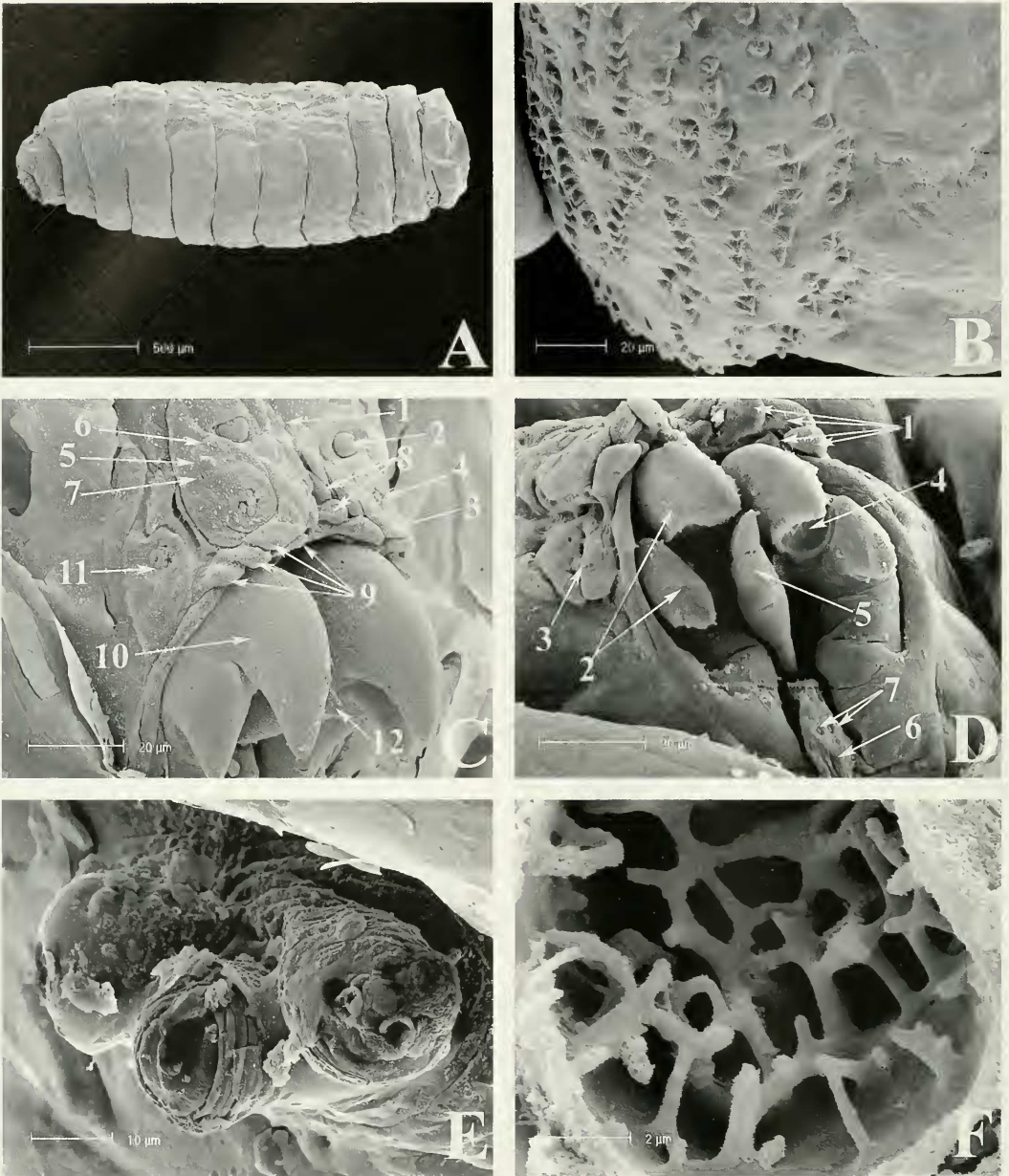


Fig. 3. Third instar of *Goedenia steyskali*: (A) habitus, anterior to left; (B) lateral view of venter of second abdominal segment showing minute acanthae; (C) gnathocephalon in frontolateral view, 1—vertical cleft, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—terminal sensory organ, 5—lateral sensory organ, 6—supra-lateral sensory organ, 7—pit sensory organ, 8—medial integumental petals, 9—lateral integumental petals, 10—mouthhook, 11—stomal sense organ, 12—median oral lobe; (D) oral cavity, ventral view, 1—lateral integumental petals, 2—teeth of mouthhook 3—stomal sense organ, 4—posterior concavity on anterior tooth of mouthhook, 5—median oral lobe, 6—labial lobe, 7—pores; (E) anterior spiracle; (F) latticed interior of papillum of anterior spiracle.

terspiracular processes, each ca. 0.003 mm long (Fig. 4E-2).

The habitus of the third instar of *G. steyskali* (Fig. 3A) resembles that of *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), *G. setosa* (Goeden 2002b), and *G. stenoparia* (Goeden 2002c). In all five species, the venters of the thorax, anterior abdominal segments, and the caudal segment are darkly pigmented (Fig. 6B; Goeden et al. 1995; Goeden 2002a, b, c) and minute acanthae circumscribe the meso- and metathorax and abdomen, and especially noteworthy, the central, posterior surface of the caudal segment is dotted with scattered pores (Fig. 4D-2, 3; Goeden et al. 1995; Goeden 2002b, c). This central area is ringed by concentric series of shallow, elliptical depressions in all five species (Figs. 3A-2, B-4; Goeden et al. 1995; Goeden 2002a, b, c). The prothorax and gnathocephalon of *G. timberlakei* and *G. rufipes* are smooth and free of minute acanthae; whereas, the prothoracic venters of *G. steyskali* (not shown), *G. setosa* (Goeden 2002b) and *G. stenoparia* anteriorly each bear a few minute acanthae (Goeden 2002c).

The third instars of all five species of *Goedenia* studied to date lack oral ridges on either side of the mouth opening, and ventral or ventrolateral to the stomal sense organ (Fig. 3C, Goeden et al. 1995; Goeden 2002a, b, c, and unpublished data).

Two medial and four lateral integumental petals are present in *G. stenoparia* (Goeden 2002c), as in *G. rufipes* (Goeden 2002a); whereas, *G. timberlakei* has six lateral integumental petals (Goeden et al. 1995, unpublished data), *G. setosa* has five (Goeden 2002b), and *G. steyskali* has four (Figs. 3C-9, D-1). The lateral-most integumental petal apparently is fused with the stomal sense organ in *G. steyskali* (Fig. 3D-1, 3), but this petal is separated from the stomal sense organ in the other four species (Goeden et al. 1995; Goeden 2002a, b, c).

The mouthhooks of the third instar of *G. steyskali* (Figs. 3C-10, D-2), like those of

G. timberlakei (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), *G. setosa* (Goeden 2002b), and *G. stenoparia* (Goeden 2002c), are bidentate. Moreover, a ventral view of the oral cavity (Fig. 3D), like that also figured and described for *G. rufipes* (Goeden 2002a) and *G. stenoparia* (Goeden 2002c), but not obtained for either *G. timberlakei* (Goeden et al. 1995, unpublished data) or *G. setosa* (Goeden 2002b), shows the concavely scalloped, posterior surface of the anterior tooth (Fig. 3D-3).

The anterior spiracle of the third instar of *G. steyskali* bears three papillae (Fig. 3E) differing from the other four *Goedenia* species studied, in which this spiracle bears only two papillae (Goeden et al. 1995, Goeden 2002a, b, c). The latticed interior of one of the papillae of *G. steyskali* is shown in Fig. 3F.

The lateral spiracular complex of the mesothorax of *G. steyskali* (Fig. 4A-4) contains at least five verruciform sensilla in a vertical series. In *G. rufipes* (Goeden 2002a) and *G. stenoparia* (Goeden 2002c), this complex contains six verruciform sensilla, but in *G. timberlakei*, it includes only two verruciform sensilla (Goeden et al. 1995). Likewise, the metathoracic lateral spiracular complex of *G. steyskali* (Figs. 4A-5, 6) contains five verruciform sensilla in a vertical series. Those of *G. rufipes* and *G. steyskali* include four verruciform sensilla (Goeden 2002a), again like *G. stenoparia* (Goeden 2002c); whereas, only two such sensilla occur in *G. timberlakei* (Goeden et al. 1995). Finally, four verruciform sensilla in a vertical series comprise the lateral spiracular complex of the first abdominal segment of *G. steyskali* (Figs. 4A-7, 8), but five such sensilla comprise this complex in *G. stenoparia* (Goeden 2002c), three such sensilla occur in *G. rufipes* (Goeden 2002a), and only one verruciform sensillum is found on this segment in *G. timberlakei* (Goeden et al. 1995).

The number of minute acanthae and pores dorsomedial of and between the posterior spiracular plates (Figs. 4D-1, 2, 3) are

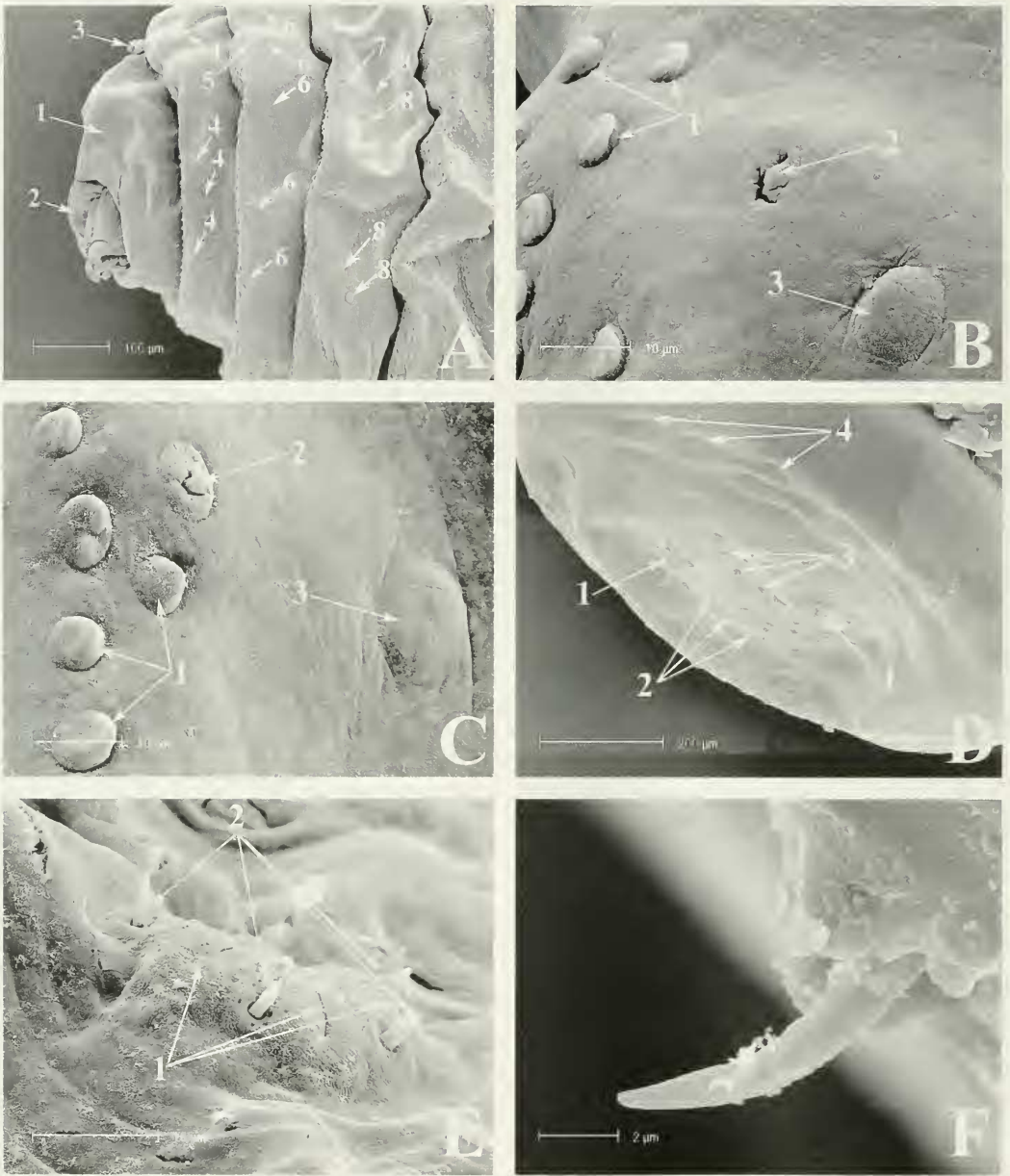


Fig. 4. Third instar of *Goedenia steyskali*, continued; (A) anterior spiracular complexes, anterior to left, 1—prothorax, 2—gnathocephalon; 3—anterior spiracle, 4—verruciform sensilla on mesothorax, 5—lateral spiracle on metathorax, 6—verruciform sensilla on metathorax, 7—lateral spiracle on first abdominal segment, 8—verruciform sensilla on first abdominal segment; (B) close-up of lateral spiracle on metathorax, 1—minute acanthae, 2—spiracle, 3—verruciform sensillum; (C) close-up of lateral spiracle on first abdominal segment, 1—minute acanthae, 2—spiracle, 3—verruciform sensillum; (D) caudal segment, 1—posterior spiracular plates, 2—minute acanthae, 3—pores, 4—elliptical depressions; (E) posterior spiracular plate, 1—rimae, 2—interspiracular processes. (F) stalex sensillum.

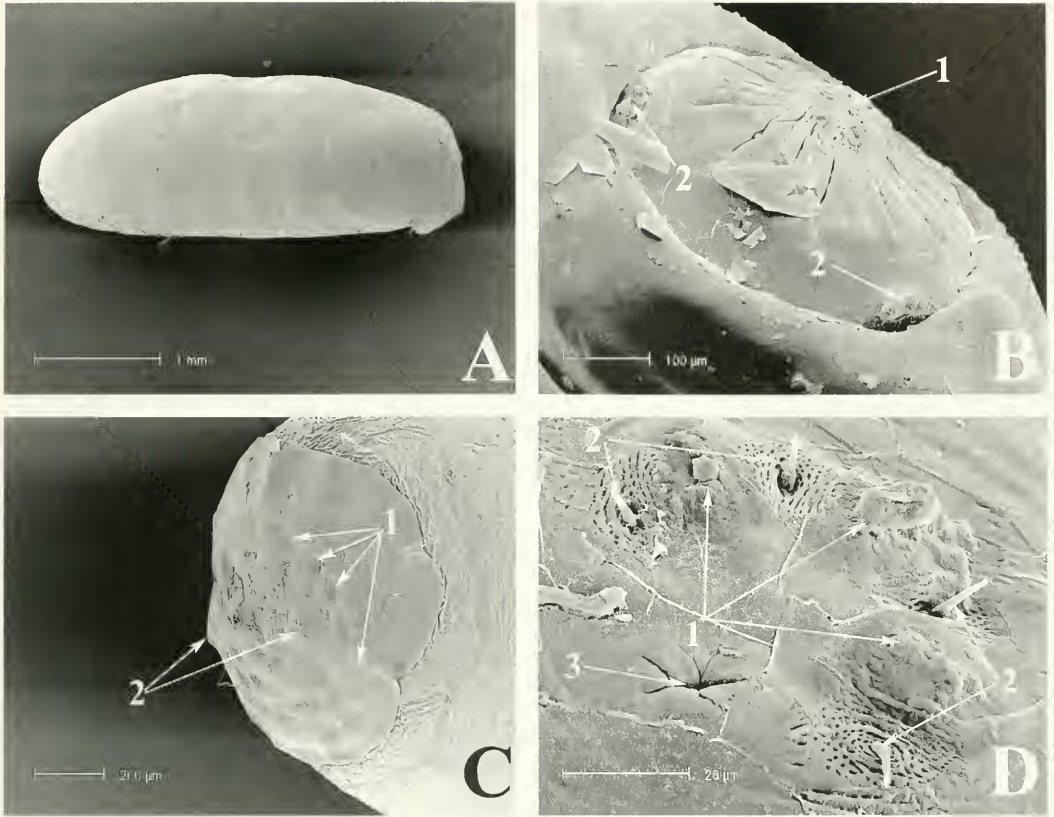


Fig. 5. Puparium of *Goedenia steyskali*: (A) habitus, anterior to right, (B) anterior end, 1—invagination scar, 2—anterior spiracles; (C) caudal segment, 1—shallow elliptical depressions, 2—posterior spiracular plates.

the least of those found on the five congeners studied to date (Goeden et al. 1995, Goeden 2002a, b, c).

Puparium: Light to dark, reddish brown with dark brown to black, anterior stripe or series of spots on venters of meso- and metathorax and abdominal segments A-1 to A-2, and similarly dark, caudal segment. Elongate-ellipsoidal, with smoothly rounded anterior end, and truncated posterior end (Fig. 5A). Anterior end bears invagination scar (Fig. 5B-1) and raised, trilobed, anterior thoracic spiracles (Fig. 5B-2). Posterior end of caudal segment studded with a few, smoothly rounded, hemispherical, minute acanthae interspersed with a few open pores surrounded by shallow elliptical depressions (Fig. 5C-1). A pair of raised, hemispheroidal, posterior spiracular plates (Fig. 5C-2, D) each bearing three elliptical rimae

(Fig. 5D-1) interspersed with four, peg-like, interspiracular processes (Fig. 5D-2). Eleven puparia dissected from flower heads averaged 3.40 ± 0.10 (range, 2.70–3.99) mm in length; 1.48 ± 0.55 (range, 1.44–1.79) mm in width.

DISTRIBUTION AND HOSTS

Goedenia steyskali was studied on *Grindelia hirsutula* var. *halli* which is locally common but localized, in meadows, dry slopes, and open pine/oak woodlands in southern San Diego County, where it is listed as a rare species by Hickman (1993). The only other host that I have reared *Goedenia steyskali* from is *Grindelia camporum*, possibly var. *camporum* Greene (Hickman 1993), that is more widespread in southern and central California; however, my record for the single specimen that I

reared from this plant species requires confirmation and additional collection records in order to define the distribution of this tephritid. Both host plants of *Goedenia steyskali* belong to the family Asteraceae, tribe Astereae, subtribe Solidagininae (Bremer 1994), as do all other, reported and confirmed hosts of *Goedenia* spp. (Goeden 1987, Freidberg and Norrbom 1999). Accordingly, *G. steyskali* is classed as narrowly oligophagous (on two spp. in one host subtribe in the Asteraceae) (Goeden 1987, Headrick and Goeden 1998).

BIOLOGY

Egg.—No flower head of *Grindelia hirsutula* var. *halli* containing an egg of *Goedenia steyskali* was sampled; however, it is assumed that one or more eggs are inserted individually into a young preblossom flower head based upon dissections of flower heads. Moreover, individual flower heads containing separate second and third instars, third instars in different stages of development, or larvae and puparia suggest oviposition by more than one female in the same flower heads.

Larva.—Upon eclosion, the first instars commence to feed on the ovules. The receptacle was neither abraded nor pitted by such feeding.

An average of 1.4 ± 0.2 (range, 1–2) second instars were found feeding on ovules in five, separate flower heads (three preblossom, two postblossom) (Fig. 6A). They usually fed individually on a succession of ovules or soft achenes with their bodies perpendicular to, but always above, the receptacles (Fig. 6A). These larvae destroyed an average of 12 ± 5 (range, 17–22) ovules/soft achenes in these flower heads, the receptacles of which averaged 5.9 ± 1.0 (range, 4.0–10.0) mm in diameter. These larvae had damaged about 25% of the average total of 48 ± 6 (range, 24–80) ovules counted within a total of nine pre- and postblossom, flower heads. The flower heads are extremely sticky with sap, thus difficult to handle and dissect when fresh. Shortly

before or after the molt to the third instar, the larvae began to feed with their long axes oriented perpendicular to the receptacles, and with their mouthparts directed towards the receptacles, in which they begin to tunnel (Fig. 6B).

Similarly, third instars fed on receptacles as above in all but two (96%) of 48 infested flower heads examined. The 48 flower heads (9 closed preblossom, 16 live and postblossom, and 23 dead and overwintered) each contained an average of 1.5 ± 0.2 (range, 1–7) third instars. These 48 flower heads averaged 6.03 ± 0.22 (range, 4.56–8.62) mm in diameter, and as noted above, nine contained an average total of 48 ovules/achenes. The receptacles were pitted by the third instars in all 48 flower heads, indeed, some individuals tunneled deeply into the receptacle and buried themselves completely (Fig. 6C-1), horizontally beneath the receptacle surface. A few larvae tunneled through the receptacle into the peduncle of the flower head. Such deeply pitted receptacles indicated that sap constituted at least part of the diet of third instars of *G. steyskali*, as also reported for *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), *G. setosa* (Goeden 2002b), and *G. stenoparia* (Goeden 2002c). Goeden (1988), Headrick and Goeden (1990), Goeden and Headrick (1992), Goeden et al. (1995), Headrick et al. (1996), Goeden and Teerink (1997) also first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea*, *Paracantha*, *Neaspilota*, *Tephritis*, *Dioxya*, and *Xenochaeta*, respectively. Upon completing feeding in flower heads, the larva constructed a thin-walled, vasiform cell consisting of ovule/achene/floret fragments impregnated with and hardened by dried, liquid feces and sap and basally extending into the receptacle. As noted elsewhere, the flattened, sclerotized caudal segment of the third instar, nicely serves as a plug that tightly closes the mouth of the cell, yet allows respiration, and thus apparently also may serve to shield the larva

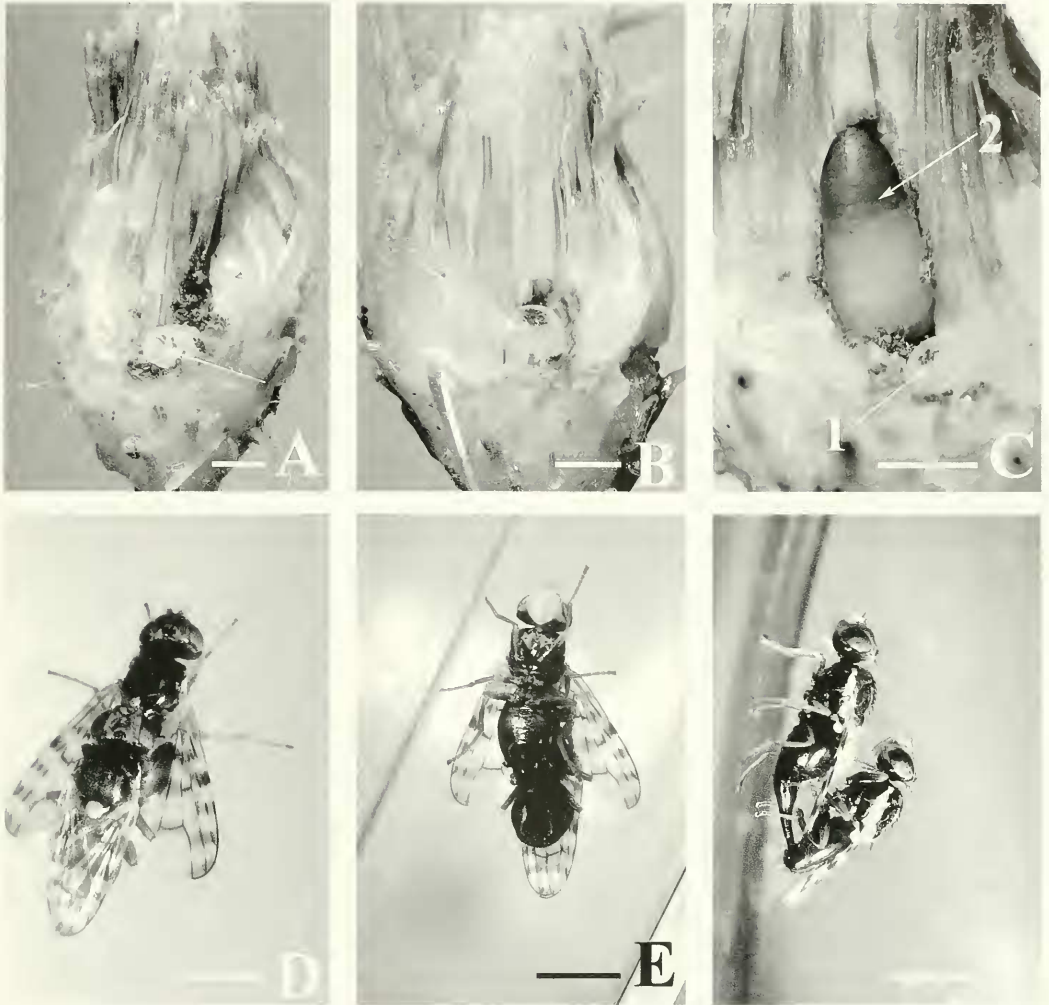


Fig. 6. Life stages of *Goedenia steyskali* in flower heads of *Grindelia hirsutula*: (A) second instar (arrow), (B) third instar (arrow) feeding in receptacle (note dark infuscation on caudal plate); (C) 1—third instar and 2—puparium in flower head, (D) mating pair, dorsal view; (E) mating pair, ventral view; (F) mating pair, lateral view. Lines = 1 mm.

from arthropod predators during overwintering (= phragmosis; Goeden 2002b, c). Prior to pupariation the prepupa turns 180° and orients with its anterior end away from the receptacle, retracts its mouthparts, and forms a puparium (Figs. 6C-2).

Pupa.—Postblossom, mature flower heads of the F₁ generation and overwintered, dead flower heads still attached to plants usually each contained a single puparium, but as many as four. The posterior

of the puparium faced the receptacle, rested in the cuplike base of the cell (Fig. 6C-2).

Adult.—Under insectary conditions, 14 males of *G. steyskali* lived an average of 52 ± 5 (range, 17–77) days, and 21 females lived an average of 49 ± 3 (range, 22–78) days. These longevities were more than the mean longevities of 39 and 31 days reported for *G. timberlakei* (Goeden et al. 1995) and 28 and 25 days for *G. stenoparia* (Goeden 2002c), but comparable to 49 and 58

days for *G. setosa* (Goeden 2002b), respectively. These adult longevities are commensurate with the aggregative type of life histories possessed by all four of these tephritids (Headrick and Goeden 1994, 1998; Goeden et al. 1995).

The pre-mating and mating behaviors of *G. steyskali* were not studied in the field, but were observed for six pairs (one male and one female each) in separate petri dish arenas. These arenas were of the type found to be useful in studying mating behaviors of many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). Both sexes exhibited wing hamation (Headrick and Goeden 1994) throughout the day concurrent with other behaviors, i.e., grooming, resting, and feeding; this also was the most common wing movement reported for *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), *G. setosa* (Goeden 2002b), and *G. stenoparia* (Goeden 2002c). Premating behaviors observed with *G. stenoparia* included males and females tracking individuals of the opposite sex, during which males sometimes swayed and usually exhibited abdominal pleural distension. During mating, the wings of the male were overlapped (Figs. 6D, E) or parted at 10–20°, the wings of the female were parted at 60–80° (Figs. 6D, E), with both pairs of parted wings centered over the midlines of the flies (Figs. 6D, E). The foretarsi of the male grasped the dorsum of the abdomen of the female laterally at the thoracic juncture, the midtarsi grasped the abdomen laterally or the oviscapae at its base, and the hindtarsi touched the substrate or crossed under the oviscapae (Fig. 6F). The bodies of both flies paralleled the substrate with the oviscapae elevated about 30° (Fig. 6F). In arenas, the flies mated at least once on successive days at different times during daylight and were observed eight times to mate twice in one day. Another pair was observed mating three times during one day. A total of 15 matings were observed that lasted an average of 147 (range, 50–280) min. Females *in copula* were observed to

walk about the arenas. Females became restless before termination of mating and pushed against the males with their hind tarsi, they also lofted their wings so as to push against the males and fully extended their aculei. The male in turn countered this agonistic behavior with copulatory induction behavior (CIB), i.e., rubbed his hind tarsi along the oviscapae, grasped the female tightly, or rocked from side to side to regain purchase or to avoid the female's pummeling, all of which appeared to calm the female and allow coitus to continue. During postcoital separation, the male turned and rapidly walked off and away from the female while pulling his genitalia free, a process lasting just 6 and 10 s in two cases.

Seasonal history.—The life cycle of *Goedenia steyskali* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the prepuparia, puparia, and adults variously are the overwintering stages. *Grindelia hirsutula* has a long bloom period, with young, immature through fully mature flower heads found on single plants. Overwintered adults and adults emerged from overwintered puparia in spring (March–May) aggregate the following summer (June–July) on their preblossom host plants, to mate, and subsequently to begin to oviposit in the small, newly-formed flower heads. The new generation emerges from puparia formed in late summer (August) through late-fall (October–November), whereas, later-formed larvae overwinter as prepuparia as noted above.

Natural enemies.—Overwintered puparia of *G. stenoparia* were parasitized by chalcidoid Hymenoptera in the genera *Eurytoma* (Eurytomidae), *Pteromalus* (Pteromalidae), and *Torymus* (Torymidae) as probable primary, solitary, larval-pupal endoparasitoids.

ACKNOWLEDGMENTS

I thank Andrew C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California,

Riverside, for identifications of plants mentioned in this paper. Krassimer Bozhilov in the Institute of Geophysics and Planetary Physics, University of California, Riverside, greatly facilitated my scanning electron microscopy. I also am grateful to Jeff Teerink for his technical assistance and to David Headrick for his helpful comments on an earlier draft of this paper.

LITERATURE CITED

- Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc. Portland, Oregon.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca, New York.
- Freidberg, A. and A. L. Norrbom. 1999. A generic reclassification and phylogeny of the Tribe Myopitini (Tephritinae). Chapter 23. In Aluja, M. and A. L. Norrbom, eds. Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior. CRC Press, Boca Raton, Florida. 944 pp.
- Goeden, R. D. 1987. Host-plant relations of native *Urophora* spp. (Diptera: Tephritidae) in southern California. Proceedings of the Entomological Society of Washington 89: 269–274.
- . 1988. Life history of *Tripanea imperfecta* (Coquillett) on *Bebbia juncea* (Bentham) Greene in the Colorado Desert of southern California (Diptera: Tephritidae). Pan-Pacific Entomologist 64: 345–351.
- . 2001a. Life history and description on immature stages of *Neaspilota footei* Freidberg and Mathis (Diptera: Tephritidae) on *Aster occidentalis* (Nuttall) Torrey and A. Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 103: 191–206.
- . 2001b. Life history and description on immature stages of *Tephritis joanae* Goeden (Diptera: Tephritidae) on *Ericameria pitifolia* (A. Gray) H. M. Hall (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 103: 586–600.
- . 2001c. Life history and description of immature stages of *Tephritis teerinki* Goeden (Diptera: Tephritidae) on *Hulsea vestita* A. Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 103: 807–825.
- . 2002a. Life history and description of immature stages of *Goedenia rufipes* (Curran) (Diptera: Tephritidae) on *Isocoma acradenia* (E. Greene) E. Greene in southern California. Proceedings of the Entomological Society of Washington 104: 576–588.
- . 2002b. Life history and description of immature stages of *Goedenia setosa* (Foote) (Diptera: Tephritidae) on *Ericameria brachylepsis* (A. Gray) H. M. Hall in southern California. Proceedings of the Entomological Society of Washington 104: 629–639.
- . 2002c. Life history and description of immature stages of *Goedenia stenoparia* (Steyskal) (Diptera: Tephritidae) on *Gutierrezia californica* (De Candolle) Torrey and A. Gray and *Solidago californica* Nuttall (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 104: 702–715.
- Goeden, R. D. and D. H. Headrick. 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 94: 59–77.
- Goeden, R. D., D. H. Headrick and J. A. Teerink. 1993. Life history and descriptions of immature stages of *Tephritis arizonaensis* Quisenberry (Diptera: Tephritidae) on *Baccharis sarothroides* Gray in southern California. Proceedings of the Entomological Society of Washington 95: 210–222.
- . 1995. Life history and description of immature stages of *Urophora timberlakei* Blanc and Foote (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 97: 779–790.
- Goeden, R. D. and A. L. Norrbom. 2001. Life history and description of adults and immature stages of *Procecidochares blanci* n. sp. (Diptera: Tephritidae) on *Isocoma acradenia* (E. Greene) E. Greene (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 103: 517–540.
- Goeden, R. D. and J. A. Teerink. 1997. Life history and description of immature stages of *Xenochaeta albiflorum* Hooker in central and southern California. Proceedings of the Entomological Society of Washington 99: 597–607.
- Headrick, D. H. and R. D. Goeden. 1990. Resource utilization by larvae of *Paracantha gentilis* (Diptera: Tephritidae) in capitula of *Cirsium californicum* and *C. proteanum* (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 92: 512–520.
- . 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.
- . 1998. The biology of nonfrugivorous tephritid fruit flies. Annual Review of Entomology 43: 217–241.

- Headrick, D. H., R. D. Goeden and J. A. Teerink. 1996. Life history and description of immature stages of *Dioxya picciola* (Bigot) (Diptera: Tephritidae) on *Coreopsis* spp. (Asteraceae) in southern California. *Proceedings of the Entomological Society of Washington* 98: 332-349.
- Hickman, J. C. (ed.) 1993. *The Jepson Manual*. University of California Press, Berkeley and Los Angeles.
- Steyskal, G. C. 1979. Taxonomic studies on fruit flies of the genus *Urophora* (Diptera: Tephritidae). Special Publication, Entomological Society of Washington. 61 pp.
- Teerink, J. A. and R. D. Goeden. 1999. Description of the immature stages of *Trupanea imperfecta* (Coquillett). *Proceedings of the Entomological Society of Washington* 101: 75-85.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology Occasional Papers 19, 172 pp.