

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF  
*NEASPILOTA SIGNIFERA* (COQUILLET) (DIPTERA: TEPHRITIDAE) ON  
*HEMIZONIA PUNGENS* (HOOKER AND ARNOTT) TORREY AND A. GRAY  
(ASTERACEAE) IN SOUTHERN CALIFORNIA**

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*Abstract.*—*Neaspilota signifera* (Coquillett) is a bivoltine, monophagous fruit fly (Diptera: Tephritidae) apparently developing solely in the flower heads of *Hemizonia pungens* (Hooker and Arnott) Torrey and Gray in southern California. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The mouth-hooks of the first and second instars are bidentate, but tridentate in the third instar. The pair of flattened integumental petals are fused laterally with the well developed, stomal sense organs in the first instar; whereas, the integumental petals are papilliform and progressively more numerous in the second and third instars. The dorsal sense organ is well defined in all three instars. The six oral ridges in the second and third instars are dentate ventrally. The life cycle is of the aggregative type. Most eggs are laid singly between the chaff and ovules of preblossom flower heads and perpendicular to the receptacle. First instars feed on ovules, as do the second instars, which also feed on soft achenes in open flower heads, like all third instars. A third of the third instars examined also pitted the receptacles and apparently supplemented their diet with sap. Pupariation occurs inside the mature flower heads, but no protective cell is formed, as with congeners that overwinter as prepuparia. Instead, F<sub>1</sub> adults emerge from their cells in early summer (June) and either produce a partial second generation in late-blooming flower heads or pass the summer, fall, and winter in riparian habitats as long-lived adults. Surviving, overwintered adults aggregate the next year in early spring (March–April) on preblossom host plants to mate and subsequently oviposit. A *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from puparia as a solitary, larval-pupal endoparasitoid.

*Key Words:* Insecta, *Neaspilota*, *Hemizonia*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, seed predation, parasitoid

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Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae (Goeden 1989) and stimulated several life-history studies, including those on *N. viri-*

*descens* Quisenberry (Goeden and Headrick 1992) and *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999). This paper describes the immature stages and life history of a third species from California, *Neaspilota signifera* (Coquillett).

## MATERIALS AND METHODS

The present study was based in large part on dissections of subsamples of flower heads of *Hemizonia pungens* (Hooker and Arnott) Torrey and Gray collected during March–May, 1995–1997 from the San Jacinto Wildlife Area at 390-m elevation, Lakeview, Riverside Co., administrated by the State of California, Department of Fish and Wildlife. One-liter samples of excised, immature and mature flower heads containing eggs, 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. Five first-, 11 second-, and 15 third-instar larvae, and 11 puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional 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 increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated 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 and sexual maturation 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. Single pairs of virgin males and females obtained

from emergence cages also were held in each of six, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1998a, b), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997, 1998, 1999a, b, c), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means  $\pm$  SE are used throughout this paper. Voucher specimens of *N. signifera* immature stages, adults, and parasitoids reside in my research collections.

## RESULTS AND DISCUSSION

## Taxonomy

*Adult.*—*Neaspilota signifera* was described by Coquillett (1894). Freidberg and Mathis (1986) designated a male lectotype from Los Angeles, California, and pictured the unpatterned wing [as did Foote et al. (1993)] along with drawings of the lateral aspect of the head, male right foretarsus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

*Immature stages.*—The egg, larvae, and puparium heretofore have not been described nor illustrated.

*Egg:* Twenty-five ova dissected from four, field-collected, mature females of *N. signifera* plus nine eggs measured *in situ* in dissected, field-collected flower heads (Fig. 5A) were white, opaque, smooth, elongate-ellipsoidal,  $0.72 \pm 0.01$  (range, 0.54–0.85) mm long,  $0.20 \pm 0.003$  (range, 0.16–0.24) mm wide, smoothly rounded at tapered basal end; pedicel also tapered,  $0.025 \pm 0.001$  (range, 0.02–0.03) mm long.

All eggs found in flower heads were damaged during removal and unsuitable for

scanning electron microscopy. The egg of *N. signifera* is similar in shape to those of *N. viridescens* and *N. wilsoni* but longer and wider on average than that of *N. viridescens* (Goeden and Headrick 1992) and shorter and narrower than that of *N. wilsoni* (Goeden and Headrick 1999).

**First instar:** White, elongate-cylindrical, bluntly rounded anteriorly and posteriorly (Fig. 1A), minute acanthae circumscribe intersegmental lines; gnathocephalon with pair of prominent, flattened, integumental petals dorsad to mouthhooks (Fig. 1B-1); mouthhook bidentate (Fig. 1B-2); median oral lobe laterally flattened, apically pointed (Fig. 1B-3); each integumental petal fused laterally with prominent, stomal sense organ (Fig. 1B-4). Posterior spiracular plate bears two ovoid rimae, ca. 0.01 mm in length (Fig. 1C-1), and four interspiracular processes, each with two to four branches, longest measuring ca. 0.01 mm (Fig. 1C-2).

The poor condition of my specimens of first instar *N. signifera* allowed few comparisons with those of *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999); however, their general habitus is similar and their mouthhooks also are bidentate. Like *N. wilsoni*, but not *N. viridescens*, the integumental petal is fused laterally with the stomal sense organ in first instar *N. signifera*, a condition first reported in *Trupanea vicina* (Wulp) by Goeden and Teerink (1999b).

**Second instar:** White, elongate-cylindrical, rounded anteriorly, truncated postero-dorsally (Fig. 2A), minute acanthae circumscribe intersegmental lines (Fig. 2B-1); gnathocephalon conical (Fig. 2B); dorsal sensory organ a well-defined, dome-shaped papilla with a basal pore sensillum on each side (Fig. 2C-1); anterior sensory lobe (Fig. 2C-2, D-1) bears the terminal sensory organ (Fig. 2C-3, D-2), lateral sensory organ (Fig. 2D-3), supralateral sensory organ (Fig. 2D-4), and pit sensory organ (Fig. 2D-5); stomal sense organ prominent, ventrolaterad of anterior sensory lobe (Fig. 2D-6); mouthhook bidentate (Fig. 2C-4); median oral

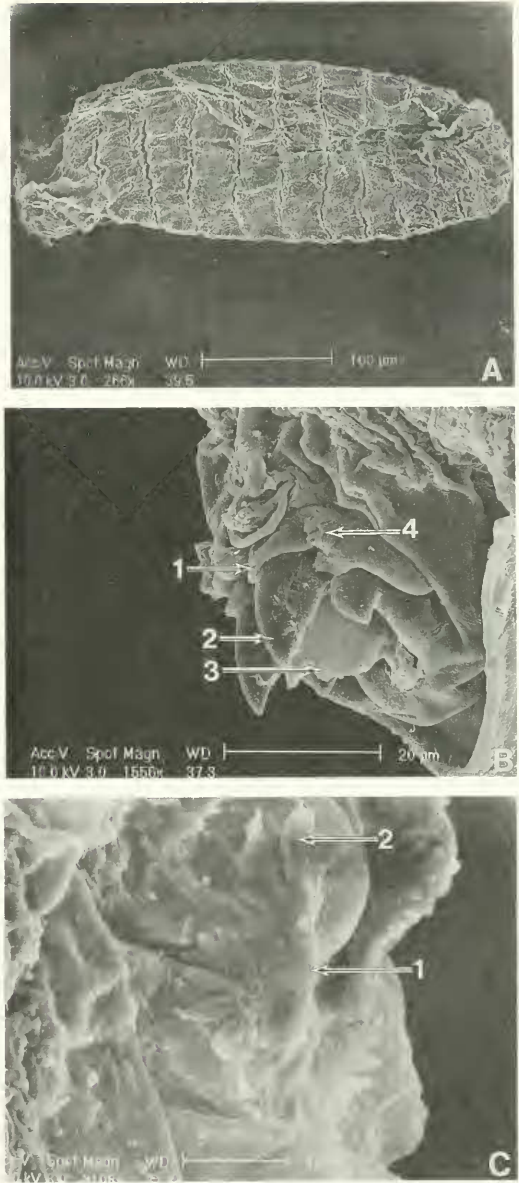


Fig. 1. First instar of *Neaspilota signifera*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1— integumental petal, 2— mouth hook, 3— median oral lobe, 4— stomal sense organ; (C) posterior spiracular plate, 1— rima, 2— interspiracular process.

lobe laterally flattened (Fig. 2C-5); single row of four, papilliform, integumental petals dorsal to each mouth hook (Fig. 2C-6, D-7); six oral ridges with long axes parallel in row lateral to mouth hooks, oral ridges

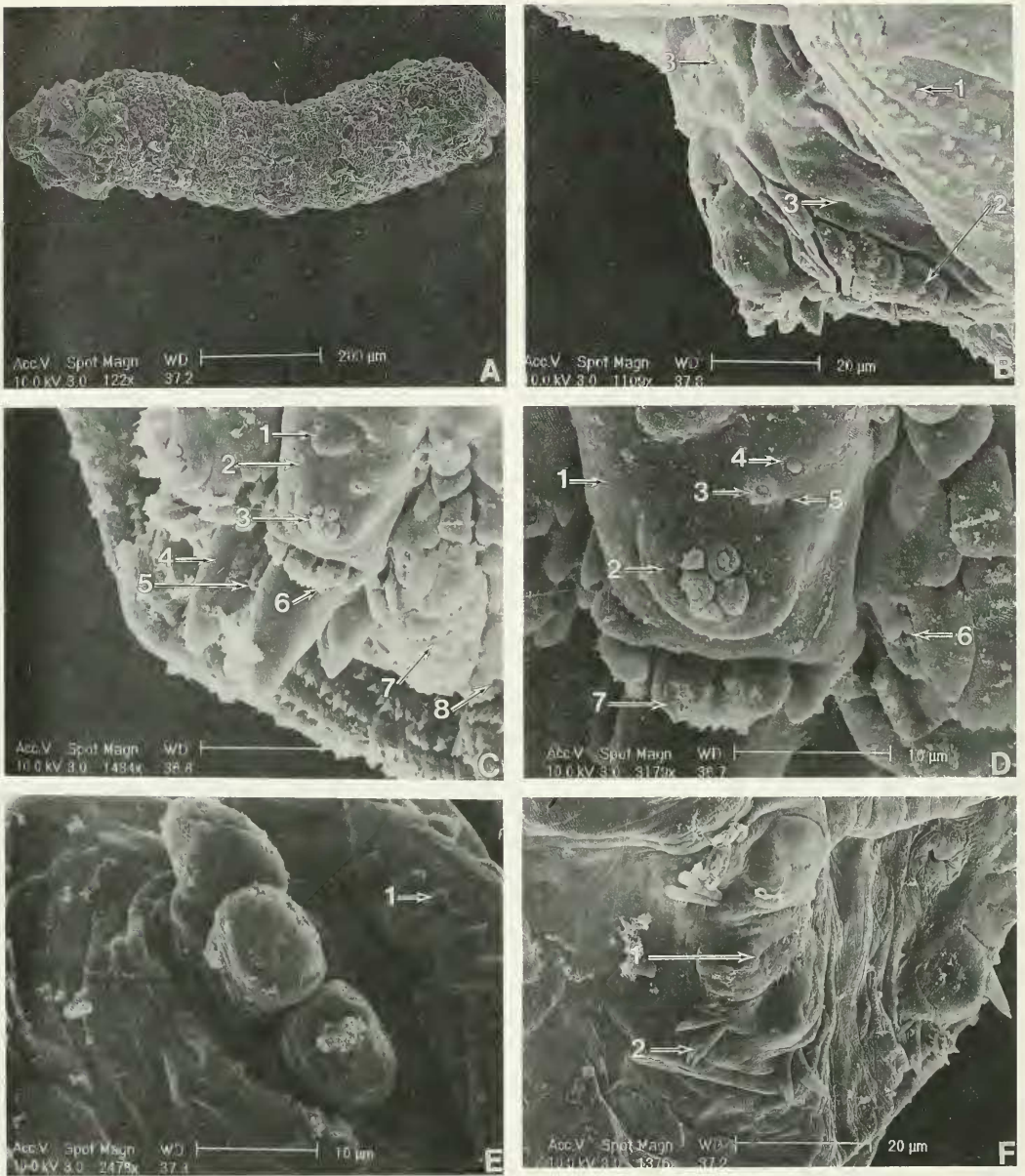


Fig. 2. Second instar of *Neaspilota signifera*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1— minute acanthae, 2— oral ridge, 3— pit sensillum; (C) gnathocephalon, 1— dorsal sensory organ, 2— anterior sensory lobe, 3— terminal sensory organ, 4— mouthhook, 5— median oral lobe, 6— integumental petal, 7— oral ridge, 8— pit sensillum; (D) gnathocephalon, 1— anterior sensory lobe, 2— terminal sensory organ, 3— lateral sensory organ, 4— supralateral sensory organ, 5— pit sensory organ, 6— stomal sense organ, 7— integumental petal; (E) anterior thoracic spiracle, 1— minute acanthae; (F) posterior spiracular plate, 1— rima, 2— interspiracular process.

dentate along ventral margins (Fig. 2B-2, C-7); pit sensilla circumscribe gnathocephalon posteriorad of oral ridges (Fig. 2B-3, C-8); anterior thoracic spiracle with three

oblong papillae (Fig. 2E); minute acanthae circumscribe anterior margin of prothorax (Fig. 2B-1, B-1); lateral spiracular complexes not seen; posterior spiracular plate

bears three ovoid rimae, ca. 0.01 mm long (Fig. 2F-1), and four interspiracular processes, each with two to four branches, longest measuring 0.009 mm (Fig. 2F-2).

The habitus of the second instar of *N. signifera* is more like *N. wilsoni* (Goeden and Headrick 1999) than the barrel-shaped second instar of *N. viridescens* (Goeden and Headrick 1992). Unlike both *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), the dorsal sensory organ of *N. signifera* is well defined in the second instar. However, one distinction between the first and second instar common to all three species of *Neaspilota* is the presence of oral ridges with dentate margins in the latter instar (Goeden and Headrick 1992, 1999). The stomal sense organs of the second instar of all three species are well developed and bear sensory structures, variously described as conical in *N. viridescens* (Goeden and Headrick 1992), papillose in *N. wilsoni* (Goeden and Headrick 1999), but verruciform in *N. signifera* (Fig. 2D-6). Also, the integumental petals of the second instars of all three species are papilliform and about four in number above each mouthhook in *N. signifera* (Fig. 2C-6, D-7); whereas, in the first instars these structures are broad, flattened, and paired (Goeden and Headrick 1992, 1999). The mouthhooks of the second instar of *N. signifera* are bidentate, like those of *N. wilsoni* (Goeden and Headrick 1999); whereas, those of *N. viridescens* are tridentate (Goeden and Headrick 1992). Similar, apparent interspecific differences in dentation were noted among mouthhooks of second instar *Trupanea* spp. (Goeden and Teerink 1999b and references therein). Finally, the interspiracular processes each bear two to four branches (Fig. 2F-2), not five to nine branches like those of *N. viridescens* (Goeden and Headrick 1992), nor two to six branches like those of *N. wilsoni* (Goeden and Headrick 1999).

*Third instar:* White to pale yellow, with posterior spiracular plate dark brown to black, elongate-cylindrical, tapering anteri-

orly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 3A), minute acanthae circumscribe thoracic and abdominal segments anteriorly, acanthae more numerous on posterior segments; gnathocephalon conical (Fig. 3B); dorsal sensory organ a well-defined, dome-shaped papilla (Fig. 3D-1), pit sensillum on each side at base of dorsal sensory organ (Fig. 3D-2); anterior sensory lobe (Fig. 3C-1) bears the terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); eight to 10 papilliform, integumental petals in double row above each mouth hook (Fig. 3C-6, D-3); six oral ridges laterad of mouthhook, oral ridges dentate along ventral margins (Fig. 3B-1, C-7); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 3C-8, D-4); mouth hook tridentate (Fig. 3B-2, C-9, D-5); median oral lobe laterally flattened, apically pointed (Fig. 3C-10, D-6); prothorax circumscribed anteriorly with minute acanthae (Fig. 3B-3); anterior thoracic spiracle on posterior margin of prothorax bears three to four oblong papillae (Fig. 3E); spiracle of metathoracic lateral spiracular complex absent or not seen, this complex otherwise consisting of vertical row of four verruciform sensilla and verruciform sensillum posterior to upper verruciform sensillum (not shown, but otherwise like Fig. 3F); abdominal lateral spiracular complex consists of a spiracle (Fig. 3F-1), vertical row of four verruciform sensilla (Fig. 3F-2), and a single verruciform sensillum posterior to upper verruciform sensillum in vertical series (Fig. 3F-3); caudal segment broadly circumscribed by minute acanthae (Fig. 3G-1); stlex sensilla dorsolaterad and ventrolaterad of posterior spiracular plates (Fig. 3G-2), lateral stlex sensilla not seen; posterior spiracular plate bears three ovoid rimae, ca. 0.029 mm in length (Fig. 3G-3), and four interspiracular processes (Fig. 3G-4), each with one to three, simple, pointed branches, longest branch measuring 0.009 mm; inter-

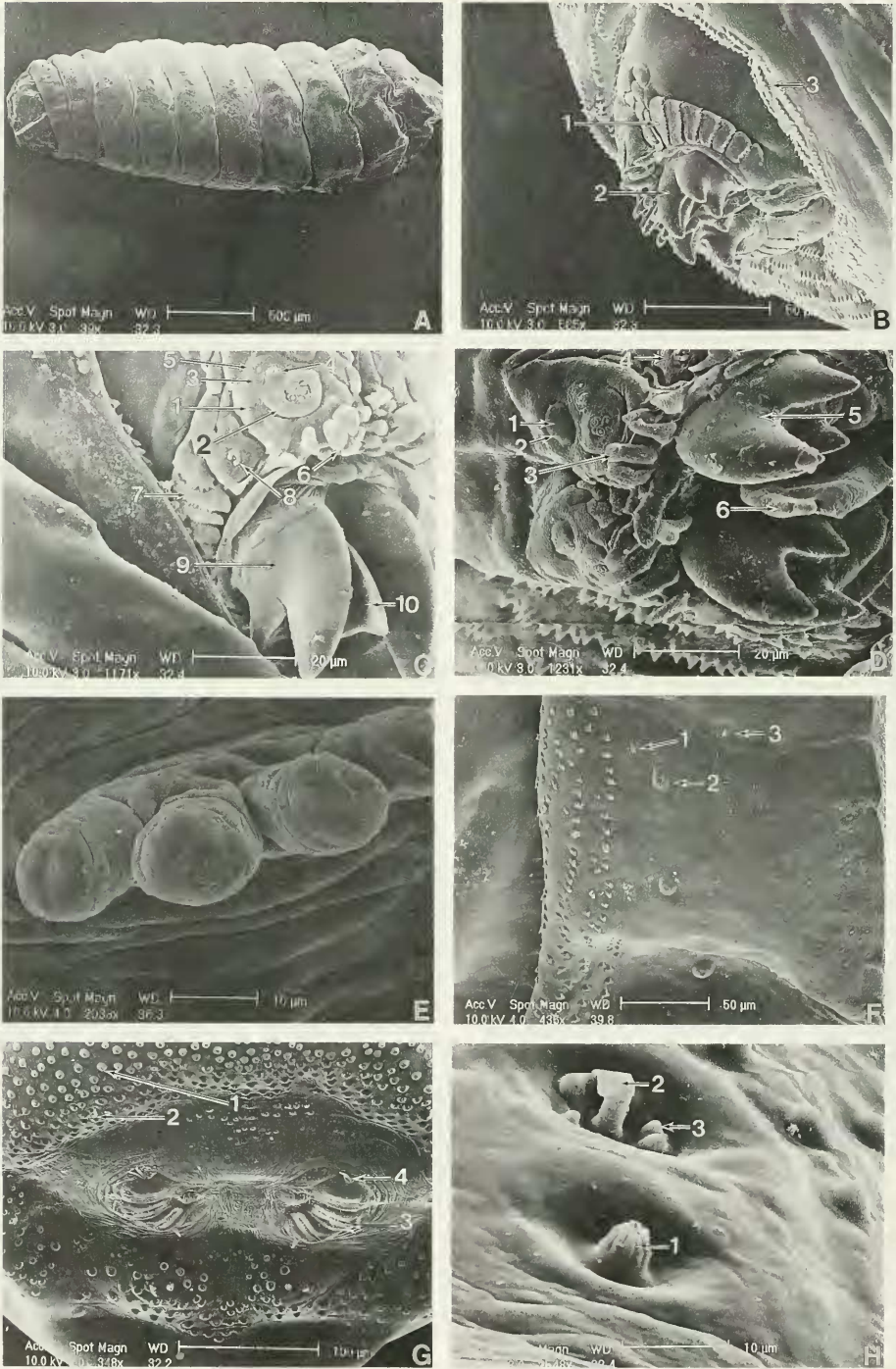


Fig. 3. Third instar of *Neaspilota signifera*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1—oral ridge, 2—mouthhook, 3—minute acanthae; (C) 1— anterior sensory lobe, 2— terminal sensory organ, 3— pit sensory organ, 4— lateral sensory organ, 5— supralateral sensory organ, 6— integumental petal, 7— oral ridge, 8— stomal sense organ, 9— mouth hook, 10— median oral lobe; (D) gnathocephalon, anterior view, 1— dorsal sensory organ, 2— pit senillum, 3— integumental petal, 4— stomal sense organ, 5— mouthhook, 6— median oral lobe; (E) anterior thoracic spiracle; (F) first abdominal spiracular complex, 1— spiracle,

mediate sensory complex with a medusoid sensillum (Fig. 3H-1) and a stelex sensillum (Fig. 3H-2) ringed by minute acanthae (Fig. 3H-3).

The habitus of the third instar of *N. signifera* generally is like that reported for *N. viridescens* Goeden and Headrick (1992) and *N. wilsoni* (Goeden and Headrick 1999), except that the minute acanthae circumscribe the body segments differently; i.e., in *N. signifera*, the anterior part of each segment is circumscribed; in *N. wilsoni*, all intersegmental areas and all abdominal segments except the pleura are circumscribed; and in *N. viridescens*, the intersegmental areas are free of acanthae. Unlike these two congeners, the dorsal sensory organ is well defined in the third instar of *N. signifera* (Fig. D-1) as well as in the second instar; however, I was unable to determine whether this also held for the first instar. The dorsal sensory organ is well defined in the first instar of both congeners. Thus, speculation by Goeden and Headrick (1992, 1999) that this intraspecific, differential degree of definition of the dorsal sensory organ may be a consistent generic character has now been invalidated by comparison with a third species of *Neaspilota*.

Additional bases for differentiation between instars were noted. The integumental petals in the third instar *N. signifera* are papilliform and arranged in a double row above each mouthhook, but are less numerous and form a single row in the second instar. The integumental petals in the second and third instars of *N. viridescens* also are papilliform and situated similarly (Goeden and Headrick 1992), but in *N. wilsoni* are fewer in the third instar (Goeden and Headrick 1999). The stomal sense organs of the third instars of all three species are well developed and bear different sensory structures,

described as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992); as papilliform and pit-type in *N. wilsoni* (Goeden and Headrick 1999); and as verruciform (Fig. 3C-8), or what might be termed "compound verruciform", as shown in Figure 3D-4. Like the second instar of *N. signifera*, the third instar has oral ridges with dentate margins, also reported in the second and third instars of *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999). Counting only those oral ridges with dentate margins in a single row ventral to the stomal sensory organ, these apparently number six in the second and third instars of all three species examined to date; therefore, further comparison with additional species may show this to be a consistent generic character. The third instars of *Trupanea imperfecta*, *T. jonesi*, *T. nigricornis*, *T. pseudovicina*, *T. signata*, and *T. wheeleri* also bear serrated oral ridges (Goeden and Teerink 1997, 1998, 1999b, Goeden et al. 1998a, Knio et al. 1996, Teerink and Goeden 1998), but these oral ridges appear to be fewer in number, and not arranged in a more or less regular, vertical row laterad to the oral cavity, as in *Neaspilota*. Also, the mouth hooks of the third instars of *N. signifera* and *N. viridescens* are tridentate (Goeden and Headrick 1992); whereas, those of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation are supported by our findings that the mouth hooks of third-instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 1999b and citations therein).

*Puparium*: Mostly white to yellow, with posterior 2-3 segments grayish to blackened posteriorly, broadly ellipsoidal and

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2— verruciform sensillum, 3— verruciform sensillum: (G) caudal segment, 1— minute acanthae, 2— stelex sensillum, 3— rima, 4— interspiracular process; (H) intermediate sensory complex, 1— medusoid sensillum, 2— stelex sensillum, 3— minute acanthae.

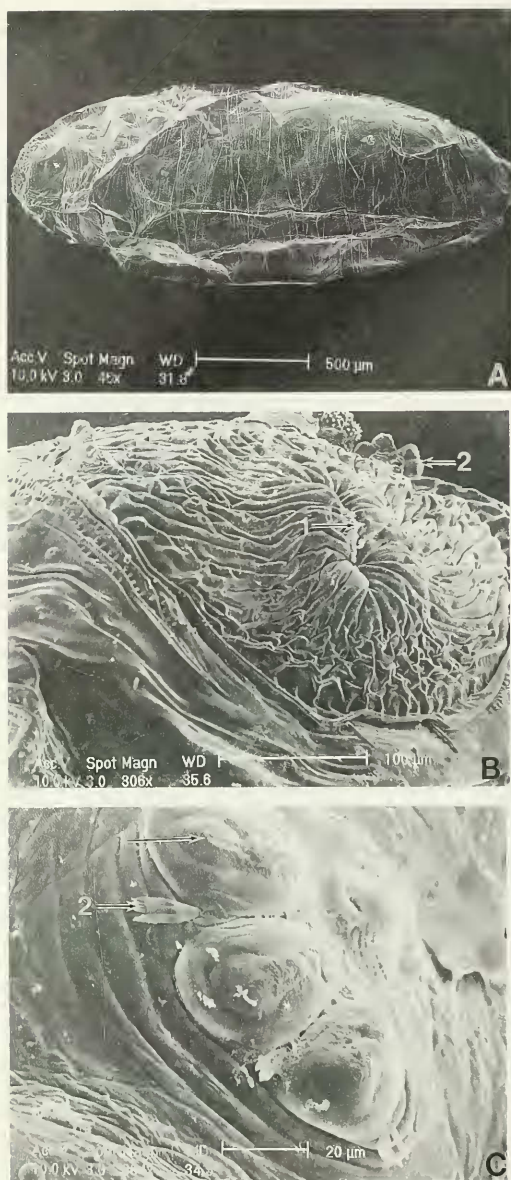


Fig. 4. Puparium of *Neaspilota signifera*: (A) habitus, anterior to left; (B) anterior end, 1— invagination scar, 2— anterior thoracic spiracle; (C) caudal segment, 1— rima, 2— interspiracular process.

smoothly rounded at both ends (Fig. 4A), minute acanthae circumscribe body segments anteriorly; anterior end bears the invagination scar (Fig. 4B-1) and anterior thoracic spiracles (Fig. 4B-2); caudal segment circumscribed by minute acanthae, two stalex sensilla, dorsad and ventrad of

posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 4C-1), and four interspiracular processes, each with two to three branches (Fig. 4C-2); intermediate sensory complex consists of a medusoid sensillum and a stalex sensillum. Twenty-five puparia averaged  $2.43 \pm 0.03$  (range, 2.20–2.70) mm in length;  $1.10 \pm 0.02$  (range, 0.92–1.28) mm in width.

#### DISTRIBUTION AND HOSTS

The distribution of *N. signifera* as mapped by Foote et al. (1993) restricted this tephritid to Arizona, California, Oregon, and Washington in the western United States North of Mexico. The distribution of its main, probably sole, host plant, *H. pungens*, apparently does not extend far into Mexico (Shreve and Wiggins 1964, Hickman 1993), nor, perhaps, does *N. signifera*. Accordingly, Freidberg and Mathis (1986) listed only two collection records for *N. signifera* from northern Mexico, one from Baja California Norte, and one from Sonora.

*Hemizonia pungens* belongs to the subtribe Madiinae of the tribe Helenieae of the family Asteraceae (= Compositae) (Bremer 1994). I have not reared *N. signifera* from six other species of *Hemizonia* from California, involving a total of 11, 1-liter samples of mature flower heads. Freidberg and Mathis (1986) also listed *Lasthenia* (as *Baeria fremontii* (A. Gray) E. Greene as another host, apparently based on two separate series of specimens labelled “ex” or “on” this plant and collected over 5- and 18-day periods, respectively, from California. *Lasthenia fremontii* belongs to a different subtribe Baeriinae of the Helenieae. I have not reared *N. signifera*, nor any other species of *Neaspilota* (only *Trupanea* spp.), from 18 samples of mature flower heads from three species of *Lasthenia*, but not including *L. fremontii* (a northern California species, Hickman 1993). Furthermore, 11 of the 12 described species of *Neaspilota* in California for which hosts are now known



(Goeden 1989 and unpublished data) have hosts belonging solely to the tribe Astereae, with only *N. sp. prob. punctistigma* Benjamin or near, besides *N. signifera*, having been reared by me from flower heads of a host in the tribe Helenieae (subtribe Pectidinae). In addition, the generalist species, *N. viridescens*, has now been reared from 21 host species in the tribe Astereae and a single host in the Tribe Senecioneae (Goeden, 1989, Goeden and Headrick 1992, and unpublished data). Therefore, the above information suggests that the host record for *L. fremontii* in Freidberg and Mathis (1986) is suspect, possibly based on sweep records for adults, which are problematic predictors of reproductive hosts (Headrick and Goeden 1998), and that *N. signifera* is a true monophage on *H. pungens*.

#### BIOLOGY

**Egg.**—In 10, closed, preblossom, immature flower heads of *H. pungens*, 12 eggs were inserted pedicel-last, usually between the chaff and ovules, and perpendicular to the receptacle (Fig. 5A). No flower head contained any floret damaged by oviposition. The diameters of the receptacles of these 10 flower heads containing eggs averaged  $3.64 \pm 0.13$  (range, 2.42–4.56) mm, and these heads held an average of  $1.2 \pm 0.1$  (range, 1–2) eggs.

**Larva.**—Upon eclosion, the first instars usually tunneled into an ovule, or into a corolla before entering an ovule (Fig. 5B). One first instar was found feeding within each of 18, closed, preblossom flower heads, the receptacles of which averaged  $3.63 \pm 0.18$  (range, 2.0–5.13) mm in diameter. An average of only  $1.3 \pm 0.3$  (range, 0–3) ovules was damaged in these 18 heads, or based on  $93 \pm 4$  (range, 52–150) as the average number of ovules/achenes counted in 51 preblossom to postblossom flower heads, about 1.4% (range, 0–3.2%) of the ovules were damaged. No receptacles within these 18 infested flower heads were abraded or pitted by feeding of first instars.

Second instars continued feeding on ovules in preblossom flower heads or in soft achenes in open flower heads (Fig. 5C). All fed with their bodies horizontal to and their mouthparts directed towards the receptacles within a series of adjacent ovules/soft achenes, but always well above the receptacles. Receptacles of 23 flower heads containing second instars were not fed upon and averaged  $4.15 \pm 0.12$  (range, 3.13–5.15) mm in diameter. These flower heads contained an average of  $1.3 \pm 0.1$  (range, 1–3) second instars that had destroyed an average of  $6.7 \pm 0.9$  (range, 2–18) ovules/soft achenes, as calculated for the preceding instar, about 7% (range, 2–19%) of the average total of 93 ovules/soft achenes per flower head.

Third instars fed mainly on soft achenes in the centers of open flower heads, or in one case, a postblossom flower head. Thirty-four flower heads that averaged  $4.09 \pm 0.14$  (range, 2.85–5.70) mm in diameter contained an average of  $1.3 \pm 0.14$  (range, 1–4) third instars. An average of  $25 \pm 2.4$  (range, 7–80) of the soft achenes therein were damaged, or about 27% (range, 8–86%) of the average total of 93 ovules/soft achenes per flower head. Third instars fed with their long axes oriented horizontal or perpendicular to, and mouthparts directed towards the receptacles (Fig. 5D). One-third of the third instars in the 34 infested heads examined pitted the receptacles, and thus supplemented their diet with sap that presumably collected in these depressions. Goeden and Headrick (1992, 1999) described and discussed this type of feeding by *N. viridescens* and *N. wilsoni*. However, unlike the third instars of these congeners, the third instar of *N. signifera* did not surround itself by a protective cell within which most individuals pupariated and overwintered. Instead, upon completing their feeding, the larvae of *N. signifera* simply oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated, as described for other florivorous tephritids that do not overwinter

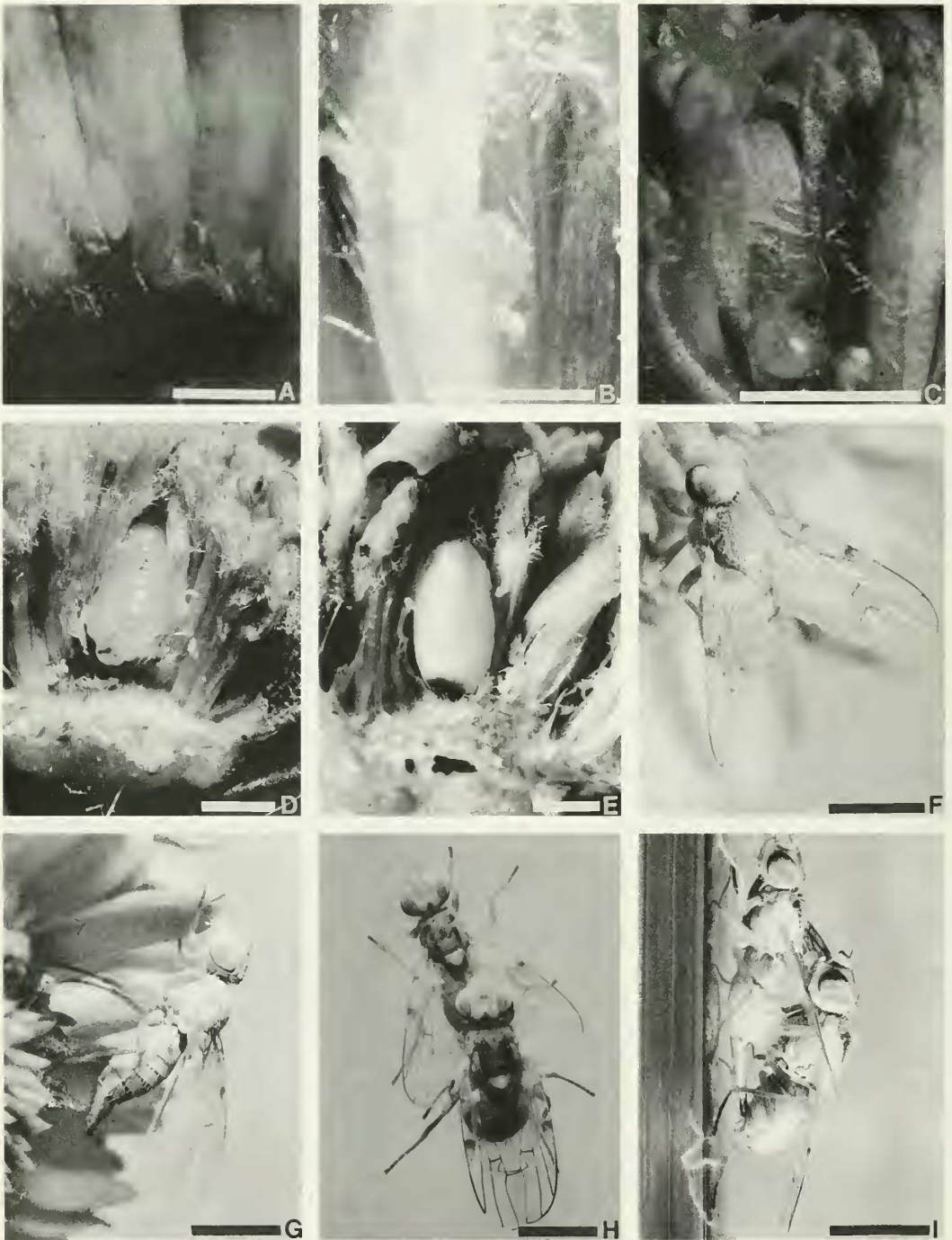


Fig. 5. Life stages of *Neaspilota signifera* in *Hemizonia pungens*: (A) egg laid between florets in preblossom flower head, (B) first instar tunneling into corolla, (C) second instar feeding on ovule, (D) third instar feeding on soft achenes in center of open flower head, (E) puparium in postblossom flower head, (F) male on open flower head, (G) female on open flower head, (H) mating pair, dorsal view; (I) mating pair, lateral view. Lines = 1 mm.

in flower heads, e.g., *Trupanea* spp. (Headrick and Goeden 1998).

**Pupa.**—The receptacles of 24 flower heads containing puparia (Fig. 5E) averaged  $4.51 \pm 0.11$  (range, 3.42–5.70) mm in diameter and bore an average total of  $21.2 \pm 2.0$  (range, 8–38) soft achenes, or calculated as above, 23% (range, 7–78%) that were damaged by larval feeding. The receptacles of seven (29%) of the 24 flower heads were pitted. These 24 heads contained an average of  $1.1 \pm 0.07$  (range, 1–2) puparia. All puparia of *N. signifera* were found in the center of the flower heads with their anterior ends facing away from the receptacles and their long axes perpendicular to the receptacles (Fig. 5E).

**Adult.**—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as six unmated males (Fig. 5F) averaged  $67 \pm 13$  (range, 40–88) days, and five virgin females (Fig. 5G) averaged  $129 \pm 15$  (range, 91–179) days. Such lengthy lifespans are commensurate with the aggregative type of life cycle described below for this tephritid, and compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999).

The premating and mating behaviors of *N. signifera* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other non-frugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors observed with *N. signifera* were abdominal pleural distension, side-stepping, and swaying by males (Headrick and Goeden 1994), and wing hamation, sometimes combined with lofting 10–20°, by both sexes (Headrick and Goeden 1994). However, no trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). Eighteen matings (Fig. 5H, I) were observed that usually began during the early to late afternoon. These matings involved 12 different pairs of flies and lasted an average of 238 min, very

close to the average duration of 235 min. reported for *N. wilsoni* (Goeden and Headrick 1999), and similarly long to mating durations reported with *N. viridescens* (Goeden and Headrick 1992). A post-copulatory behavior reminiscent of the mate guarding observed with *Dioxya picciola* (Bigot) (Headrick et al. 1996) and *Euaresta stigmatica* Coquillett (Headrick et al. 1995) was observed repeatedly. Six males remained atop females after copulation for a few minutes to as long as 50 min, during which time females bent their ovipositors upward nearly 90° while extruding their aculei. Sometimes this behavior was followed by additional copulations by the same pair; other times, the males did not engage the extended aculei.

**Seasonal history.**—The life cycle of *N. signifera* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the long-lived adults are the principal overwintering stage. Come spring (March–April), surviving, overwintered adults aggregate on preblossom host plants for mating and oviposition. By early summer (June),  $F_1$  adults emerge from flower heads. A partial second generation is produced on late-flowering plants. Like other monophagous, nonfrugivorous tephritids in southern California, the adults probably pass the dry, hot summer and fall in riparian habitats, including mountain streams and meadows, then overwinter in riparian habitats at lower elevations (Headrick and Goeden 1994, 1998, Goeden and Teerink 1998a, b).

**Natural enemies.**—Four specimens of *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from puparia of *N. signifera* as solitary, larval-pupal endoparasitoids.

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