PAN-PACIFIC ENTOMOLOGIST
July 1981, Vol. 57, No. 3, pp. 402–410

LIFE HISTORY OF THE GALL-FORMING MOTH, *CAROLELLA BEEVORANA* COMSTOCK, ON THE RAGWEED, *AMBROSIA DUMOSA* (GRAY) PAYNE, IN SOUTHERN CALIFORNIA (LEPIDOPTERA: COCHYLIDAE)

R. D. GOEDEN AND D. W. RICKER
Department of Entomology, University of California, Riverside 92521

Native, southern California ragweed insects include a diversity of noneconomic, little-studied, stenophagous species. We herein describe field, laboratory, and insectary studies on a heretofore little-known, gallicolous moth. Insectory conditions were 27 ± 1°C, 40–70% relative humidity, and a 12/12-hr (light/dark) photoperiod.

Taxonomy.—*Carolella beevorana* adults first were described and the female moth pictured by Comstock (1939b). The larva was described from *Ambrosia dumosa* by Comstock (1939b) as being similar to, but darker than that of *C. busckana* Comstock, which forms galls on the stems of the composite shrub, *Encelia californica* Nuttall (Comstock, 1939a). A brief comparison of the pupae of *C. beevorana* and *C. busckana* and photographs of the former pupa also were provided by Comstock (1939b).

Distribution and host plant.—*Carolella beevorana* apparently occurs in small demes discontinuously distributed throughout the range of its sole host plant, *A. dumosa,* in southeastern California (Goeden and Ricker, 1976) and, probably, adjacent parts of Arizona, Nevada, and Mexico. Comstock (1939b) described this moth from specimens collected at Ludlow and Yermo, San Bernardino County, in the high elevation Mojave Desert. Our study site was located in a Creosote Bush Scrub-type community (Munz, 1974) in the low elevation Sonoran Desert, ca. 3 km southeast of Niland, Imperial County. The only other record for *C. beevorana* from our faunistic survey of *A. dumosa* (Goeden and Ricker, 1976) involved a single plant bearing old, empty galls observed on the east shore of the Salton Sea, ca. 3 km south of the Riverside/Imperial County line.

Biology.—*Egg.*—The egg (Fig. 1A, B) is lustrous, translucent, ivory colored, sub-ovoid, but flattened and smooth-surfaced along one side where loosely glued to the plant surface. The chorion is transversely, irregularly, but smoothly ridged or wrinkled. This type of sculpturing also was reported for eggs of *Carolella sartana* (Hübner) by Peterson (1967). Ten, newly deposited, infertile eggs averaged (±S.D.) 0.72 ± 0.043 mm, 0.48 ± 0.036 mm, and 0.32 ± 0.036 mm in length, width, and greatest thickness, respectively.

In insectary cagings on potted *A. dumosa,* most eggs (ca. 80%) were

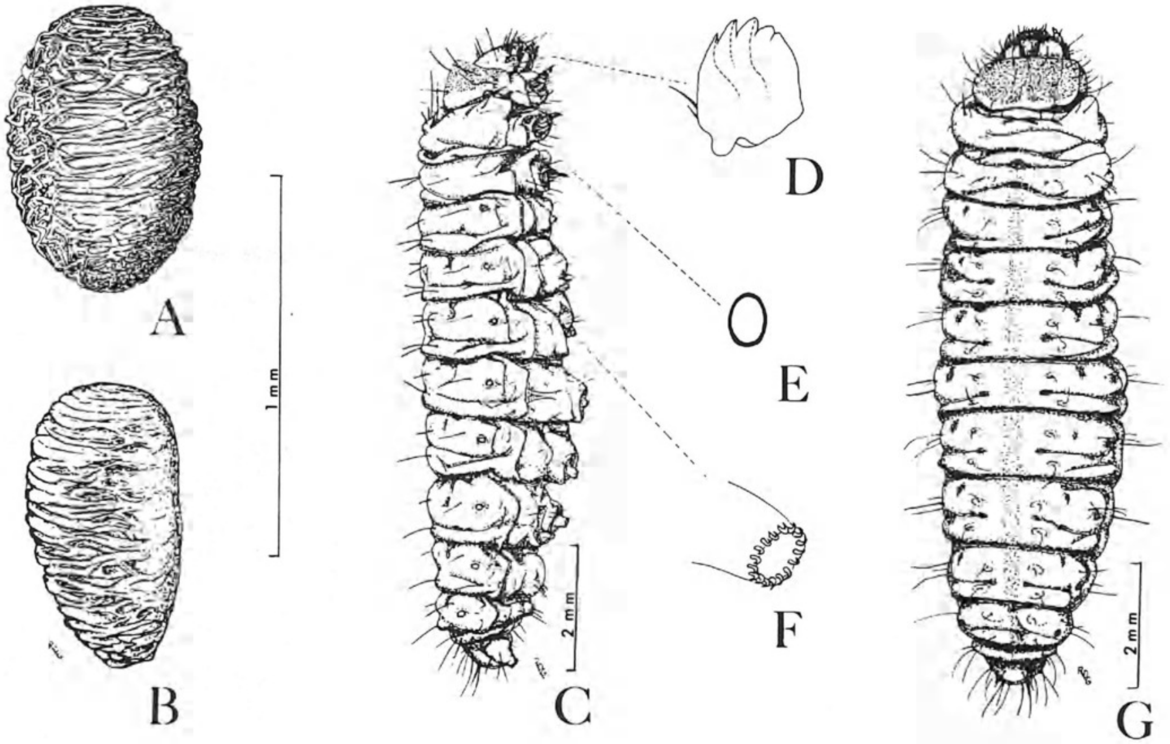

Fig. 1. Egg and mature larva of *Carolella beevorana*. A. egg, top view, B. egg, side view, C. larva, lateral view, D. right mandible, enlarged (semidiagrammatic), E. prothoracic spiracle, enlarged, F. proleg, ventral lateral view (semidiagrammatic), G. larva, dorsal view.

attached singly to the undersides of leaf laminae along the midribs and veins; the remainder, to leaf petioles, branches near axils, or cage surfaces. No eggs of *E. beevorana* were observed in nature, but such individual egg placement on foliage agrees with observed post-eclosion larval behavior described below, as well as with ovipositional behavior described for *C. sartana* by Peterson (1967).

Larva.—The first instar (Fig. 2A) differs markedly from the last instar (Figs. 1C, 1G, 2B) in gross appearance. The heart-shaped head capsule of the first instar is black, the prothoracic shield is prominent and dark brown, and the cylindrical body is a translucent, dirty pale yellow-green color principally derived from the chlorenchyma in its gut. The mature larva, in contrast, has a light reddish-brown head capsule, a much less sclerotized and prominent prothoracic shield, a dorsoventrally flattened body, and a soiled whitish-yellow color derived from the copious fatty tissue accumulated internally.

The number of larval instars was not determined with certainty because of their endophytic habit and the broad variation encountered in widths of head capsules sampled, which included those of starved larvae held for emergence in excised galls. Six instars were indicated.

The newly hatched larva crawled to and entered a herbaceous, photosyn-

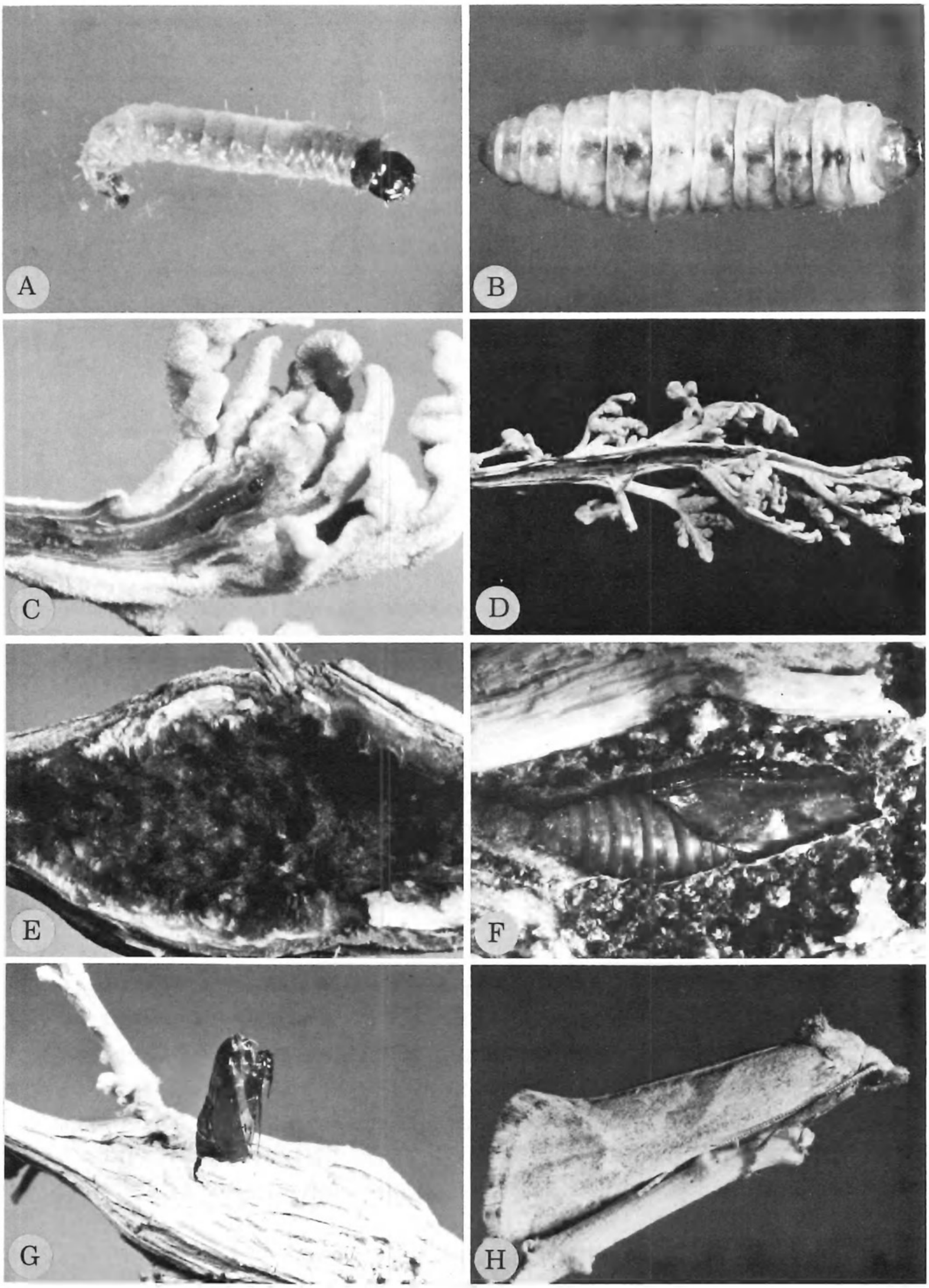

Fig. 2. Life stages of *Carolella beevorana*. A. first instar, 20×, B. mature larva, 5.3×, C. young larva tunneling near apical meristem, 7×, D. young gall in cross-section, 1.5×, E. inner, pitted surface of mature gall, 3×, F. pupa in cocoon, 5×, G. pupal exuvium projecting from exit hole in gall, 2.5×, H. adult at rest, 3.7×.

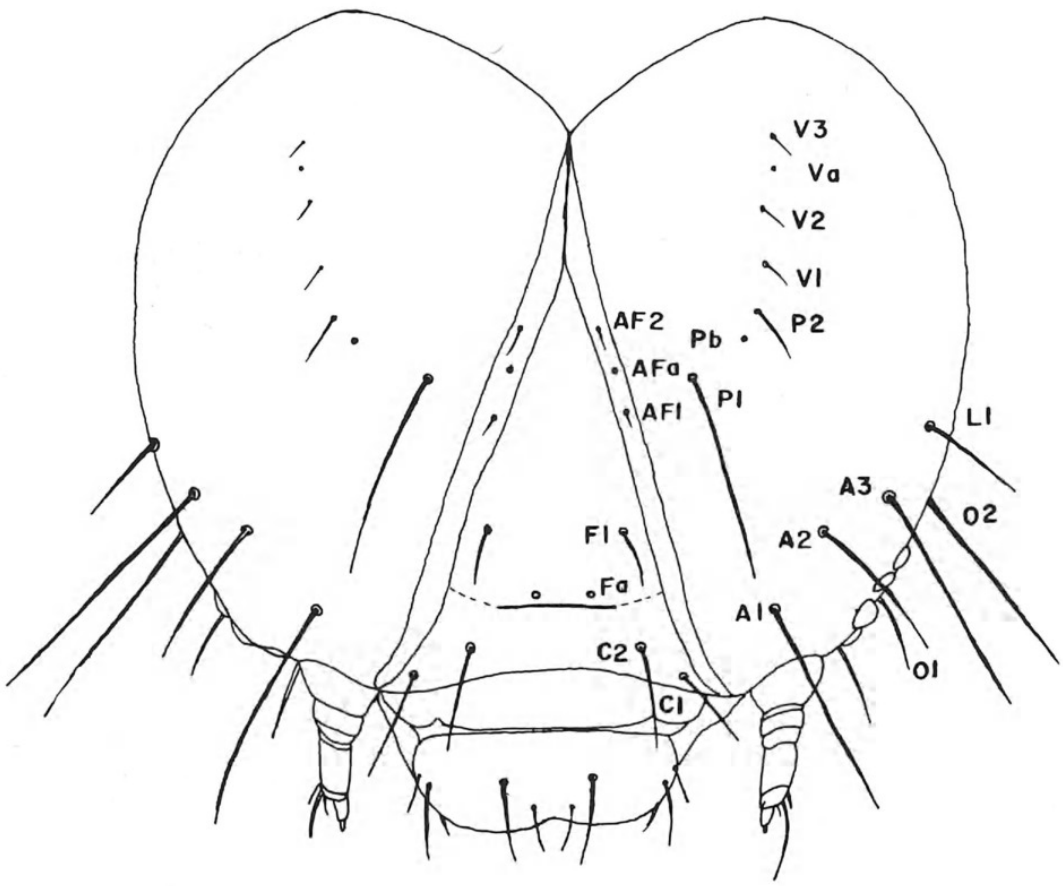

Fig. 3. Dorsal view of head of *Carolella beevorana* last instar (semidiagrammatic). Nomenclature and abbreviations after Hinton (1946) and format after Common (1970).

thetic, terminal branch basally, usually tunneling into the smooth epidermis just distal to a petiole base. A transverse, 2-lipped, entrance hole (0.4 to 0.8-mm wide), usually plugged with feces, marked this point of entry. The larva tunneled directly into the central pith, and then within the pith towards the branch apex (Fig. 2C). The open lumens of 10 young galls, initially comprised of excavated pith (Fig. 2D), began 10 ± 2.8 (range: 6–15) mm distal to the entrance holes. External recognition characters for these incipient galls were chlorotic and slightly swollen apical branches that bore fully expanded leaves along their entire lengths, reflecting slowed branch elongation resulting from reduced apical meristem activity. Although the infested terminal branches usually remained alive, the apical meristems occasionally were killed by the young larvae (Fig. 2C). This prematurely halted the elongation of the infested branch and led to the formation of subspherical galls. Of the first 100, fully formed galls containing larvae collected for laboratory measurement on March 9–17, 1976, at Niland, 21 were subspherical; the remainder, the more typical, fusiform shape (Figs. 2E, 2G).

The young larvae defended their galls against intruding, younger larvae of their own species. Combat usually resulted in the death of the younger

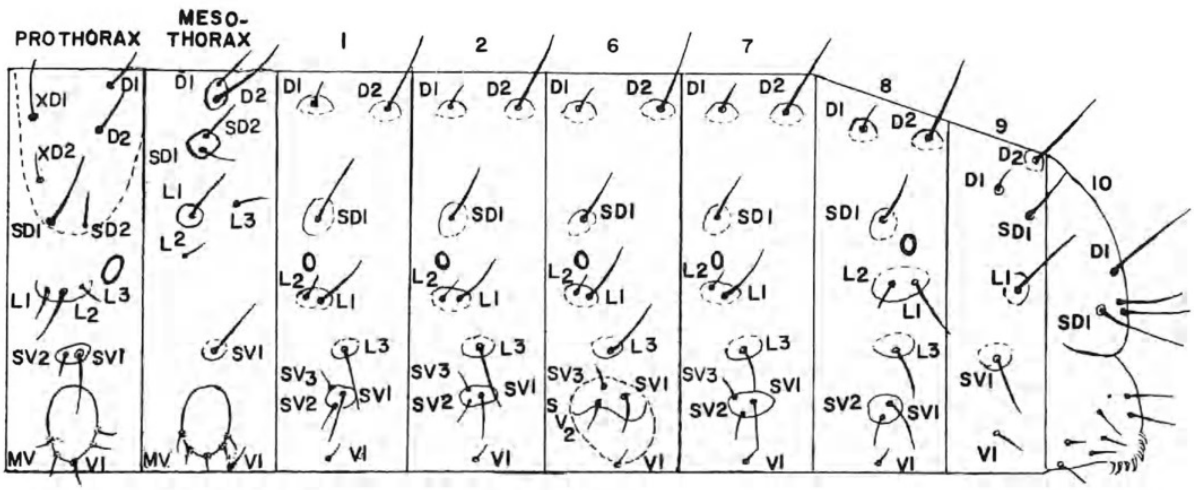

Fig. 4. Setal map of *Carolella beevorana* last instar. Nomenclature and abbreviations after Hinton (1946) and format after Common (1970).

invader and the ejection of its corpse, as with feces and exuviae, through one of up to 3, 0.3 to 0.5-mm diameter, frass ejection holes chewed in the gall walls. These holes usually were located in the basal half of the gall in expanded ray tissue. The larvae pick up and thrust fecal pellets through these ejection holes by means of their mouthparts. The lumens of galls that contained developing larvae were kept free of debris in this manner. Ejection holes in disuse were covered with a silken web sealed by impregnation with an oral secretion that dried hard and black. The covered holes provide translucent windows to the outside through which the larvae apparently perceive photoperiodic stimuli. Small, externally caused breaks in the gall walls were repaired in the same manner.

Only 1 larva developed per gall. The gall expanded in width mainly through the proliferation of parenchyma comprising the longitudinally directed rays, a wound reaction by the host plant to the constant erosion of the inner gall wall by the feeding larva. The inner surface was pitted with concave feeding scars (Fig. 2E) in the expanded rays located between longitudinally directed fibrous ribs. The larva left a silken trail as it moved about and fed within the gall, and completely covered the inner surface with a thin layer of silk as a measure of its activity. The gall thus provided a humid, protected, nutritionally fully supportive microhabitat in an otherwise harsh, arid environment.

The mature larva expanded the gall lumen to its ultimate dimensions and partly filled this space with its coarse feces. It then spun a fusiform, thin-walled, white, silken, centrally located cocoon surrounded by loose fecal pellets (Fig. 2F). The cocoon extended distally as a short, tubular "exit channel" (terminology of Comstock, 1939a) that ended in an exit hole cut laterally in the apical third of the gall wall. The exit hole remained covered by a thin remnant of bark. A few exit channels were directed proximally,

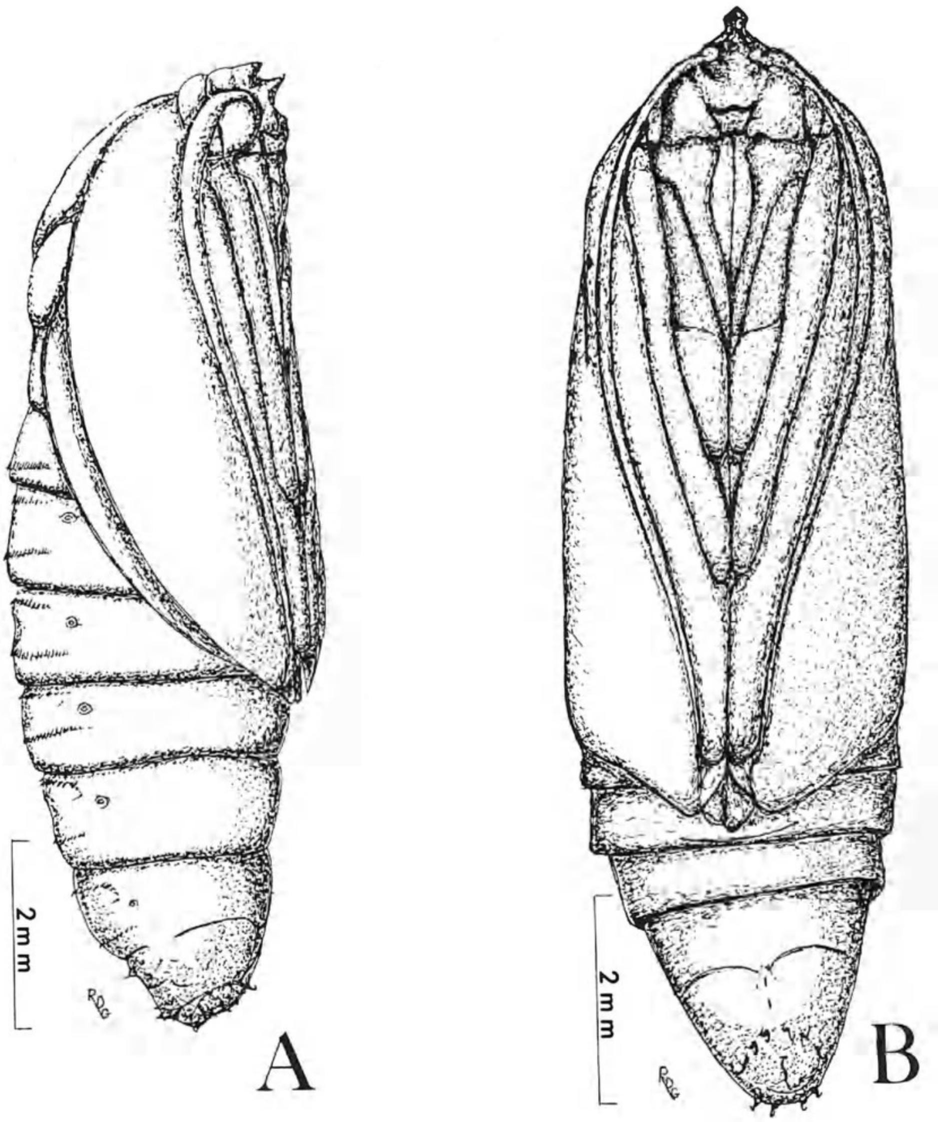

Fig. 5. Pupa of *Carolella beevorana*. A. lateral view, B. ventral view.

and the exit holes thus were located basally. *Carolella busckana* showed similar prepupal behavior (Comstock, 1939a).

The mature larva, which measured 9–12 mm in length, is illustrated in Figs. 1C–G, 2B, 3, and 4. The setal maps (Figs. 3 and 4) employ the nomenclature and abbreviations of Hinton (1946) and the format used to illustrate *Epiphyas* sp. (Lepidoptera: Tortricidae) in Common (1970, pp. 774 and 776).

Mean dimensions of 79 mature fusiform galls were: external length, 29.8 ± 6.29 (range: 18–45) mm; external maximum width, 9.4 ± 2.47 (range: 5–18) mm; and lumen length, 24.5 ± 6.08 (range: 11–38 mm). Sixteen of the 100 fully developed galls containing larvae, noted above, bore no live terminal or lateral branches, 29 bore live lateral branches only, 3 bore live terminal branches only, and 52 bore live terminal and lateral branches. Exit

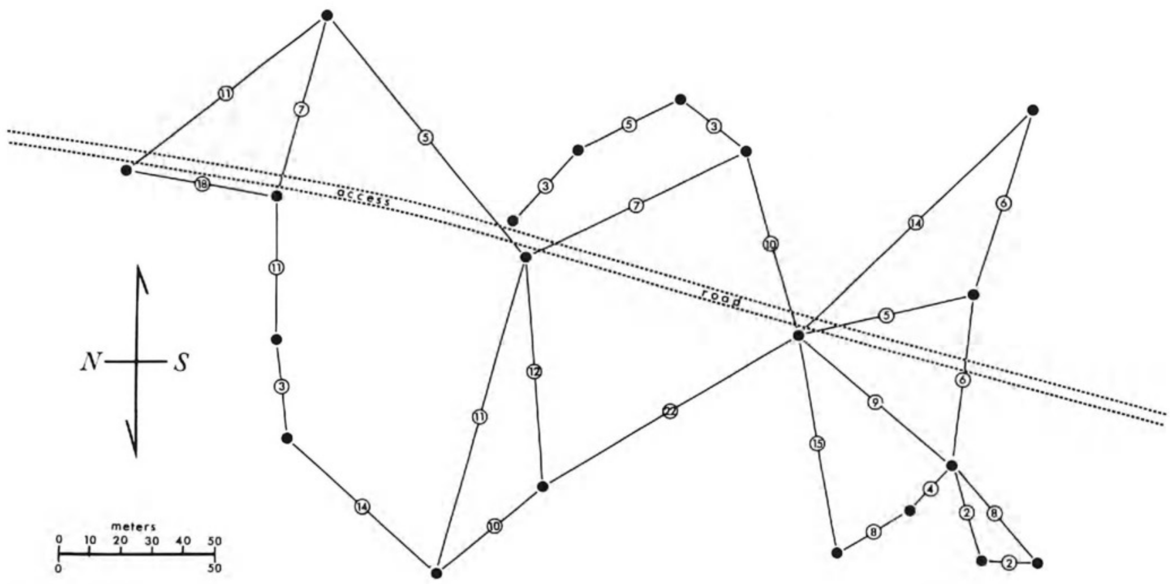

Fig. 6. Map of locations of 20 *Ambrosia dumosa* that bore galls of *Carolella beevorana* (black dots) at the Niland, California, study site in 1976. The numbers of gall-free *A. dumosa* located between selected gall-bearing plants are encircled.

channels in cross-section approximated the shape and diameter of the exit holes, 35 of which ranged from circular to elliptical and measured 3.3–3.8 mm across. The long axes of 24 galls measured on 2 plants in nature pointed to all quarters of the compass. Only 3 of 24 (12.5%) galls formed descending angles of 20° and 30° with the horizon; the remainder formed ascending angles that averaged ca. 14° and ranged from 0° to 80°.

Pupa.—Forty-four pupae averaged 9.2 ± 1.18 (range: 6.5–11.6) mm in length, apparently slightly larger than pupae of *C. busckana,* as well as darker and more cylindrical, according to Comstock (1939a, 1939b). The pupa is illustrated in Fig. 5.

Pupation occurred in the central cocoon (Fig. 2F), with the head directed towards the exit hole. The abdomen moved freely. The emerging pupa worked its way out of the cocoon and through the exit channel using the 2 rows of short, serrate, posteriorly-directed spines on the dorsum of each abdominal segment for traction (Fig. 5A). With the aid of the sclerotized, 2-pronged process on its vertex (Fig. 5), it broke through the bark window and projected from the exit hole, with its head, thorax, and upper abdomen free, anchored by the cremasteric hooklets at the tip of the abdomen (Fig. 5).

Adult.—Adults (Fig. 2H) were not observed in nature. The fragile pupal exuviae remained projecting for a few days from the exit holes as evidence of adult field emergence (Fig. 2G).

In the insectary, the preovipositional periods of 8 females caged on potted

A. dumosa averaged 4.4 ± 1.65 (range: 2.0–6.5) days. These females laid an average of 54 ± 29.9 (range: 7–106) eggs during an average ovipositional period of 5.5 ± 3.26 (range: 1.5–10.5) days and lived an average of 11.6 ± 1.6 (range: 9–13.5) days. A single female laid as many as 29 eggs and an average of ca. 10 eggs during a 12-hr photoperiod. Three non-ovipositing females and 5 males also lived ca. 12 days in the same cagings.

Host-plant relations.—The 20 plants attacked by *C. beevorana* represented only ca. 0.5% of the potential host individuals contained in the part of the study area mapped in Fig. 6. Five gall-bearing plants were located along an unpaved access road. No obvious differences were noted in the location, crown size, and vigor of these plants compared to uninfested *A. dumosa*.

When surveyed during March 9–16, 1976, the 20 galled plants averaged 62 ± 8.8 (range: 50–80) cm in height and ca. 134 ± 19.4 (range: 100–175) cm in diameter. They bore an average total of 80 ± 96.6 (range: 1–357) galls, of which an average of 7 ± 11 (range: 0–45) were nearly fully formed, intact, and contained mid-instar larvae. Of the 1603 galls excised from these 20 plants, 1463 (91.3%) were old and empty. Galls were distributed throughout the crowns, with 22%, 28%, 27%, and 23% found in the north, east, south, and west quadrants, respectively. More galls occurred in the lower (52%) and middle (41%) thirds of the crowns.

Seasonal history.—Only 11 of the 20 (55%) gall-bearing plants (Fig. 6) bore current generation galls, indicating that not all plants were re-attacked during successive years. *Carolella beevorana* usually is a univoltine species, with overlapping generations that principally result from a protracted, winter, emergence period. Comstock (1939b) reported the occurrence of mature galls along with immature galls, containing very young larvae. This, he suggested, indicated a 2-year period of development or a protracted emergence period. Both interpretations were correct. Field observations and insectary cagings of excised galls indicated that most adult emergence at Niland occurred in mid-December 1976 and 1977, following pupation in late November and early December that apparently coincided with the first winter rainfall, which also re-initiated host-plant growth. A smaller segment of this population pupated, emerged, and oviposited during January and February. A still smaller segment, i.e., 3 individuals in labelled galls, took 2 years to emerge as adults. Comstock (1939a) reported adult emergence during December 4–31 from excised galls collected at Ludlow and the trapping of 2 adults near Yermo on January 28.

Natural enemies.—Intraspecific, internecine combat accounted for some early-instar, larval mortality, as noted above. *Spilochalcis* sp., nr. *mariae* (Riley) and *Spilochalcis* sp., nr. *flavopicta* (Cresson) (Hymenoptera: Chalcididae) were reared as solitary, larval-pupal endoparasites from galls collected at Niland during November 1976–January 1977. Larvae and pupae of *C. beevorana* were preyed upon by larvae of *Cymatodera fuchsii* Schaeffer (Coleoptera: Cleridae).

Acknowledgments

Carolella beevorana was identified by Dr. D. C. Ferguson, Systematic Entomology Laboratory, IIBII, USDA, %U.S. National Museum of Natural History, Washington, D.C. Mr. R. J. LaSalle, Division of Biological Control, Department of Entomology, University of California, Riverside, identified the chalcidids.

Literature Cited

Common, I. F. B. 1970. Lepidoptera (moths and butterflies). Pp. 765–866 *In:* The Insects of Australia. Melbourne Univ. Press, 1029 pp.

Comstock, J. A. 1939a. The fauna and flora of the El Segundo Sand Dunes. 7. Two new phaloniid moths. Bull. S. California Acad. Sci., 38:112–119.

Comstock, J. A. 1939b. Four new California moths with notes on early stages. Bull. S. California Acad. Sci., 38:172–182.

Goeden, R. D., and D. W. Ricker. 1976. The phytophagous insect fauna of the ragweed, *Ambrosia dumosa,* in southern California. Environ. Entomol., 5:45–50.

Hinton, H. E. 1946. On the homology and nomenclature of the setae of Lepidoptera larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Royal Entomol. Soc. London, 97:1–37.

Munz, P. A. 1974. A Flora of Southern California. Univ. of California Press, Berkelely, Los Angeles, London, 1086 pp.

Peterson, A. 1967. Some eggs of moths from several families of Microlepidoptera. The Florida Entomol., 50:125–132.