

LIFE HISTORY AND DESCRIPTIONS OF IMMATURE STAGES OF
NEASPILOTA VIRIDESCENS QUISENBERRY
(DIPTERA: TEPHRITIDAE) ON NATIVE ASTERACEAE IN
SOUTHERN CALIFORNIA

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Abstract.—*Neaspilota viridescens* Quisenberry is a multivoltine, oligophagous tephritid reproducing in flower heads of species of *Aster*, *Chrysopsis*, *Chrysothamnus*, *Erigeron*, *Gutierrezia*, *Haplopappus*, and *Machaeranthera* in the tribe Astereae and *Lepidospartum* in the tribe Senecioneae of the Asteraceae in California. The larvae feed mainly on the ovules and immature achenes as first and second instars; however, as third instars, they usually extend their feeding chambers into the receptacle and additionally feed on sap. The chamber walls of plant fragments become impregnated with excess sap and liquid feces that harden when dry to protect the overwintering larvae. *Neaspilota viridescens* mainly overwinters as a diapausing “prepuparium,” a non-feeding, mostly quiescent, fully grown third instar with its gnathocephalon retracted. The egg, first, second and third instar larvae, prepuparium, and puparium are described and figured. Premating and mating behavior is described, including the use of the asymmetrical foretarsi of the male. Nuptial gift formation and presentation by the male also is described as part of courtship behavior.

Key Words: Insecta, *Neaspilota viridescens*, nonfrugivorous Tephritidae, courtship behavior, mating behavior, immature stages, nuptial gift, host plants, Asteraceae

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from capitula of native California Asteraceae (= Compositae), and allowed Goeden (1989) to report on the host plants of this taxon in California. It also stimulated several life-history studies, among which this report on *N. viridescens* Quisenberry is the first completed for the genus from the western United States.

MATERIALS AND METHODS

This paper was based on study of selected subsamples of mature flower heads of Asteraceae infested by *N. viridescens* from among many samples collected annually

throughout California in the manner described by Goeden (1985, 1989). Adults studied were reared in glass-topped sleeve cages in the insectary of the Department of Entomology from bulk flower-head samples at 14-h photoperiod and $27 \pm 1^\circ\text{C}$. Additional adults and parasitoids were reared from larvae and puparia of *N. viridescens* dissected from flower heads and held separately in cotton-stoppered, glass, shell vials within humidity chambers in the laboratory at $23 \pm 2^\circ\text{C}$ and 76% R.H.

Adult longevity and oviposition were studied in 850-ml, clear-plastic cages fitted with screened lids for ventilation and basal water reservoirs in which absorbant cotton wicks and cut ends of bouquets of flower-



Fig. 1. Egg of *Neaspilota viridescens*. A. Habitus, aeropyle at left. B. Detail of aeropyle, arrow denotes aeropyle pore.

head bearing peduncles were emersed through a hole in each cage bottom. Honey striped on the underside of the lids provided food for the flies (Headrick and Goeden 1990b, Goeden and Headrick 1990, 1991a, b). Mating behavior was observed and photographed in 9-cm diam., clear-plastic Petri dishes used only once per pairing. Unlike Jenkins (1990), we provisioned these arenas with honey and water renewed daily and applied to a pad of absorbant cotton pressed flat onto the arena floor. Arenas were carried between home and laboratory for extended viewing at room temperatures under natural and artificial lighting during waking hours for 2 or 3 days.

Plant names used in this paper follow Munz (1974). The materials, methods, format, and nomenclature used to describe the

immature stages follow Headrick and Goeden (1990a, 1991) and Goeden and Headrick (1990, 1991a, b). Means \pm SE are used throughout this paper. Voucher specimens of reared adults of *N. viridescens* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae, and puparia in the research collection of immature Tephritidae of DHH.

RESULTS AND DISCUSSION

Taxonomy

Quisenberry (1949) first described *N. viridescens*. Freidberg and Mathis (1986) redescribed this species and illustrated important adult characters, including its dark-veined unpatterned wings, dark pterostigma, and asymmetrical male foretarsi. The useful key for *Neaspilota* that they also provided was based in large part on such wing characters, male foretarsi, setal color, and chaetotaxy. The immature stages of *N. viridescens* heretofore have been neither illustrated nor described.

Egg.—The egg (Figs. 1A, 8A) is smooth, shiny, white, elongate-ellipsoidal, sometimes flattened along one side, and rounded at the end opposite the peg-like, 0.02-mm pedicel. Fifteen eggs recovered from flower heads of *Aster spinosus* L. (Asteraceae) measured 0.57 ± 0.12 (range, 0.46–0.64) mm in length and 0.17 ± 0.12 (range, 0.14–0.18) mm in greatest width. These measurements were shorter and narrower on average than (and the ranges did not include) the length and width of the egg of *N. alba* (Loew) reported by Schwitzgebel and Wilbur (1943), who also described this egg as slightly curved and pointed at one end.

Scanning electron microscopy revealed an egg virtually free from distinguishing surface features (Fig. 1B). Even the pedicellar end, usually bearing symmetrical and well-defined aeroscopic pores in other non-frugivorous tephritids, e.g. *Tephritis baccharis* (Coquillett) (Goeden and Headrick 1991b, DHH unpublished data), was highly re-

duced and irregular (Fig. 1B). The egg body lacked polygonal reticulations, which are present even on the typically featureless eggs of frugivorous species, i.e. *Ceratitis captitata* (Wiedemann) (DHH unpublished data). Why this flower head-infesting species should have an egg with such highly reduced features is unclear. After processing for SEM, eggs of *N. viridescens* were observed to collapse more at the basal end opposite the pedicel (Fig. 1A), which suggested more structural strength to the chorion nearer the pedicel. This explanation would be consistent with other more structurally complex tephritid eggs, e.g. *Tephritis baccharis*, that have highly developed reticulation of the chorion near the pedicel, where these reticulations provide strength and protection to the end of the egg which is exposed after oviposition (Goeden and Headrick 1991b).

Larva.—The third instar larva provides the basis for our general description, and descriptions of the first and second instars are limited to observed differences. The third instar larva (Fig. 2A, B) is elongate and dorso-ventrally flattened with well-defined segmentation. The anterior end is bluntly rounded and the posterior end has a unique and characteristic shape (Fig. 2A). The caudal segment is upturned ca. 60° and distinctly flattened, such that the posterior spiracular plate is borne dorsally and the ventral portion of the segment juts posteriorad. In the fully grown larva, the integument of the last two or three posterior segments is hardened and often darkly discolored. This is a reliable character for distinguishing this species from species in other genera, e.g. *Trupanea*, that may sometimes share the same flower head.

The gnathocephalon is smooth anteriorly, though rugose pads surround the anterior sensory lobes and the perimeter of the mouth lumen (Fig. 2C). These lateral pads are rectangular, with their posterior margin dentate (Fig. 2D—1). The mouth hooks are tridentate and the median oral lobe is smooth ventrally (Fig. 2D—3). The ventral margin

of the median oral lobe in *N. viridescens* is attached to the floor of the mouth lumen, as illustrated in Belcari (1987) for the Italian species, *Acanthiophilus helianthi* (Rossi). The independent mobility, morphology, and use of this fleshy lobe located between the mouth hooks was first described by Headrick and Goeden (1990) for *Paracantha gentilis* Hering. No feeding larva of *N. viridescens* was examined to determine the comparative degree of movement of its attached median oral lobe. All non-frugivorous tephritid larvae described thus far have median oral lobes (Headrick and Goeden 1990a, 1991, Goeden and Headrick 1990a, 1991b, DHH, unpublished data). However, only the larva of *N. viridescens* among North American species of non-frugivorous tephritids is known to have the median oral lobe attached basally to its mouth lumen.

The dorsal sensory organ is not well defined in *N. viridescens*. There is a distinct flattened area that lies medial of the anterior sensory organs (Fig. 2E—1). This area had small pores associated with it that were irregular in number and placement among the six larvae examined. The dorsal sensory organ is typically very distinct and not a part of the anterior sensory lobe. This species also has two sensilla not observed before, a pair of small depressions with a small central papilla dorsad of the anterior sensory lobes (Fig. 2E—2); these sensilla are bilaterally symmetrical and were consistent in placement on both second instars and all six third instar larvae examined.

The anterior sensory lobe bears the terminal sensory organ, the lateral sensory organ, the pit sensory organ and a sensillum that lies dorsal to the lateral sensory organ (Fig. 2F—2). The last, uncommon sensillum was previously described in *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991a), but it is not a constant feature of the anterior sensory lobe among other tephritid species from southern California examined to date (DHH, unpublished data). This sensillum and the lateral sensory organ

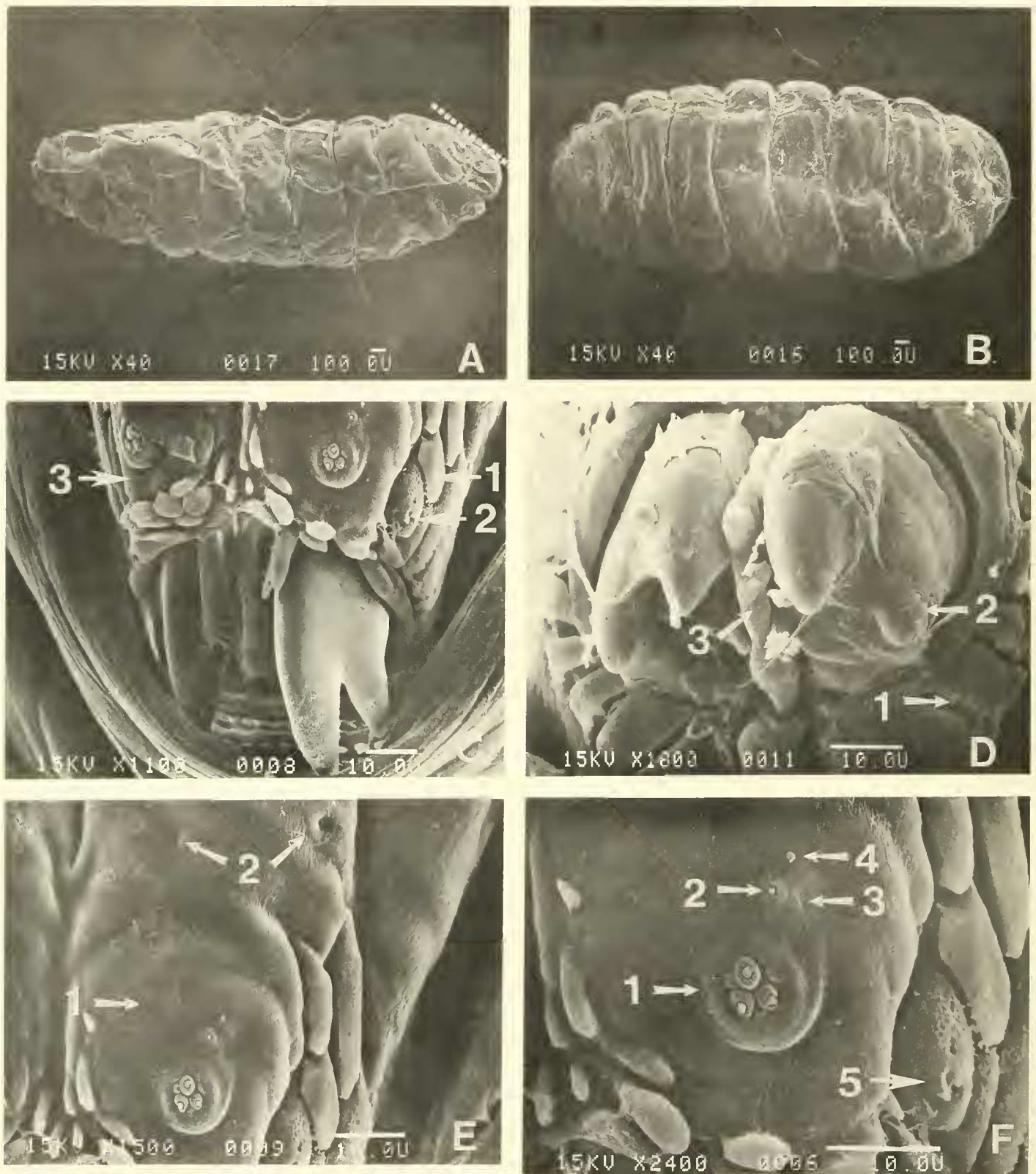


Fig. 2. Third instar larva. A. Habitus, lateral view. Dashed line marks the upturned caudal segment. B. Habitus, ventral view. C. Anterior view; 1—rugose pads, 2—lateral sensory lobe, 3—anterior sensory lobe. D. Anterior view; 1—rugose pads, 2—mouth hooks, 3—median oral lobe. E. Anterior sensory lobe; 1—probably dorsal sensory organ, 2—paired sensory depressions. F. Anterior sensory lobe, detail; 1—terminal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—dorsal sensillum, 5—stomal sense organ.

in *N. viridescens* are composed of a single papilla in a raised cuticular ring (Fig. 2F—2, 4). The terminal sensory organ is composed of three ringed structures and two sin-

gle papillae all surrounded by a raised cuticular ring (Fig. 2F—1). The lack of a well-defined dorsal sensory organ and the presence of supernumerary anterior sensilla are

noteworthy in *N. viridescens*, as the anterior sensory complex is usually highly conserved among tephritid species (Carroll and Wharton 1989, Headrick and Goeden 1990a, DHH, unpublished data). The stomal sense organs lie ventral of the anterior sensory lobes on the lateral aspect of the mouth lumen and are composed of several cone-shaped sensilla on a flattened lobe (Fig. 2F).

The prothorax is smooth, circumscribed by several flattened sensilla (Fig. 3A), and bears the anterior thoracic spiracles on its posterior margin (Fig. 3B). In the third instar larvae and puparia we examined ($n = 12$), the number of papillae varied from two to three among individuals and between sides of individuals. This supports the suggestion of Freidberg and Mathis (1986) that this character is useful to diagnose the larvae of the subgenera of *Neaspilota*, although the range in the number of papillae in *Neorellia* is slightly greater, two to four rather than three to four. Later instars of *Neaspilota* (s. str.) generally have six to eight papillae.

The surface features of the body segments of *N. viridescens* larvae also are unique compared with other tephritid larvae examined to date. The segments are demarcated by shallow longitudinal depressions which circumscribe the body. The rows of acanthae that are usually restricted to this intersegmental area in other species form a band around the middle of each segment in *N. viridescens*, and the intersegmental area is smooth (Fig. 3C). The acanthae of *N. viridescens* are mostly rounded and dome-shaped (Fig. 3D), with only a few of the more typical, posteriorly directed spines as described for *P. gentilis* (Headrick and Goeden 1990a).

On the lateral midline of each body segment between the prothorax and caudal segment is the lateral spiracular complex (Fig. 3E). In *N. viridescens* this complex is composed of a lateral spiracle, which is round and sometimes open, as first reported in *Trupanea californica* Malloch by Headrick

and Goeden (1991), and a single dome-shaped sensillum with a central pore. Each lateral spiracular complex lies near the anterior margin of the segment within the band of acanthae.

The caudal segment is dorsally flattened and in the fully grown larva is hardened and dark. It bears the posterior spiracular plates. The associated sensilla that are usually very pronounced and often quite complex in other tephritid species are only small and dome-shaped in *N. viridescens*, but they lie in positions typical for tephritid larvae (Phillips 1946, Headrick and Goeden 1990a). The posterior spiracular plates bear three, nearly contiguous, elongate-oval rimae, the interspiracular processes, and the ecdysial scar (Fig. 3F). The interspiracular processes are small and reduced to four or fewer branches. They are also inserted between the rimae closer to the midline of the body than has been described for other tephritid species (Phillips 1946, Carroll and Wharton 1989, Headrick and Goeden 1990a).

Second instar larva: The second instar larva is barrel-shaped, white, and about one-third the size of the fully grown third instar larva (Fig. 4A). The gnathocephalon is smooth, with rugose pads around the anterior sensory lobes and mouth lumen, whose posterior margins are dentate (Fig. 4B). The mouth hooks are tridentate, and the median oral lobe has no ventral papillae; it is also ventrally attached to the floor of the mouth lumen (Fig. 4C).

The anterior sensory lobes bear four sensory structures with the same placement as observed in the third instar larva (Fig. 4D). As reported for *P. gentilis* (Headrick and Goeden 1990a), there is considerable morphogenesis of structures between instars thus, the sensory organs on the anterior sensory lobe are not as well developed as in the third instar larva. Again, a distinct, flattened area that is not clearly separated from the anterior sensory lobe in the second instar may serve as the dorsal sensory organ (cf. *P. gentilis*, Headrick and Goeden 1990a).

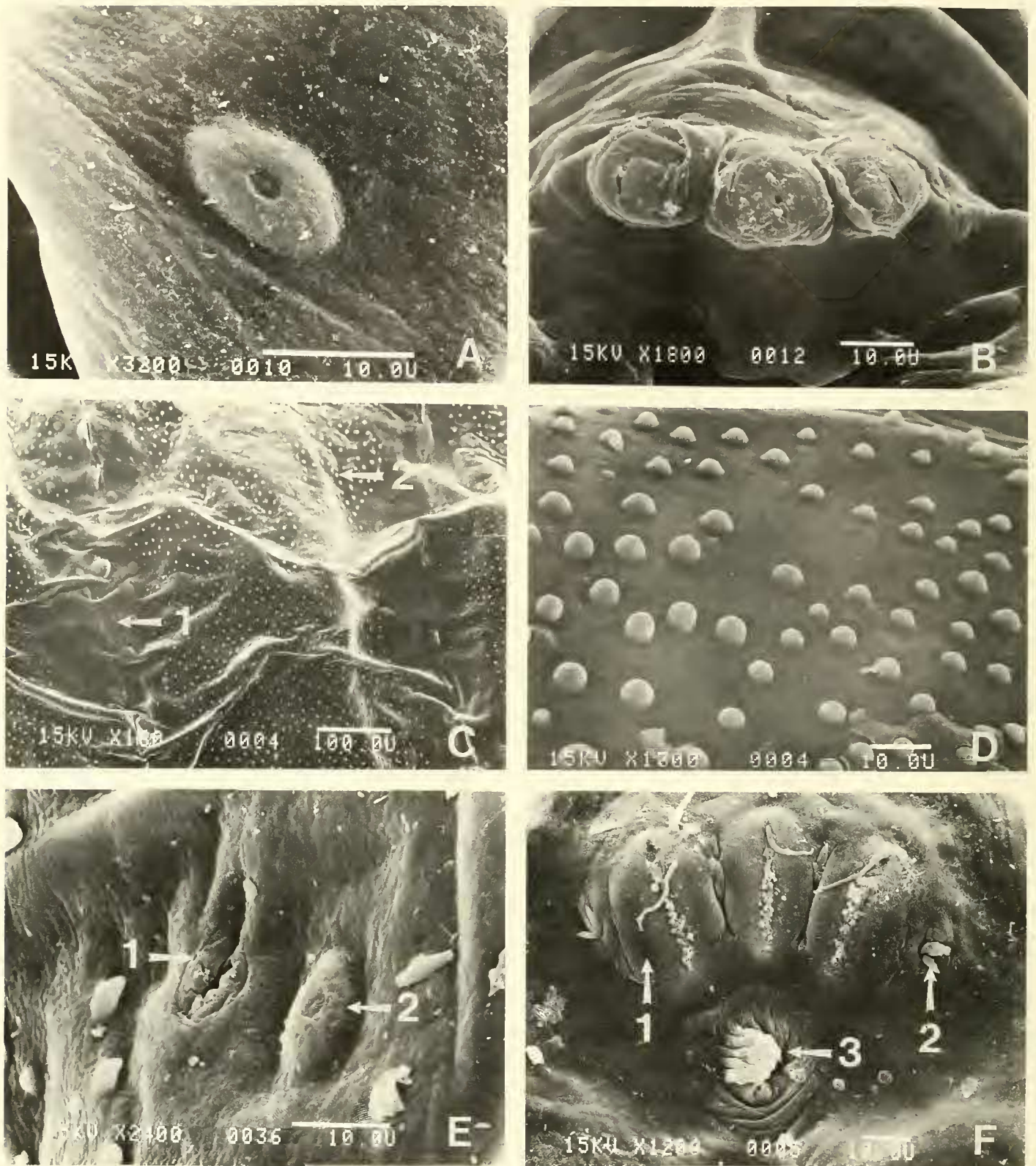


Fig. 3. Third instar larva. A. Prothoracic sensillum. B. Anterior thoracic spiracle. C. Intersegmental area; 1—intersegmental depressions, 2—acanthae. D. Acanthae, detail. E. Lateral spiracular complex, 1—lateral spiracle, 2—lateral sensillum. F. Posterior spiracular plate, 1—rima, 2—interspiracular process, 3—ecdysial scar.

The stomal sense organs are located ventral of the anterior sensory lobes and bear three cone-shaped sensory structures (Fig. 4E).

The posterior spiracular plate bears three elongate oval rimae, four interspiracular processes, and an ecdysial scar (Fig. 4F).

The interspiracular processes are two-branched at most, and again are short and located more toward the midline of the body.

First instar larva: The body of the first instar larva is translucent, parallel-sided, cylindrical, and bluntly rounded at both ends

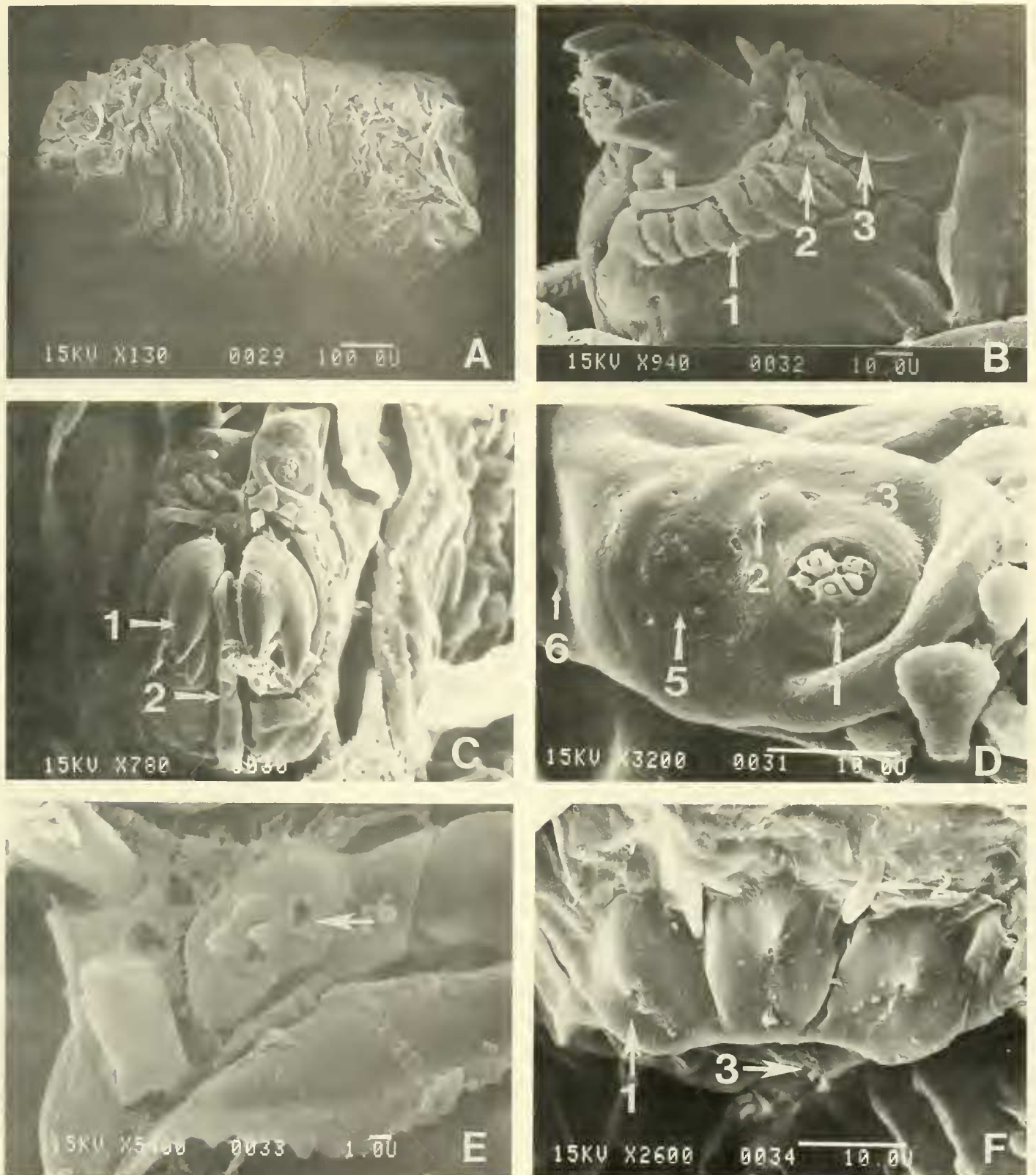


Fig. 4. Second instar larva. A. Habitus. B. Anterior end, left lateral view; 1—rugose pads, 2—lateral sensory lobe, 3—anterior sensory lobe. C. Anterior view; 1—mouth hooks, 2—median oral lobe. D. Anterior sensory lobe; 1—terminal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—dorsal sensillum, 5—probably dorsal sensory organ, 6—paired sensory depression. E. Stomal sense organ. F. Posterior spiracular plate; 1—rima, 2—interspiracular process. 3—ecdysial scar.

(Fig. 5A). The gnathocephalon has extremely reduced features composed of three lobes on either side of the midline. Dorsally to ventrally, they are a large lobe that may bear

the dorsal sensory organ, the anterior sensory lobe, and a lobe that develops in later instars into the integumental petals surrounding the mouth lumen. The anterior

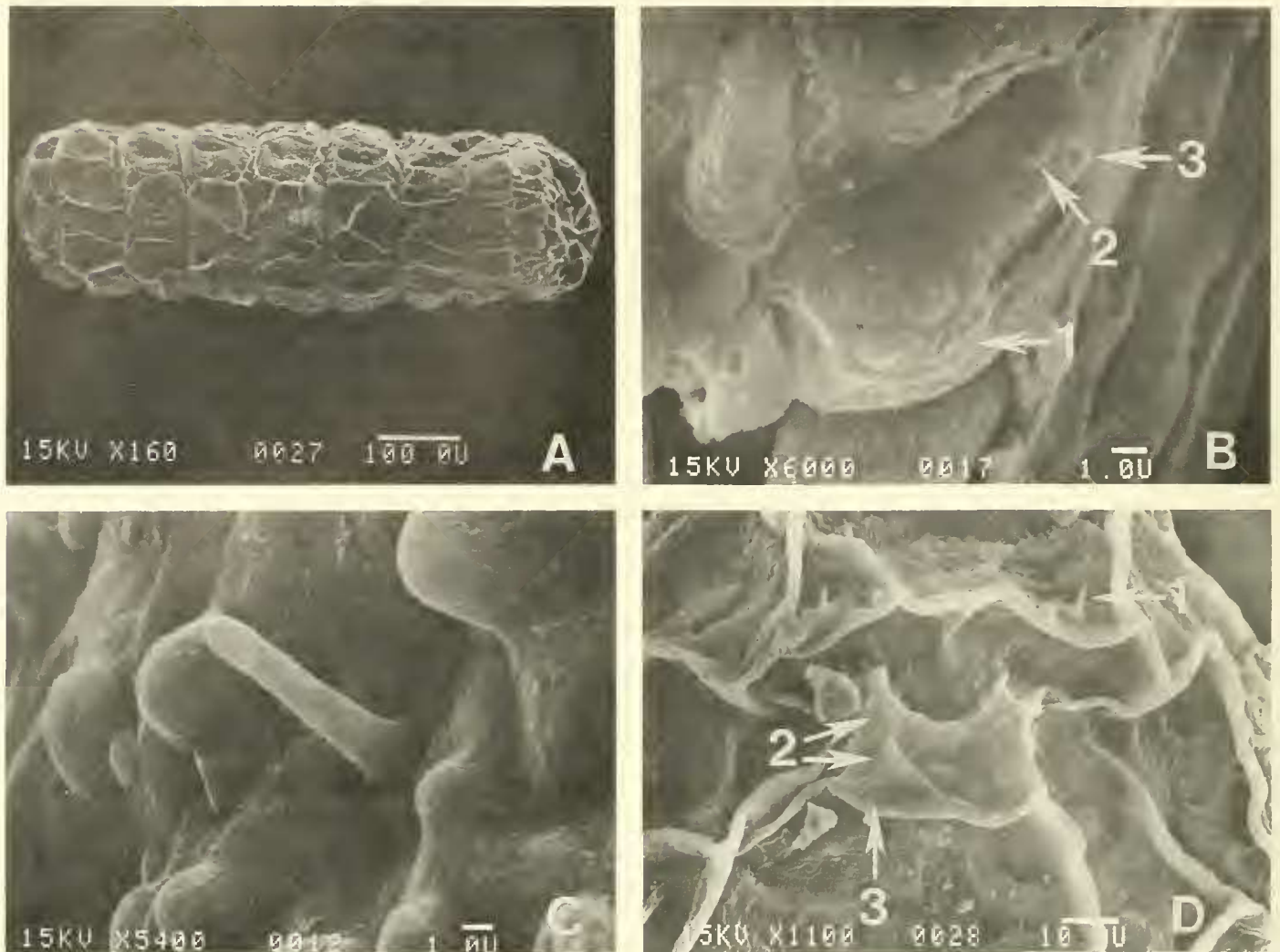


Fig. 5. First instar larva. A. Habitus. B. Anterior sensory lobe; 1—terminal sensory organ, 2—lateral sensory organ, 3—dorsal sensillum. C. Typical sensillum on lateral aspect of abdominal segment. D. Posterior spiracular plates; 1—caudal sensillum, 2—rima, 3—interspiracular process.

sensory lobe bears three distinguishable sensilla, but the pit sensory organ was not visible (Fig. 5B). The terminal sensory organ is composed of three ringed papillae and at least one of the two single papillae observed in later instars (Fig. 5B). Again, these structures are indistinct in the early instars and only reach full development in the third instar larva. The segments posterior to the gnathocephalon of the first instar bear several finger-like sensilla (Fig. 5C). These sensilla often change form in later instars to a more flattened dome-shaped sensillum, but retain their relative placement. The first instar larvae of *Paracantha gentilis* also have these same finger-like sensilla, which take on different forms in later instars (Headrick and Goeden 1990a). The caudal segment bears ten finger-like sensilla on its margins

(Fig. 5D). The posterior spiracular plate bears two small, barely perceptible spiracular slits, and four interspiracular processes, with up to four branches (Fig. 5D). The median ecdysial scar does not form until the first instar larva molts. The spiracular slits are easier to observe under a dissecting microscope as they are sclerotized and show up against the translucent white of the integument.

Prepuparium.—This “stage” in the phenology of *N. viridescens* will be described separately from the third instar larva and the puparium from which it differs morphologically and behaviorally, and occupies a significant amount of time in the life history. However, no molt separates it from the other stages; instead, this is a transitory step towards pupariation. The third instar,

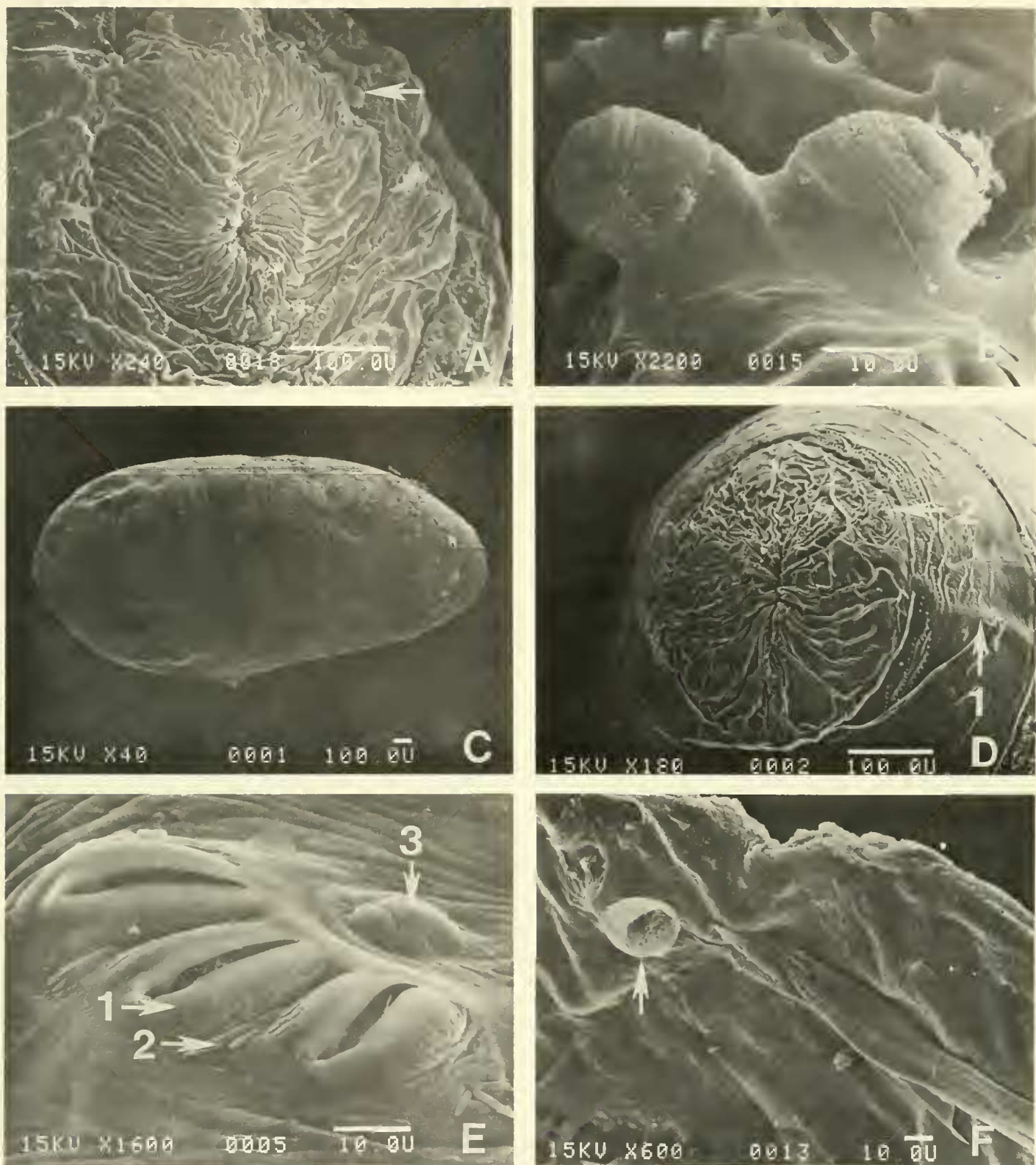


Fig. 6. A, B.—Prepuparium, C, F.—Puparium. A. Anterior view; arrow denotes anterior thoracic spiracles. B. Anterior thoracic spiracles, detail. C. Habitus. D. Anterior view; 1—fracture line, 2—anterior thoracic spiracles. E. Posterior spiracular plate; 1—rima, 2—interspiracular process, 3—ecdysial scar. F. Interior view of cephalic cap; arrow denotes open tracheal attachment to the anterior thoracic spiracle.

while feeding head down in a flower head, withdraws its gnathocephalon into the body almost to the margin of the prothorax, forming a heavily ridged cephalic cap (Fig. 6A). The larva does not go through the pro-

cess of tanning and hardening as it would to form a puparium, but remains soft, pliable, and “waxy” appearing. The integument is very wrinkled, and does not become smooth until pupariation, at which time

muscle contractions form the body into the typical barrel-shaped puparium. The anterior spiracles remain exposed (Fig. 6B), but their role in gas exchange is questionable. The posterior spiracles are possibly more important for gas exchange as they are held up and directed away from the receptacle in the air space at the top of the feeding chamber. Pupariation takes place only after the pre-puparium reverses itself in the flower head.

Puparium.—The puparium of *N. viridescens* (Fig. 6C) is elongate-oval, superficially smooth, rounded and dark brown to black at both ends, and off-white or unpigmented centrally. Thirty-seven puparia averaged 2.7 ± 0.3 (range, 2.4–3.2) mm in length and 1.2 ± 0.2 (range, 1.0–1.5) mm in width. The cephalic cap is heavily ridged with distinct fracture lines (Fig. 6D). The anterior spiracles lie nearer to the midline than in other tephritid species examined to date (Fig. 6D). The posterior end is superficially smooth. The spiracular slits are distinct and open (Fig. 6E); however, just before pupariation the prepuparium turns head upward, which makes the anterior spiracles the primary sites of air entering the puparium for the developing pupa. The taenidia maintain an open tracheal attachment to the anterior spiracles to permit gas exchange (Fig. 6F).

This is the first description of the immature stages of *N. viridescens*. Thus, it is worth noting several features of taxonomic interest that separate *N. viridescens* from species in other genera. The ventrally attached median oral lobe is the first reported for any of the 16 species in eight other genera examined thus far by DHH (unpublished data). The poorly defined dorsal sensory organ may be the most easily determined feature for this species, as the anterior sensory structures are visible under a dissecting microscope. Another difference is the band of acanthae that occurs only around the middle of each body segment, and not on the intersegmental lines. Lastly, there are the much reduced interspiracular processes,

which species of *Procecidochores* also possess (DHH and Teerink, unpublished data).

Adult: The asymmetrical foretarsi of the male are currently one of the main characters used to separate the genus *Neaspilota* from other genera in the Terelliinae (Freidberg and Mathis 1986). However, this rather unusual morphological feature has only been documented with SEM in *N. alba* (Freidberg and Mathis 1986). We provide here a detailed description of the male foretarsus of *N. viridescens*, and later provide behavioral evidence of its use.

The fifth tarsomere of the male is more elongate, but not wider than preceding tarsomeres (Fig. 7A). Each tarsomere is cylindrical, longitudinally wrinkled, and invested with several types of spines. One type is a straight, thin, acantha drawn into a fluted spiral (Fig. 7A—1, B). These acanthae are arranged in somewhat regular longitudinal rows in which each is directed distally. There are also larger setae which are much stouter, especially at their base. These setae are drawn out into a long, parallel-fluted sharply pointed structure (Fig. 7A—2).

The fifth tarsomere has a cluster of setae on its anterodistal margin that are short, stout, bluntly tapered, and fluted (Fig. 7A, B). The sockets are drawn out from the parallel ridges of the integument to form a pad of 11 sockets in three parallel rows. The anterior-most row has three setae, the middle row has four setae, and the posterior row has four setae. In comparison, the SEM micrographs published in Fig. 2 for *N. alba* in Freidberg and Mathis (1986: 13) show that the anterior row has six setae and the posterior row has four for a total of ten setae. The smaller, thin acanthae occur up to and project beyond the pad of stout setae in *N. viridescens*, and several of the long setae surround the pad. The setae on the pad project distad except for the two most proximal setae which project proximad.

On the ventral aspect of the fifth tarsomere is a subapical empodium (Fig. 7C—1, D). The empodium is a ventral projection

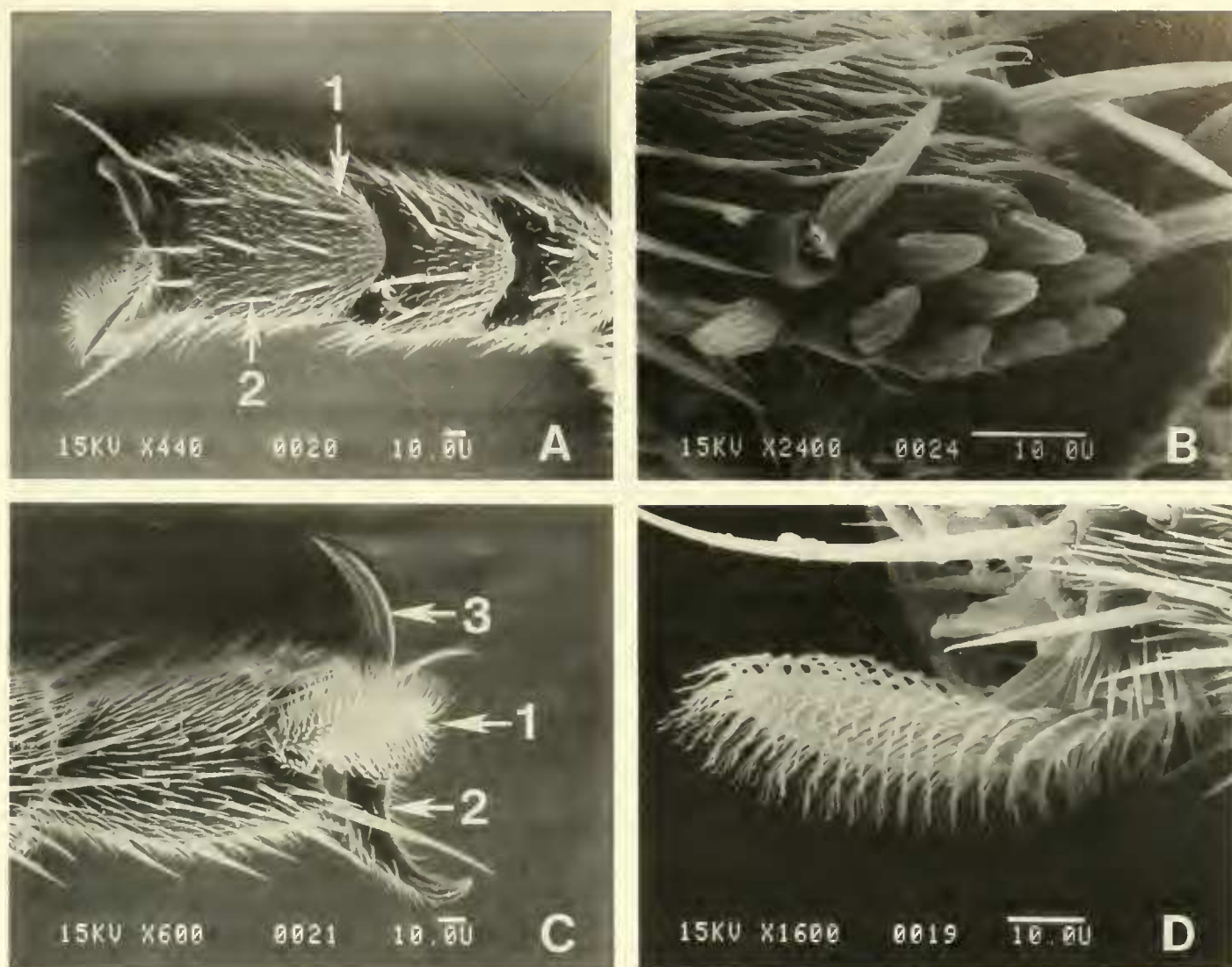


Fig. 7. Male foretarsus. A. Fifth tarsal segment, lateral view; 1—Socketless acantha, 2—Socketed spine. B. Anteriodistal pad. C. Fifth tarsomere, medial view; 1—empodium, 2—anterior claw, 3—posterior claw. D. Empodium, lateral view.

of the integument, the base of which is fluted, and surrounded by a brush of sharply pointed, flattened projections. The empodium extends from the fifth tarsomere foramen to form a foot-like pad invested with 20 rows of thinly tapered ventrally projecting spines. Each spine is bent ventrally once at about half its length, and again laterally near its apex.

The claws are asymmetrical both in size and orientation (Fig. 7A, C). Each claw is a fluted spiral. The anterior claw is the larger of the two; it is curved such that the apex of the claw is proximally projected. Each claw bears several small, sharp acanthae near its base, and is smooth distally. The posterior claw is somewhat flattened and tapers

to a ventrally projecting fluted point. The acanthae are the same size and shape as the smaller ones found on the tarsomeres.

DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) mapped collection records for *N. viridescens* and described its geographic distribution as "... Western North America from Alaska and the Yukon Territory southward through Washington and Montana to California and Colorado." Their collection records and sole rearing record for *Aster spinosus* L. represented 11 counties in California. Goeden (1989) reported rearing records from six additional California counties, from two additional species of *Aster*, and from 13 other

host species in the genera *Chrysothamnus*, *Erigeron*, *Gutierrezia*, *Haplopappus*, *Lepidospartum*, and *Machaeranthera*. All reported host genera belong to the tribe Astereae of the Asteraceae, except *Lepidospartum* in the tribe Senecioneae (Goeden 1989). We add the following new rearing records recently acquired by RDG: *Aster foliaceus* Lindley, 1 ♂, Indian Creek, E. side of White Mountain, Inyo National Forest, Esmeralda Co., Nevada, 26.vii.1989 (apparently the first published record for this fly from Nevada); *A. intricatus* (Gray) Blake, 1 ♂, 5-bridges Road N of Bishop and bridge over Owens River at 1207 m, Inyo Co., 9.x.1990; *Chrysopsis villosa* (Pursh) Nuttall, 1 ♂ and 1 ♀, Frenchman Lake, Plumas National Forest, Plumas Co., California, 22.viii.1989 (new host-genus, and -species records). *Chrysopsis* also belongs to the Astereae; thus, there is a predictable pattern to the host range of *N. viridescens*. As currently defined, *N. viridescens* is the most commonly encountered species with the widest host range in this genus in California (Freidberg and Mathis 1986, Goeden 1989).

BIOLOGY

Egg.—The eggs are laid in the immature flower heads (so-called flower “buds”), usually singly under natural conditions (Fig. 8A). As many as four eggs were recovered from single heads of *Aster spinosus* in insectary cages. Schwitzgebel and Wilbur (1943) reported that *N. alba* oviposited a single egg “against the inside of the involucre” (i.e. on the periphery of the receptacle) inside the flower heads of *Vernonia interior* Small. In *A. spinosus*, a few eggs of *N. viridescens* were inserted in the center of a head, but most were located to one side, not touching the involucre bracts, and with their long axes parallel to the florets. The eggs were laid alongside and sometimes touching the floret perianths, usually above and not touching the ovules or young achenes, but always located among the pappus hairs (Fig. 8A). The pedicels projected

upward away from the receptacle. The eggs were loose or only lightly glued to the pappus hairs or perianths. The incubation period under insectary conditions was 5–6 days.

Larva.—The newly hatched larva immediately tunnels into an immature ovule (Fig. 8B). The first and second instars then mined through a series of ovules and soft achenes (fertilized ovules), usually around the periphery and parallel to the receptacle surface in flower heads of *Chrysopsis villosa* and *Erigeron foliosus* Nuttall (Fig. 8C). In smaller flower heads, e.g. *Aster spinosus*, *Chrysothamnus teretifolius* (Durand and Hilgard) Hall, and *Haplopappus cooperi* (Gray) Hall (Fig. 8D, E, G), the ovules and soft achenes are almost entirely consumed, then feeding is extended into the basal parts of the tubular perianths and pappus. In larger heads of *E. foliosus*, the larva began feeding on the rest of the florets only after all or most of the soft achenes were mined (Fig. 8C).

Third instar larvae usually feed within elongate-saccoidal chambers with smooth-surfaced inner walls constructed of uneaten fragments of achenes, pappus hairs, and perianths. The third instar larva also usually taps into the conductive tissues that ramify the receptacle (Romstöck 1987). It chews a smoothly rounded, cuplike feeding depression within which the sap collects, upon which it also feeds (Fig. 8D). This type of feeding behavior has been reported for the third instar larvae of other flower head-infesting Tephritidae, e.g. *Paracantha gentilis* Hering (Headrick and Goeden 1990c) and *Tomoplagia cressoni* (Goeden and Headrick 1991a). In *P. gentilis*, receptacle scoring is a density moderated behavior among third instars, but in *N. viridescens*, it was the usual feeding behavior in most host species studied. For example, only one (0.2%) of 367 larvae in separate heads of *A. spinosus* did not score a receptacle; 17 (12%) of 142 larvae in separate heads of *H. cooperi*; and one (10%) of 10 larvae in separate heads of

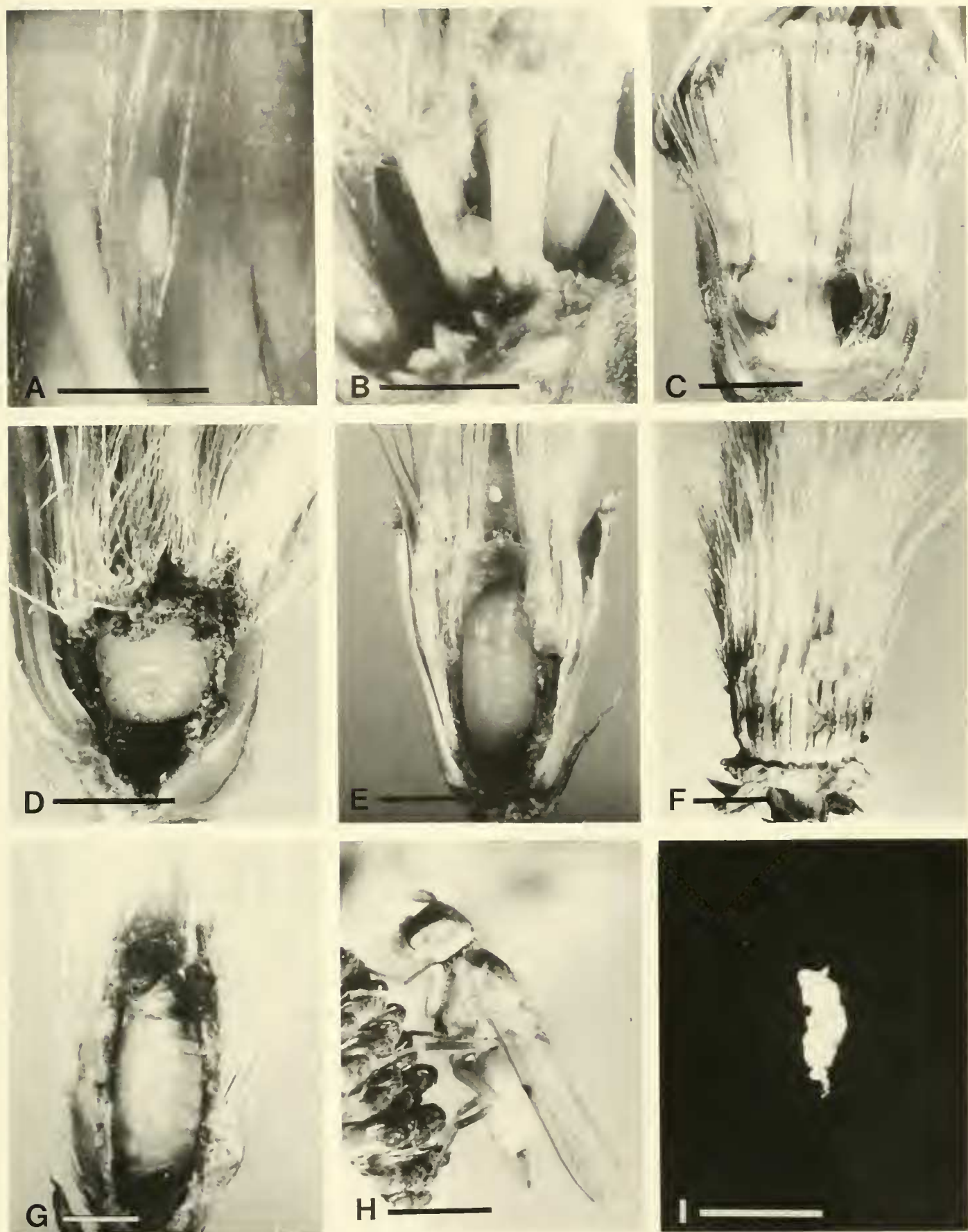


Fig. 8. Life stages of *N. viridescens*. A. Egg in flower head of *Aster spinosus*. B. First instar larva feeding on ovule of *A. spinosus*. C. Second instar larva feeding in head of *Erigeron foliosus*. D. Third instar larva and feeding depression in receptacle in head of *A. spinosus*. E. "Prepuparium" in flower head of *Haplopappus cooperi*. F. Flower head of *A. spinosus* containing overwinter larva (prepuparium). G. Empty puparium in head of *Chrysothamnus teretifolius*. H. Adult female at rest on head of *A. spinosus*. I. Nuptial gift. Lines = 1 mm.

Chrysopsis villosa. However, 23 (68%) of 34 larvae in separate heads of *Chrysothamnus nauseosus* did not score the receptacles and fed within and just above the achenes. The basal stumps of the achenes connected to the receptacles apparently also served as conduits for sap upon which the larvae fed. This latter mode of feeding is similar to that employed by at least one species each of *Neaspilota*, *Procecidochores*, and *Trupanea* (RDG, unpublished data), and by *Paracantha gentilis* at low densities (\leq three) in heads of *Cirsium* thistles (Headrick and Goeden 1990c).

Excess sap and liquid feces impregnate the walls of the feeding chambers of *N. viridescens*. These liquid wastes eventually dry to a yellow-brown (ochrous) solid after larval feeding ceases; this drying causes the wall to assume a brittle, protective hardness (Fig. 8E, G). Excised pappus hairs and other floret fragments were oriented transversely to the long axis of the flower head in the upper ends of the chamber walls, possibly reflecting the turning of the larva on its long axis as it fed. Chamber walls in heads of *Chrysothamnus teretifolius* appeared more fibrous than walls in heads of *H. cooperi*, reflecting the larger pappus of the achene of the former host (Fig. 8E, G).

The chambers were formed off-center in heads of *E. foliosus*, and occupied most of the interiors in smaller heads of *A. spinosus*, *Chrysothamnus teretifolius*, and *H. cooperi* (Fig. 8D, E, G). However, six of eight chambers were located centrally in separate heads of *Chrysopsis villosa*; the remaining two chambers were located towards one side of different heads.

Feeding chamber length was measured from the bottom of the feeding depression in the receptacle (Fig. 8D) outward to the circular, 0.6 ± 0.2 -mm diam. ($n = 31$) mouth of the chamber, where the sap- and feces-impregnated walls end (Fig. 8E, G). A ring of florets and pappus hairs forms the unimpregnated extension of the chamber walls out through which the emerging adult

passes (Fig. 8E, G). A loose plug of unimpregnated, excised floret apices and pappus hairs closes the chamber distally. In infested heads of *A. spinosus*, 22 feeding chambers averaged 4.3 ± 0.1 mm long by 1.2 ± 0.1 mm wide at their centers. The walls averaged 0.5 ± 0.1 mm wide at their thickest in the center of the chamber. This compared with mean chamber lengths of 4.7 ± 0.2 mm in 25 heads of *Chrysothamnus teretifolius* (Fig. 8G); of 3.4 ± 0.1 mm in seven heads of *Chrysopsis villosa*; and of 3.6 ± 0.5 mm in 58 heads of *H. cooperi* (Fig. 8E). Four larvae destroyed an average of 19.8 ± 2.8 achenes in heads of *A. spinosus*, whereas each of nine larvae destroyed 9.8 ± 0.3 achenes in heads of *Chrysothamnus teretifolius*. As reported by Benjamin (1934) for *N. achilleae* Johnson, *N. dolosa* Benjamin, and *N. punctistigma* Benjamin, larvae of *N. viridescens* usually feed singly in flower heads (Fig. 8C, D, E, G). However, one head of *Chrysopsis villosa* was infested by a third instar larva of *N. viridescens* and an intact puparium of *Procecidochores minuta* (Snow); another head was infested by a third instar larva of *N. viridescens* and two empty puparia of *P. minuta*. [This is a new host record for *P. minuta* (Wasbauer 1972).]

After the larva stops feeding in heads of *H. cooperi* and *Chrysopsis villosa*, it becomes quiescent and withdraws its gnathocephalon nearly up to its anterior spiracles (Fig. 6A). While still in this "prepupal stage," it reverses itself 180° such that its posterior segments lie closely cupped within the feeding depression, its anterior end facing outward (Fig. 8E). The duration of this prepupal stage was not determined, mainly because the larvae and puparia are hidden in flower heads; moreover, this period varies with the time of year and host plant involved. For example, in heads of spring-blooming hosts, cf. *H. cooperi* (Fig. 8E), and summer-blooming hosts, cf. *E. foliosus* and *Chrysopsis villosa*, it apparently is of relatively short duration, i.e. pupariation ensues once the prepupal larva has

rotated in its feeding chamber. However, in areas with temperate climates, i.e. mountains in southern California, and more northern latitudes in California and elsewhere, *N. viridescens* (and other species of *Neaspilota*; Goeden, Headrick, and Teerink, unpublished data) overwinters primarily as diapausing prepuparia in hard-walled chambers in heads of fall-blooming hosts, i.e. *A. spinosus*, *Lepidospartum squamatum*, and *Chrysothamnus teretifolius* (Fig. 8F). Nondiapausing individuals also emerge as adults from excised heads of fall-blooming hosts (see below).

Puparium.—The puparium is formed with its anterior end facing outward, away from the receptacle to facilitate emergence of the adult (Fig. 8E, G). The puparium snugly fits the feeding chamber, reaching to within 1–3 mm of the loosely plugged chamber mouth. The emerging adult pushes the plug outward with its ptilinum through the chamber mouth and exits the head via the 2–5-mm long, encircling band of florets, pappus hairs, and involucre bracts (Fig. 8E, G).

Puparia were dissected intact only with difficulty from hardened chambers in dried, overwintered heads of *A. spinosus*. Overwintering prepuparia-bearing heads also are distinguished by the whitish tufts of pappus and uneaten florets and achenes that surround the cell and remain attached to and project from the receptacle (Fig. 8F). This was in stark contrast to the bare receptacles from which the achenes of uninfested heads had long been shed.

Adult.—Females of *N. viridescens* newly emerged from flower heads of spring-, summer-, and fall-blooming hosts ($n = 3$ per season) all bore small, undeveloped ovaries and little fat body tissue. A preoviposition period during which the adults feed and gain sexual maturity is requisite, as with other flower head-infesting Tephritidae, e.g. *Neotephritis finalis* (Loew) (Goeden et al. 1987), *P. gentilis* (Headrick and Goeden 1990b), *Tomoplagia cressoni* (Goeden and Headrick 1991a), and several *Trupanea* spp. (Cav-

ender and Goeden 1982, Goeden 1987b, 1988, Headrick and Goeden 1991).

Males and females emerged together throughout the entire emergence period in a male-biased sex ratio based on analysis of the following samples of insectary-reared *Neaspilota viridescens* ($\chi^2 = 28.03$, $P < .005$, 4 df): 76 males and 71 females reared between 27.xi.1989 and 15.ii.1990 from mature flower heads of *Haplopappus palmeri* collected in N. San Jacinto Valley, Riverside Co., on 7 and 18.xi.1989. By 15.xii.1989, nine males and seven females had emerged; by 15.i.1990, 59 males and 51 females had emerged. Similarly, a total of 70 males and 89 females were reared from heads of *Aster spinosus* collected near Calipatria, Imperial Co., on 6.xii.1988, 11.i.1990, and 16.ii.1990. Again, seven males and five females emerged by 22.iii.1989; 46 males and 38 females by 7.iv.1989.

Other large samples of insectary-reared adults included: 17 males and 13 females from *Aster occidentalis* (Nuttall) Torrey and Gray, from Round Valley Reservoir, Plumas Nat. Forest, Plumas Co., 10.ix.1986; 58 males and 53 females from *Chrysothamnus teretifolius*, Mountain Springs, Imperial Co., 6.xi.1986; and 193 males and 138 females from *Haplopappus cooperi*, Walker Pass, Kern Co., 16.v.1989. Slightly male-biased sex ratios also were reported for *Trupanea conjuncta* (Adams) (Goeden 1987b) and *Procecidochares* sp. (Silverman and Goeden 1980).

Resting adults in isolated cagings exhibited no unique behavior. They held their wings over their dorsa, parallel to the substrate, and slightly parted ($\leq 30^\circ$). Their mouthparts pumped rhythmically, as they otherwise remained motionless in this resting posture for a few to many minutes, or even hours (Fig. 8H).

Interspersed among these varying periods of inactivity were spontaneous wing displays, sideways rocking movements, grooming, and droplet formation. Sponta-

neous wing displays involved episodes of rapid wing hamation at rates of two to three passes over the abdomen per s, in bursts of four to seven passes. Hamation consisted of holding the wings over the dorsum parallel to the substrate and moving them together from one side to the other through about 45°, as described for *T. californica* (Headrick and Goeden 1991). Sideways rocking, also noted with *T. californica*, and grooming behaviors were similar to that described for *Neotephritis fnalis* by Goeden et al. (1987). Droplet formation was an activity of resting, replete adults of both sexes of *Neaspilota viridescens*, as noted with other non-frugivorous species (Headrick and Goeden 1990b, 1991). Clear droplets suspended from the labellum were formed over periods of about 2 or 3 min. They grew in size to two-thirds that of the adult's head, only to be rapidly ingested in about 10 s, and another droplet started to form in about 20 s ($n = 6$). This behavior occurred with adults resting on both horizontal and vertical surfaces, so that the process appeared independent of gravity.

Freidberg and Mathis (1986) speculated that the modified male foretarsi (Fig. 7) of several species of *Neaspilota* were used to clasp the females during courtship or copulation. We describe here, for the first time for this genus, how *N. viridescens* males use their foretarsi during premating behavior based on nine pairings of virgin males and females lasting 1 to 3 days each.

After 30 h of acclimation, during the mid-afternoon of the second day of a pairing of a 15-day-old male and a 19-day-old female, premating behavior was observed for the first time. This activity initially involved, as noted by Headrick and Goeden (1991) for *T. californica*, an exaggeration of resting behaviors, i.e. frequent wing hamation and sideways rocking by both sexes as they faced each other at 3 to 5 mm distance within the confines of the arena. The male then proceeded to climb up and over the female, to turn and assume the typical mating posture

briefly, and then to dismount without copulating. This procedure was repeated during the next 10 h, with the male atop the female for 2 to 20 min before again dismounting after no copulation occurred. The female signaled her receptivity by bending her oviscape upward, rapidly hamating her wings, and even by approaching the male to reinitiate contact.

Gift presentation also was first noted with this pair of flies. The male deposited a clear oral droplet on the substrate which dried or jelled to form a low mound that was transparent and shiny along its margin, where it was thinnest, but translucent white and smoothly pustulate centrally. With other pairs of flies, this deposition sometimes was augmented between repeated dismountings and mountings to appear as a linear deposit (Fig. 8I). The male stood in front of or astride of this gift awaiting the female. Anal droplet formation by *N. viridescens* males also was observed during courtship; the droplets were dabbed onto the substrate and may have represented the contribution of an anal secretion to female attraction.

The receptive female attempted to feed on the gift by approaching the male with outstretched proboscis, lowered head, upraised oviscape, and rapid hamation of her wings. The male in turn also exhibited rapid wing hamation, but more indicative of his excitation, also displayed inflated abdominal pleura, like that reported for other non-frugivorous Tephritidae, e.g. *Trupanea bisetosa* (Coquillett) (Cavender and Goeden 1982), *Paracantha gentilis* (Headrick and Goeden 1990b), *Aciurina mexicana* (Aczél) (Jenkins 1990), *Tomoplagia cressoni* (Goeden and Headrick 1991a), and *Trupanea californica* (Headrick and Goeden 1991). It was while she stood still and fed on the offering that the male mounted her rapidly from the front, or occasionally, from the side.

Mating first was observed with a pair composed of a 34-day-old male and a 29-day-old female, and subsequently with three

pairs of similar ages. Premating behavior was as described above; however, the asymmetrical foretarsi of the male (Fig. 7) were used to grasp the wings of the female on the costal margin at the base of the costal vein, securing a hold that was difficult for the female to break. The hind legs were used to twist and hold the wings of the female down along her sides. The claws of the hind legs were hooked onto the costal vein distally and the legs pressed together such that the costal margins were brought together below her abdomen. The male then used his middle legs to further stimulate the female for copulation. The claws of his middle legs grasped the costal vein near the middle of her wings and his legs were synchronously and rapidly rubbed along her wings from anterior to posterior three to five times. The ovipositor apex was held upward against the epandrium by the lateral appression of his hind legs against her wings. The wing rubbing activity was maintained until the female exerted her ovipositor into the epandrium and coitus could be initiated. If after several minutes the female was unreceptive, the male would dismount and add to the nuptial gift. After allowing the female to feed, he would mount her again, twisting and rubbing the wings as before.

Once coitus began, the male loosened his grip on the wing bases of the female and assumed the posture common to many other mating Tephritidae, i.e. foretarsi grasping the female at the juncture of her thorax and abdomen, midtarsi grasping the base of the oviscapae, and hindtarsi on the substrate. The wings of both sexes are flattened, parallel to the substrate, and parted at about 20° in the male and 45° in the female (cf. Headrick and Goeden 1990b). Three matings by separate pairs occurred near dusk ($n = 3$) roughly between 6:30 to 7:30 PDT, and each was of longer duration, i.e. >4 h, >9 h, >3 h, than viewing opportunities permitted.

Three of 13 (23%) females began oviposition at ages 8 to 10 days when individually caged with one male each and an excised

branch of *Aster spinosus*. Each cage bore a fully open flower head, a preblossom immature head about 4 mm diam. on which the florets were as long as the phyllaries (apparently the preferred stage), and a smaller, immature, closed head ("bud"). The ovaries in these three females respectively contained 10 and 13, 13 and 15, and 15 and 23 full-size ova after each had laid a single, apparently unfertilized egg. Subsequently, fully open and postblossom, mature flower heads as well as those <4 mm in diam. received few or no eggs from the remaining 10 females. Females laid less than one egg per day on average. The oldest female to oviposit was at least 43 days old.

Adults of *N. viridescens* were long-lived in laboratory cagings. Eighteen females lived an average of 87 ± 10 (range, 42–163) days; 22 males averaged 86 ± 9 (range, 30–171) days.

Seasonal history.—*Neaspilota viridescens* is multivoltine, like some other oligophagous, nongallicolous Tephritidae in southern California, e.g. *Neotephritis finalis* (Goeden et al. 1987), *Trupanea bisetosa* (Cavender and Goeden 1982), and *T. californica* (Headrick and Goeden 1991). It reproduces in a succession of spring-, summer-, and fall-blooming Asteraceae, and primarily in the high- and low-elevation deserts and interior valleys. Unlike many other species of flower head-infesting Tephritidae in southern California, it overwinters as diapausing larvae (prepuparia), as noted above. The emergence of a few adults from samples of mature flower heads collected in late fall suggests that some individuals may overwinter as adults. These latter adults may even reproduce on yet undetected, winter-blooming, desert hosts, though 11 years of field surveys by RDG render this fairly unlikely (Goeden 1989). Some other species of *Neaspilota* currently under study also overwinter in dead flower heads as prepupal larvae in southern California; other species apparently overwinter as long-lived adults (Goeden and Teerink, unpublished

data). The same apparently holds true for southern California species of *Urophora* currently under study (Goeden 1987a, Goeden and Teerink, unpublished data).

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