

## Research Article

# Life History of the Camelthorn Gall Leafhopper, *Scenergates viridis* (Vilbaste) (Hemiptera, Cicadellidae)

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The world's only member of Hemiptera Auchenorrhyncha known to form true galls, the leafhopper *Scenergates viridis* (Vilbaste) (Cicadellidae), transforms leaves of camelthorn (*Alhagi maurorum* Medikus, Fabaceae) into pod-like chambers, up to 35 mm long, inside which individual leafhoppers develop, mate, and lay eggs. At the study site 40 km SE of Bukhara (Uzbekistan), two generations develop annually. First-instar nymphs cause young leaves to fold along the midrib. The subsequent development takes place inside the tightly closed growing gall, plugged at both ends with a mixture of leafhopper excrement, brochosomes, and crushed exuviae. These plugs act as mechanical barriers and sticky traps for intruders. The inner surface of the gall, lined with brochosomes and wax platelets, is hydrophobic. Adult males emerge from their galls and squeeze into female galls. Fertilized females insert an average of 146 eggs under the gall's inner epidermis and remain inside, possibly protecting the brood, until they die. The walls of the galls containing eggs are approximately three times thicker than regular leaves. The galls are subject to predation by Gelechiidae caterpillars; the eggs of the leafhopper are parasitized by two species of Trichogrammatidae and one Mymaridae (Hymenoptera), and its larvae by one species of Pipunculidae (Diptera).

## 1. Introduction

**1.1. Background.** Gall formation is arguably the most sophisticated strategy of plant parasitism. Among sap-sucking insects of the order Hemiptera, it is found mostly in the suborder Sternorrhyncha, particularly among aphids [1], jumping plant lice [2], and scale insects [3], and is rare among Heteroptera [4, 5]. Although malformations of host plants caused by feeding of some Auchenorrhyncha have also been observed [6, 7], so far, only one of the 42,000+ [8] known species of that suborder was found to induce true galls, which provide the parasite with food and shelter. Over a half century ago Ivan Mitjaev discovered that the leafhopper *Scenergates viridis* (Vilbaste) (Cicadellidae) develops inside closed pod-like leaf galls on camelthorn (*Alhagi*, Fabaceae) (Figures 1(a)–1(d)). His brief but highly informative report, two pages in Russian with a single sketch drawing [9], has remained mostly forgotten.

**1.2. *Scenergates viridis*: Taxonomy, Distribution, and Previous Research on the Biology.** The camelthorn gall leafhopper is the sole member of the genus *Scenergates* Emeljanov within the subfamily Deltocephalinae, comprising over 6,200 [10] phloem-feeding leafhopper species which inhabit virtually every terrestrial habitat and include some economically important and therefore better studied vectors of plant pathogens. All the known species except one are free-living; both nymphs and adults are capable of jumping, and the majority is capable of flight.

*S. viridis* was described almost simultaneously but independently by two authors, who even used the same species epithet, referring to the greenish color, in the Latin names they devised. Vilbaste [11] described it based on two males and several females from Golodnaya Steppe, Uzbekistan, and placed it in the newly created monotypic genus *Platyettix*. Emeljanov [12] described it based on ten males and nine females collected in Khiva, Uzbekistan, and the unknown

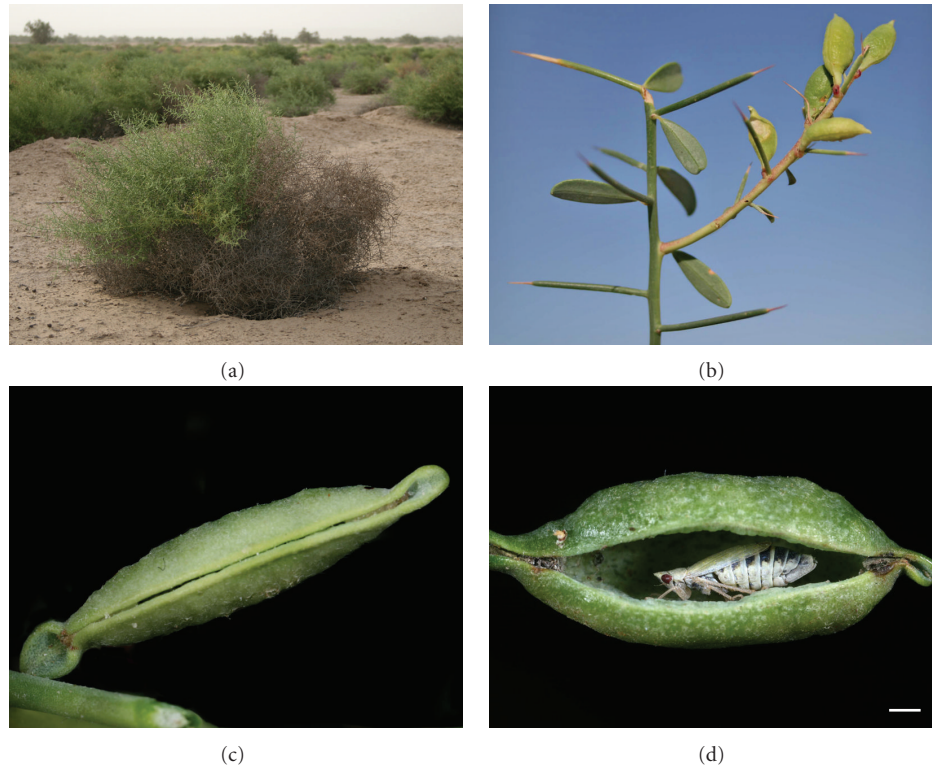


FIGURE 1: (a) Camelthorn (*Alhagi maurorum*) on the territory of the Ecocenter “Dzheiran” in Uzbekistan; note fresh green growth on the left and dead branches from the previous year on the right side of the shrub. (b) A camelthorn branch with thorns, ungalled leaves, and galls of *Scenergates viridis*. (c) An intact gall of *Scenergates viridis*. (d) An artificially opened gall with a female of *Scenergates viridis* inside. Scale bar: 1 mm (d).

locality “Nuriobay,” and placed it in the new monotypic genus *Papyrina*. The priority name *Platyettix* turned out to be preoccupied and was later replaced by the name *Scenergates* [13].

Mitjaev [9] observed *S. viridis* near the village of Baltakul’ in southern Kazakhstan. He reported that young nymphs fed on the adaxial surfaces of *Alhagi* leaves, causing their folding along the midrib into pod-like galls with individual leafhoppers developing inside, and that the exuviae were crushed and pressed together with dried leafhopper excrement, the latter forming white masses at both ends of the gall chamber. He also observed adult males on the outside of female galls, apparently waiting for copulation. Some additional data on the species were included by Dubovskii and Sulaimanov in their check-list of Auchenorrhyncha of the so-called Karshi Steppe, a semidesert plain approximately centered on the town of Karshi in southern Uzbekistan [14]. Of the 100 galls examined by the authors, 78 contained immatures or adults and also, remarkably, some eggs of *S. viridis*; 15 galls contained puparia of unidentified dipteran parasitoids, and seven contained lepidopteran larvae. Dubovskii and Sulaimanov [14] summarized the available records of this leafhopper, known mostly from Uzbekistan and a few localities in southern Kazakhstan and eastern Turkmenistan (Figure 2).

**1.3. Host Plant.** The genus *Alhagi* (Fabaceae) includes perennial shrubs with prickly thorns formed by rudimentary

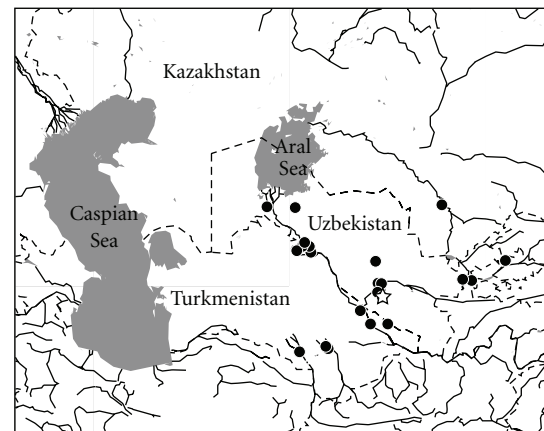


FIGURE 2: The distribution of *Scenergates viridis* based on records summarized by Dubovskii and Sulaimanov [15]. The star shows the location of the Ecocenter “Dzheiran.”

lateral shoots (Figures 1(a) and 1(b)), endemic to arid areas of the Old World and invasive in the western United States. The shrubs are usually less than one meter high, but their roots can reach depths exceeding 15 meters below the ground surface, allowing the plant to stay green and vigorous throughout the summer drought. Camelthorn propagates mostly as clones connected by long underground stolons. In Uzbekistan, the aboveground part of the shrub dies off

by late November except for a few basal centimeters of the main stem; these bear resting buds that produce new shoots in late March-early April [15]. According to Yakovlev [16], the five species of *Alhagi* previously recognized within the territory of the former Soviet Union belong to the same variable species, *Alhagi maurorum* Medikus, which occurs from North Africa and the Mediterranean throughout the Middle East to western China and northern India (see also [17]).

**1.4. Goals and Scope of the Study.** The observations of Mitjaev [9] and Dubovskii and Sulaimanov [14] have not completely elucidated the unique biology of the camelthorn gall leafhopper. Where mating takes place, how the eggs are laid, how the offspring leave the galls, how many generations develop annually, and at which stage the leafhopper overwinters all remain unknown. Therefore, the first goal of our field work in Uzbekistan was the elucidation of the complete life cycle of the leafhopper. The second goal was to find out how typical leafhopper traits are modified in this species in connection with its galling life style. In particular, disposal of dangerous sticky liquid waste is a challenge for phloem-feeding gallers [18]. In order to avoid entrapment in their liquid waste, all free-living Auchenorrhyncha forcefully eject droplets of liquid excrement; leafhoppers are additionally protected by a hydrophobic coat of brochosomes (reviewed in [19]). Therefore, among other traits, we wanted to find out how *S. viridis* maintains a safe environment inside the galls.

## 2. Study Site and Timing

The research was conducted at the Ecocenter “Dzheiran” (39.579°N, 64.723°E) near the town of Kagan in Bukhara Province, Uzbekistan, during two visits, September 4–13, 2010, and August 3–17, 2011. Additionally, at our request, 10 overwintering galls were collected at the same locality by Anastasia Shilina on December 18, 2010.

The site is located in the southwestern reaches of the Kyzylkum desert (Figure 2) and falls within the area studied by Dubovskii and Sulaimanov [14]. It is characterized by a strongly continental, hot, and arid climate with a mean annual precipitation of 110 mm and rains occurring from mid-October to mid-May, and mean January and July temperatures of  $-1^{\circ}\text{C}$  and  $+31^{\circ}\text{C}$ , respectively (data from the study by Balasheva, Sabinina, and Semenov as quoted in [20]). The site is an alluvial plain with sparse semi-desert vegetation, including camelthorn, which grows mostly on flats near the Amu-Bukhar Canal (Figure 1(a)) and along roads. According to Yakovlev [16], the area is within the range of *Alhagi maurorum* ssp. *canescens* (Regel) Yakovlev, but our plants lacked the pubescent calyx characteristic of that subspecies and must therefore be classified in the nominal *A. m. maurorum*.

## 3. Material and Methods

Hundreds of galls were observed in the field and examined intact under a stereomicroscope in the laboratory. Freshly

cut short branches with galls, inserted in moist sand, remained fresh for one to two days. Leafhopper behavior was documented using a JVC Everio camcorder with an attached macro lens. Photographs were taken with a Canon EOS camera equipped with a Canon MP-E 65 mm macro lens.

For a more detailed survey of their contents, the galls were preserved in 70% ethanol. In addition to counting the number of intact and parasitized eggs, we examined nymphal exuviae or their remains. For this purpose the masses of dried excrement (see below) were dissected in droplets of water. The number of instars was determined based on the number of stylet bundles, which remain intact even when the rest of the exuviae have been disintegrated; remains of the last-instar female exuviae were recognized based on the presence of nymphal ovipositor sheaths.

Ethanol-preserved galls were critical-point dried and examined in a Tescan Vega XMU scanning electron microscope (Tescan, Brno, Czech Republic). In order to examine wax secretions of the gall epidermis, intact galls stored in a refrigerator at  $+5^{\circ}\text{C}$  for 17 days were frozen in liquid nitrogen and examined in their frozen state in a Hitachi S-4800 cryo-scanning electron microscope (Hitachi High-Technologies Corp., Tokyo, Japan) equipped with a Gatan ALTO 2500 cryo-preparation system (Gatan Inc., Abingdon, UK).

To characterize the wettability of the gall surfaces, contact angles of small water droplets placed on the inner and outer surfaces of two galls were measured using an OCAH 200 high-speed contact angle measuring system (DataPhysics Instruments GmbH, Filderstadt, Germany). Seven measurements were taken at different points on each examined surface. Prior to measurements the galls had been stored in a refrigerator at  $+5^{\circ}\text{C}$  for 17 days. The thickness of the wall or lamina was measured under a stereomicroscope on 44 galls and 18 leaves, respectively, preserved for histological examination in a 9.0 : 0.5 : 0.5 mixture of 70% ethanol, glacial acetic acid, and neutral-buffered formalin.

## 4. Results

**4.1. Life Cycle.** The life cycle of *S. viridis*, inferred from our observations, is shown in Figure 3. First-instar nymphs cause camelthorn leaves to fold into pod-like chambers, each containing a single leafhopper. The subsequent development, including five molts, takes place inside the tightly closed growing gall. Adult females remain inside their galls, while adult males emerge from their galls and penetrate into closed female galls. The male leaves after mating, while the fertilized female stays inside and inserts eggs under the inner epidermis of the gall. First-instar nymphs eventually disperse from the galls.

Although our own observations were restricted to August and September, the entire annual cycle of *S. viridis* can be reconstructed with reasonable confidence (Figure 4). Two generations develop annually (Figure 5). According to Gushchin [15], camelthorn begins sprouting young leaves in late March-early April. Soon afterwards, first-instar nymphs must emerge from overwintered galls and initiate new galls. We refer to this as the *overwintering generation*. Mitjaev [9] observed nymphal galls from the second half of May,

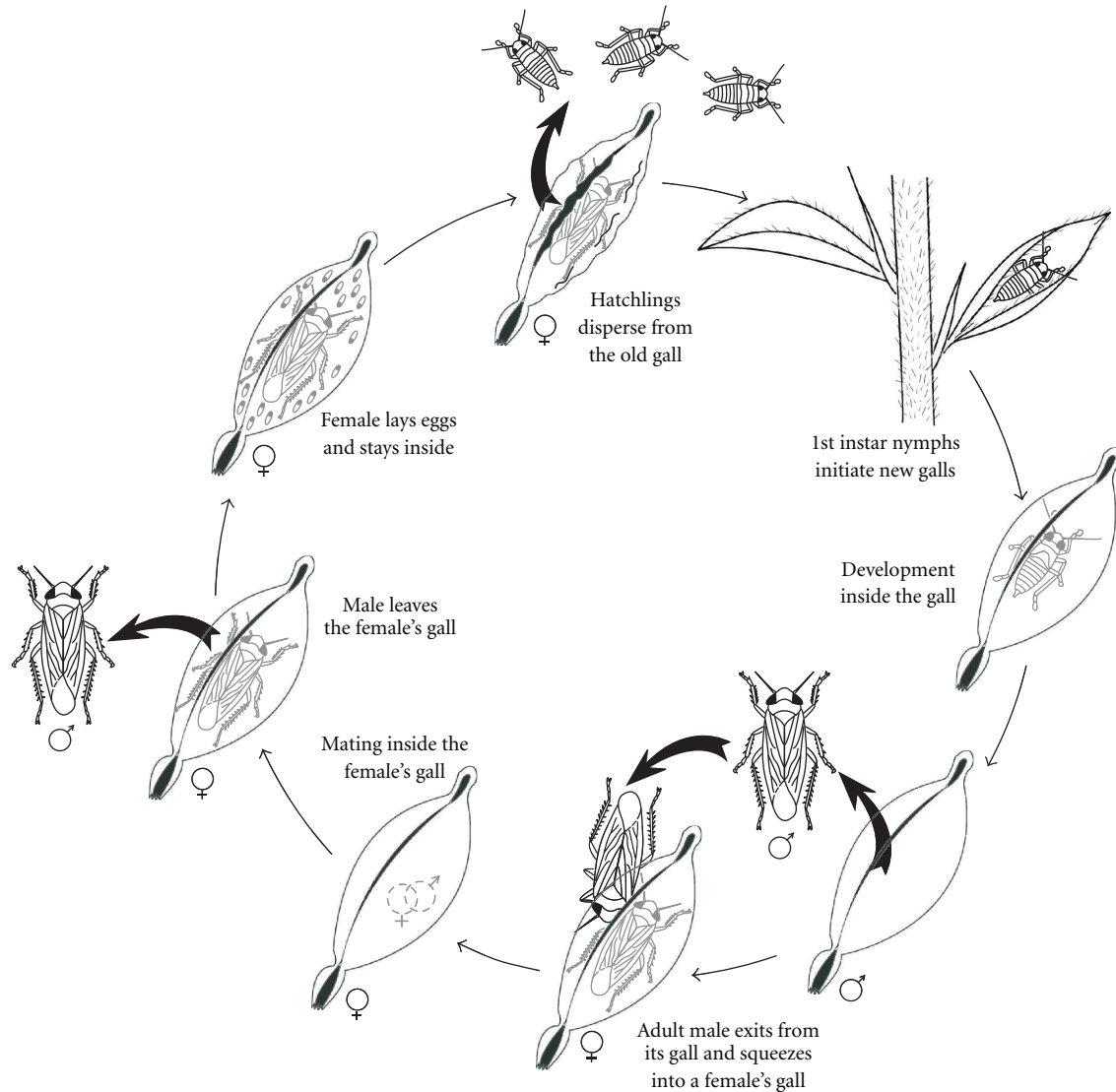


FIGURE 3: The life cycle of *Scenergates viridis*.

but already by mid-June most galls contained adults. These adults must mate and lay eggs approximately from mid-June to mid-July. During the first half of August 2011, numerous older looking galls contained live adult females of the overwintering generation next to their fully developed eggs and/or hatchlings, referred to as the *summer generation* (Figure 6(a)). This means that females of the overwintering generation remain alive inside the galls throughout the embryonic development of their offspring. Remarkably, 34 out of 38 such examined females (89.5%) had apical parts of their hindlegs injured or missing (Figure 6(b)). During the same period we observed fresher galls, which belonged to the summer generation and contained every developmental stage of the leafhopper from the first instars (very numerous) to adults (very few). By mid-August these adults had already begun mating and laying eggs of the next overwintering generation. Therefore, the two generations overlap to such an extent that some females of one overwintering generation

survive until the first eggs of the next overwintering generation are laid (Figure 4).

In early September 2010, a few galls still contained summer-generation nymphs and virgin adults, while the majority contained summer-generation females laying eggs (Figure 1(d)). Only 16 out of 50 such females (32%) had apical parts of their hindlegs injured or missing. The dry galls collected in December 2010 contained dead females next to their live overwintering eggs (Figures 7(a) and 7(b)). The aboveground parts of camelthorn shrubs die off by late November [15]; drying up of phloem sap around that time limits the potential life span of postoviposition females (Figure 4).

It appears that adult females do not typically leave their galls. Our attempts during both trips to collect *S. viridis* by beating camelthorn with a sweep net yielded no specimens of either sex. However, in August 2011 a postoviposition female was spotted walking freely; apparently it had left its



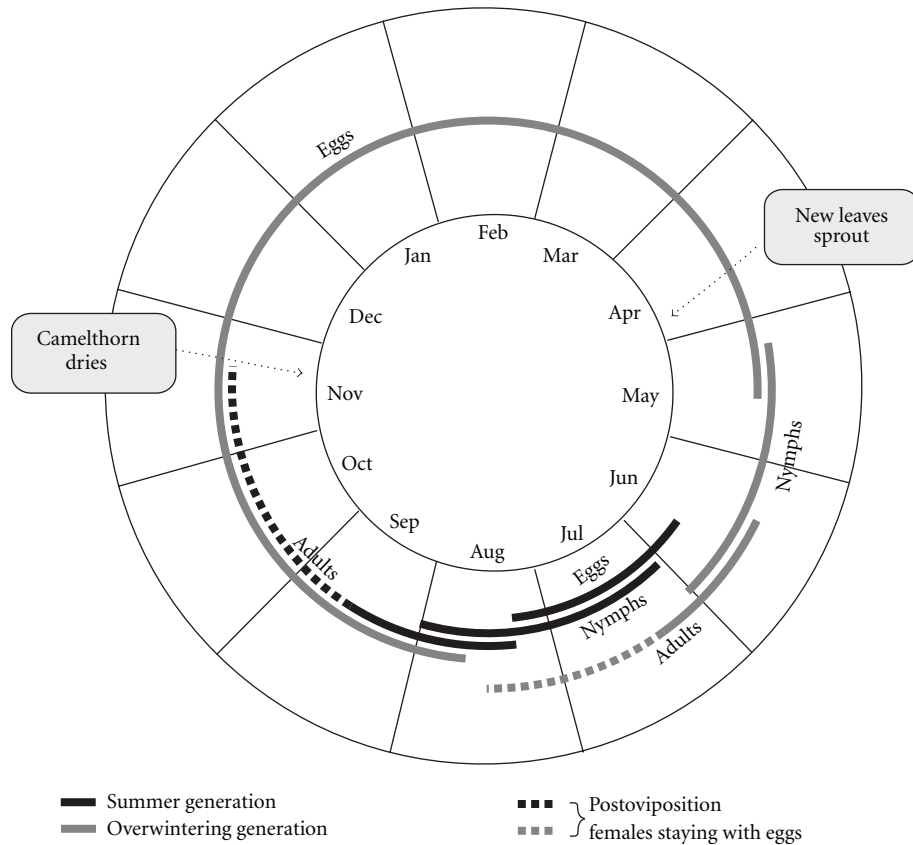


FIGURE 4: The annual cycle of *Scenergates viridis*.



FIGURE 5: A camelthorn branch with galls induced by the overwintering and summer generations of *Scenergates viridis* on the main stem and lateral shoot, respectively. Note that the older galls are slightly open.

gall through the same crack as its offspring (see below). This may explain how the females studied by Vilbaste [11]

and Emeljanov [12] were collected; in neither case were the examined specimens labeled as originating from galls.

**4.2. Gall Initiation.** Despite the abundance of first-instar nymphs, both hatching inside mother galls and having already formed galls of their own, we failed to observe initiation of new galls. In the field we never found exposed nymphs or any incompletely formed, nascent galls. Attempts to place hatchlings onto young leaves at room-temperature conditions ( $+20$ – $25^{\circ}\text{C}$ ) proved unsuccessful except in one case. After a period of feeding most nymphs escaped, but one produced a nascent gall when it was left unobserved for a few hours (Figures 8(a) and 8(b)). In the field the galls containing first-instar nymphs were 5–7 mm long; on one occasion two nymphs were discovered inside one gall.

**4.3. Gall Structure.** The number of galls per shrub varied between none and ca. 1,000. In the latter case virtually every leaf was transformed into a gall. The galls had the appearance of fusiform pods, round in cross-section or slightly flattened laterally, with a short funnel-shaped basal petiole and, typically, a similar apical lobe (Figures 1(c), 9(a)–9(d)). The orifice of each funnel was plugged from the inside by masses of dried excrement (see below). Except for these terminal openings, the valves of inhabited galls were tightly shut (Figures 1(c), 9(b)). In the galls containing



FIGURE 6: (a) A gall of *Scenergates viridis* split open to expose the female (overwintering generation) next to its offspring, first-instar nymphs (summer generation). (b) A postoviposition female with damaged apical parts of the hindlegs (insets). Scale bars: 1 mm ((a)-(b)).

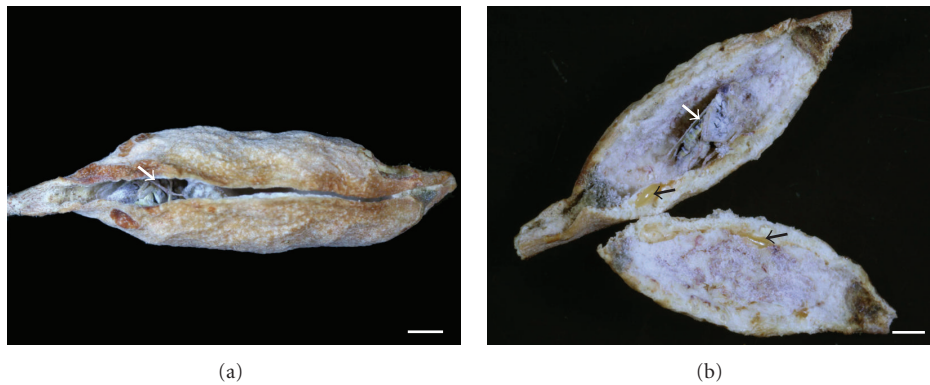


FIGURE 7: A dry overwintering gall of *Scenergates viridis*, collected in December. (a) Intact. (b) Split open. Note the dead female (white arrows) and live eggs (black arrows). Scale bars: 1 mm ((a)-(b)).

summer-generation eggs ready to hatch, the valves were slightly open (Figure 9(c)), while the galls abandoned by adult males and those of nymphs killed by pipunculids were widely open (Figure 9(d)).

The galls remain green and grow as leafhopper nymphs grow inside them. The length of the galls containing adult males we observed was  $10.1 \pm 2.10$  mm (mean  $\pm$  SD,  $n = 24$ ), and those containing adult females  $14.0 \pm 3.10$  mm ( $n = 189$ ). The largest gall observed was 35 mm long. The average length of a mature egg-containing gall is close to the average length of leaves on the same shrub. In contrast, the mean maximum wall thickness of such galls, 1.6 mm, is three times the thickness of mature leaves, 0.5 mm (Figures 10(a) and 10(b)). The wall thickness of the last-instar immature male galls only slightly exceeds that of regular leaves, but the galls of the last-instar immature females and preoviposition adult females have conspicuously thicker walls (Figure 10(b)).

The gall's inner surface corresponds to the adaxial and its outer surface to the abaxial sides of the original leaf. Young galls are variably pubescent on both sides. In older galls the outer surface is usually bare and glossy (Figure 11(a)), while the inner surface retains appressed hairs, ca.  $150\ \mu\text{m}$  in length (Figure 11(b)). On a smaller scale, the inner epidermis is coated with wax platelets and brochosomes (Figures 11(c)

and 11(d)). The latter can be found already in the youngest galls but appear to be more abundant in the egg-containing female galls. Wax platelets and brochosomes are responsible for the pruinose appearance of the gall's inner surface (Figure 11(e)). The inner surface is more hydrophobic than the outer one (Figure 11(f)). The static contact angles of small water droplets placed onto the outer and inner surfaces were  $110.2 \pm 18.94^\circ$  (mean  $\pm$  SD,  $n = 14$ ) and  $150.1 \pm 9.89^\circ$  ( $n = 14$ ), respectively.

**4.4. Disposal of Excrement and Exuviae.** The gall interior is remarkably neat and clean (Figure 12(a)). The basal and apical ends of the gall contain amorphous white or light yellow masses consisting of dried leafhopper excrement (honeydew), brochosomes, and crushed exuviae (Figures 12(a)–12(d)). These masses plug the terminal orifices of the gall cavity and therefore are referred to here as *excrement plugs*. Occasionally they also contain dead parasitoids or other small intruders (Figure 12(e)). The plugs do not melt when touched with a red-hot needle, indicating that they do not contain wax. When galls are placed in sealed plastic bags, the plugs quickly get mouldy.

Mitjaev [9] observed that the exuviae were crushed and pressed together with excrement but that the last 5th-instar

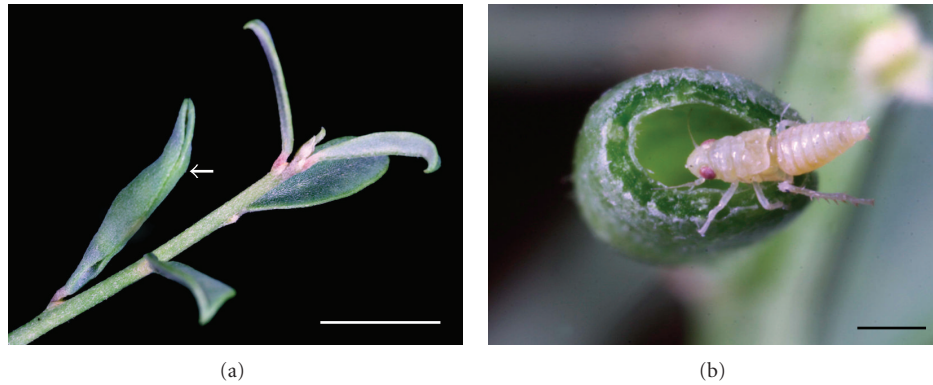


FIGURE 8: A nascent gall of *Scenergates viridis*, a few hours old, rolled in the laboratory. (a) The branch with the gall (arrow). (b) The same gall cross-sectioned, with the first-instar nymph exposed. Scale bars: 5 mm (a), 1 mm (b).

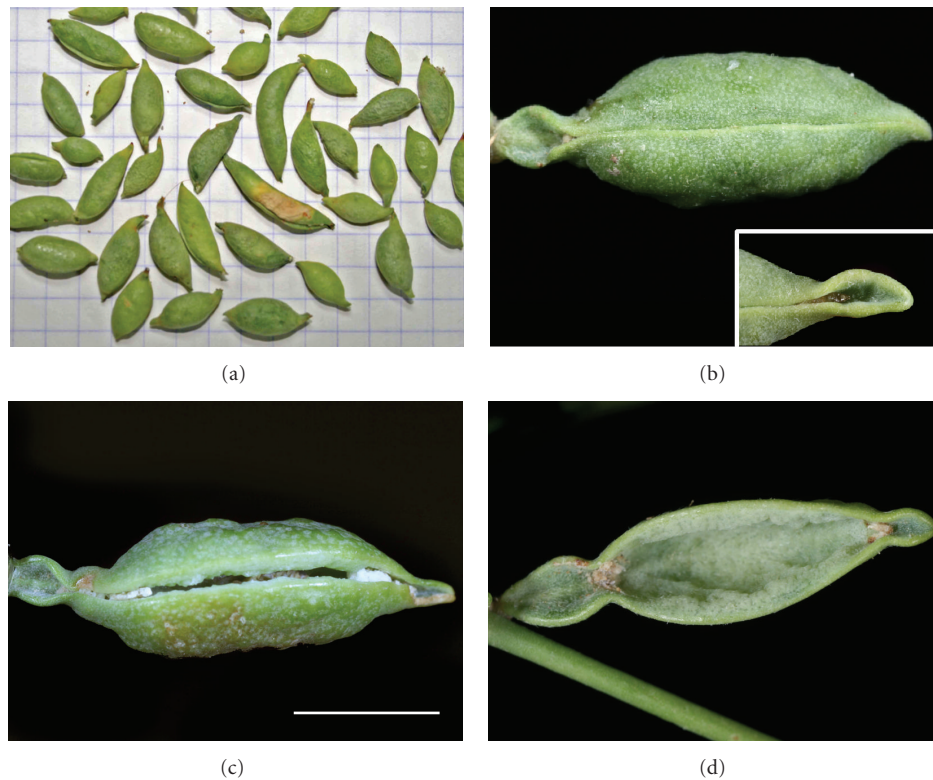


FIGURE 9: General structure of galls of *Scenergates viridis*. (a) Galls on 5 mm grid paper. (b) A closed gall containing a female and developing eggs; such galls often have funnel-shaped apices (inset). (c) A slightly open gall containing a female and ready-to-hatch eggs or first-instar hatchlings. (d) An open male gall after the male has exited. Note remnants of excrement plugs near both ends of the gall. Scale bar: 5 mm (c).

exuviae remained intact. We have found this to be true only for males, their intact last-instar exuviae lying freely in the gall cavity (recorded in 23 galls, Figure 12(f)). Females at least partly crush the exuviae of all nymphal instars (recorded in 30 galls). The exuviae are often reduced to small, hardly recognizable pieces (Figure 12(c)).

**4.5. Mating.** Mitjaev [9] observed adult males on the outside of closed female galls and suggested they were waiting

for females to come out. In August 2011 we observed such “waiting” males (Figures 13(a)–13(c)) eventually squeeze into the galls (Figures 13(d) and 14(a)–14(e)). First the male pushed one side of its body in between the valves with a lateral thrust and somewhat raised the posterior body, so that one anterolateral head margin became wedged in the slit. Then, in small increments, the rest of the body was pushed inside. During this process the male became noticeably compressed so that a part of its mesonotum normally

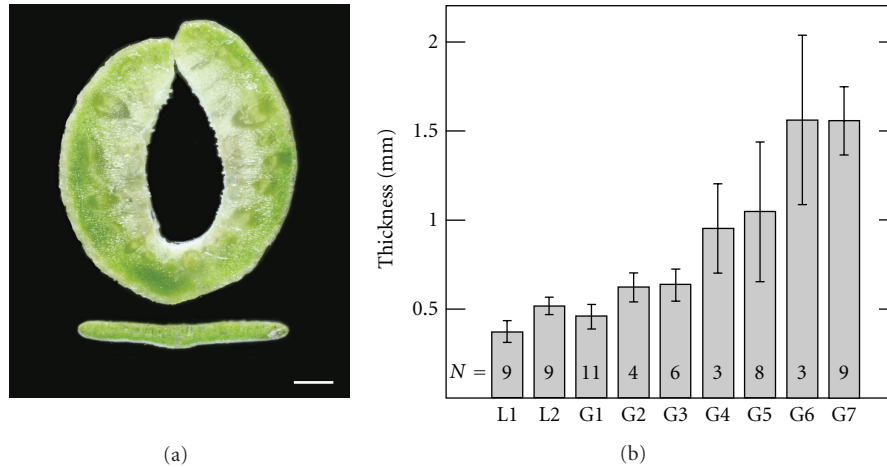


FIGURE 10: Changes of the leaf lamina thickness during the development of galls of *Scenergates viridis*. (a) Cross-sections of an egg-containing gall (top) and an ungalled camelthorn leaf of the same length (bottom). (b) The maximum thickness of camelthorn leaves (L1-L2) and *Scenergates viridis* gall walls (G1-G7). Numbers on the bars indicate sample sizes; error bars indicate the standard deviation. L1, young leaves; L2, mature leaves; G1, galls with 2nd- or 3rd-instar nymphs, sex not identified; G2, galls with 4th-instar nymphs, sex not identified; G3, galls with 5th-instar male nymphs; G4, galls with 5th-instar female nymphs; G5, galls with virgin females; G6, galls with postoviposition females and freshly laid eggs (overwintering generation); G7, galls with postoviposition females and fully developed eggs (summer generation). Scale bar: 1 mm (a).

concealed under the pronotum got exposed (Figures 13(d) and 14(b)). This strenuous process appeared to be assisted by vigorous pushing movements of all leg pairs, even though both hindlegs and at least one midleg were mostly just dangling in the air. After some time, the male left the female gall.

Altogether we observed two males penetrating into female galls and one male penetrating, obviously mistakenly, into a gall containing a last-instar immature male. In two instances, the process was recorded on video (Figures 14(a)–14(e)). In one case the penetration took 2.2 minutes and the exit 15 seconds; in the second case the penetration took 8.5 minutes and the exit 25 seconds. Additionally, we recorded an unsuccessful attempt of penetration; when the male was not able to insert more than its head margin into the slit, it eventually abandoned the task. All three penetrations observed in the field took place in full sun during the hottest hours of the day, between noon and 2 pm, when temperatures in the shade reached 37–39°C. In two cases we were able to confirm mating inside the gall upon penetration of the male. Three out of 170 examined ethanol-preserved galls containing adult females also contained a male; in two such galls the male was partly destroyed.

**4.6. Oviposition.** The eggs were inserted under the epidermis of the inner side of the gall nearly parallel to the surface (Figures 15(a)–15(c)), their anterior poles slightly protruding from the scars (Figure 15(d)). In the proximal half of the gall, the posterior poles of the eggs were directed towards, and in the apical half away, from the gall's base (Figure 15(c)), indicating that during oviposition the female turns 180°. Both the gall cavity surface (Figure 15(b)) and

the protruding egg poles (Figures 15(e)–15(f)) were densely powdered with brochosomes.

The number of eggs per gall of the overwintering generation, counted in August 2011, was  $146 \pm 53.2$  (mean  $\pm$  SD,  $n = 50$ ). Since the females do not leave their galls, this figure is an estimate of their entire lifetime reproductive output. In early September 2010, when summer-generation females were still actively laying eggs, the number of eggs per gall was just  $11.3 \pm 13.3$  (mean  $\pm$  SD,  $n = 138$ ).

**4.7. Hatching and Nymphs.** As in other Auchenorrhyncha [21, 22], the hatching phase is a pronymph, which molts into a first-instar nymph as soon as it is out of the egg (Figures 16(a) and 16(b)); the cast-off pronymphal exuvia often remains stuck to the empty chorion (Figure 16(c)). The hatchlings exit the gall through a narrow crack between the partially open valves (Figures 7(a) and 9(c)). However, we observed several galls that failed to open, with dead summer-generation hatchlings trapped inside (Figure 16(f)). The first-instar nymphs display two color morphs, one almost unpigmented and the other dark-patterned (Figure 16(d)). Although sexual dimorphism is not commonly observed among young instars of leafhoppers, these can be females and males, respectively. Coloration of the older nymphal instars is sexually dimorphic, males being darker than females (Figure 16(e)).

**4.8. Locomotion.** Nymphs and adults of both sexes were capable of jumping. The maximum recorded horizontal distance jumped was 8 cm for a first-instar nymph and 20 cm for an adult female released from its gall. Both males (Figures 13(a)–13(d)) and females (Figures 15(a) and 16(f)) were



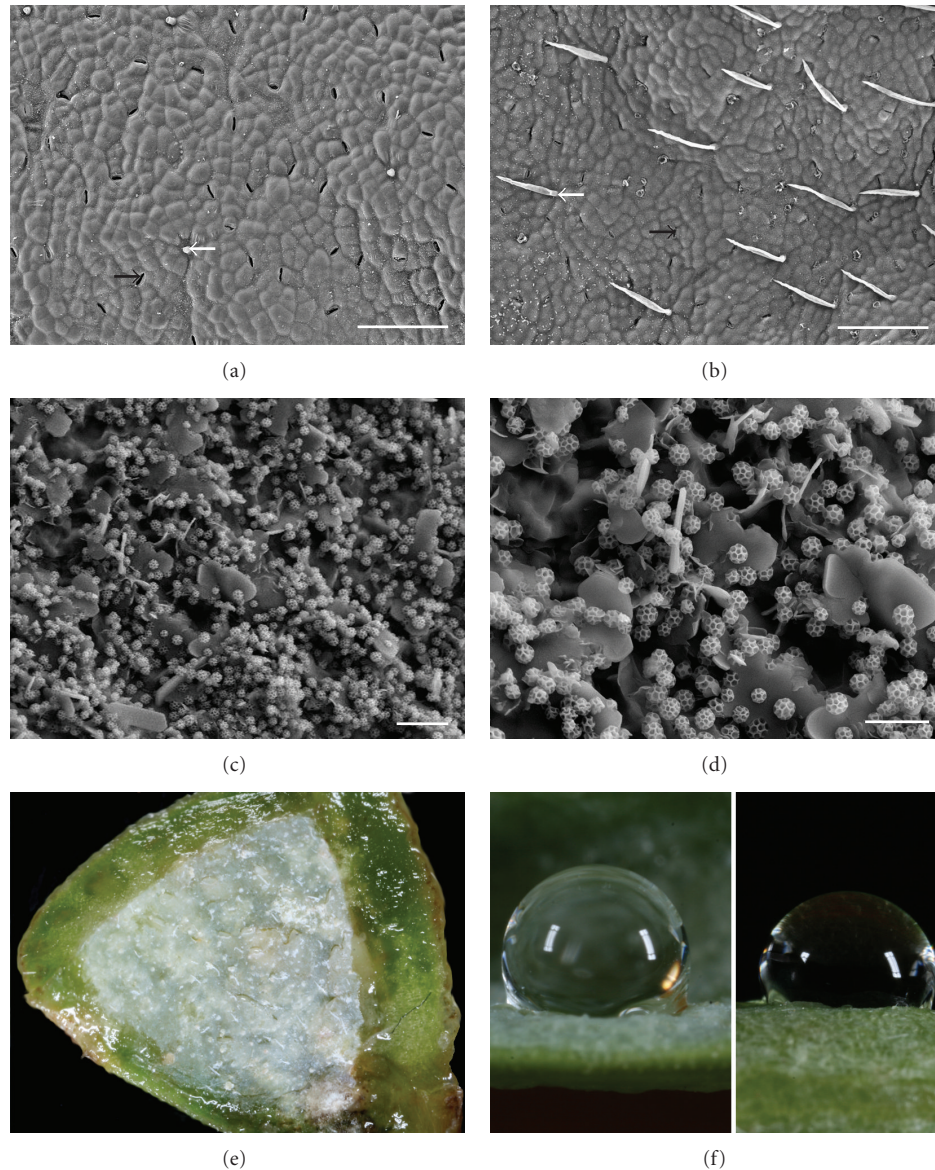


FIGURE 11: Microstructure and water repellence of the surface of galls of *Scenergates viridis*. (a) The outer surface of an ethanol-preserved gall, critical-point dried, and observed in a regular SEM: the white arrow points to the base of a broken hair, the black arrow points to a stoma. (b) Same, the inner surface: the white arrow points to a hair, the black arrow points to a stoma. (c) The inner surface of a frozen gall observed in a Cryo-SEM, showing brochosomes and wax platelets. (d) A closeup of the same. (e) A fragment of a valve of an egg-containing gall, showing its inner epidermis coated with the whitish pruinose layer of brochosomes and wax platelets. (f) Droplets of water resting on the inner (left) and outer (right) surfaces of a gall. Scale bars:  $200\ \mu\text{m}$  ((a)-(b)),  $3\ \mu\text{m}$  (c),  $2\ \mu\text{m}$  (d).

macropterous, with normally developed fore and hind wings, but flight was not observed.

#### 4.9. Natural Enemies

**4.9.1. Lepidoptera.** Numerous galls are destroyed by caterpillars of *Filatima* sp. (Gelechiidae). The younger caterpillars mine the gall valves, while the older ones devour the fleshy inner layer of the gall together with leafhopper eggs and the mother leafhopper without damaging the outer epidermis (Figures 17(a)–17(d)). Once the interior of the gall is

destroyed, the caterpillar chews an exit hole and leaves; such damaged galls remain closed (Figure 17(d): inset). We never found pupae of this moth in the field but were able to rear two adult females in captivity (Figure 17(d)); an additional female moth was collected directly from a camelthorn. In the absence of males, the moths could not be identified beyond the genus level (Alexei Bidzilya, personal communication).

**4.9.2. Diptera.** Some partially or completely open galls contained puparia of *Tomosvaryella argyrata* De Meyer (Pipunculidae) glued to their inner surface, often next to

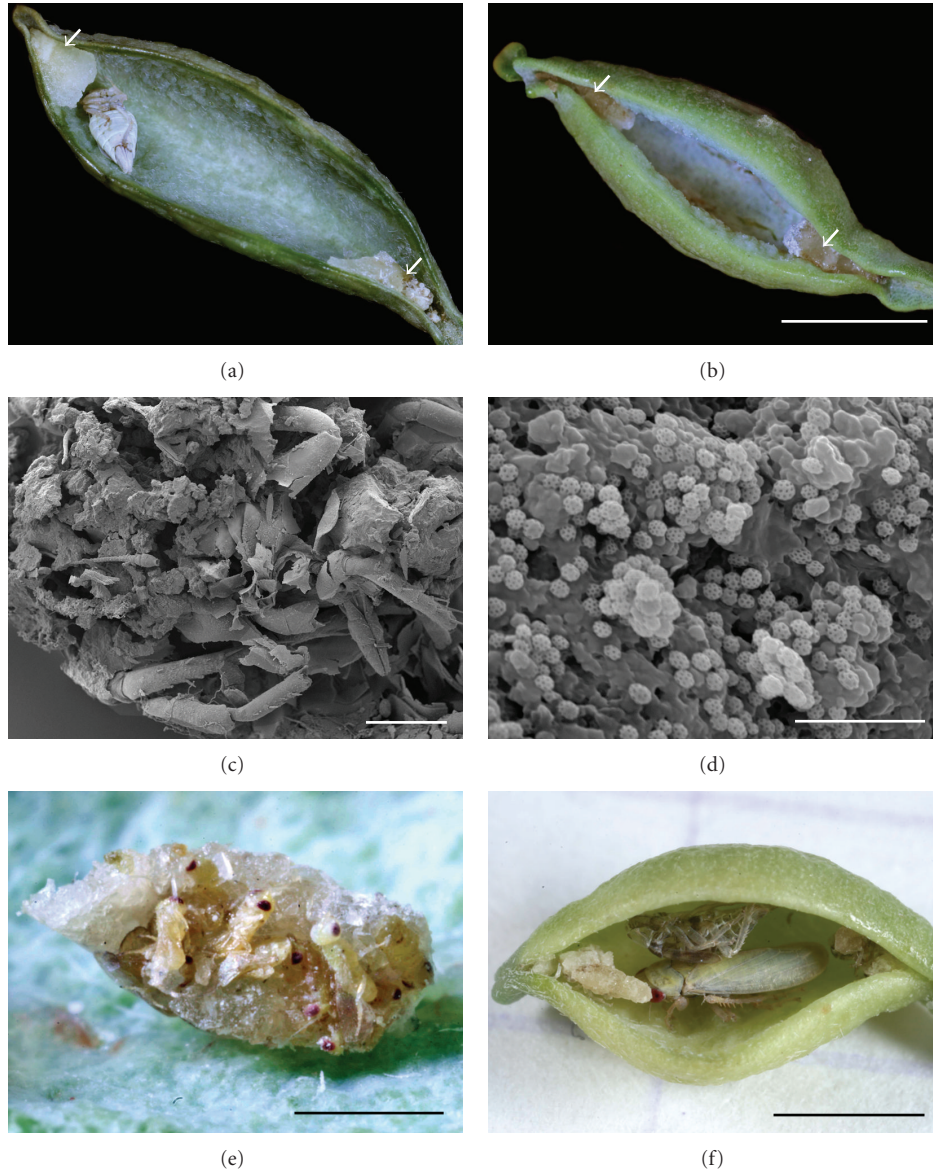


FIGURE 12: Disposal of excrement and exuvia in the galls of *Scenergates viridis*. ((a), (b)) Two adult galls opened artificially to expose their contents. Arrows point to the excrement plugs. The gall shown in (a) contains an etherized female. (c) A fragment of an excrement plug with remnants of crushed exuviae (pieces of legs, proboscis, and antenna are discernible). (d) A fragment of an excrement plug showing brochosomes. (e) A chunk of an excrement plug from the gall shown in (a); note ten trapped female *Aphelinoidea* sp. wasps. (f) A male gall artificially opened to expose the adult male and its intact last-instar exuvia; note also massive excrement plugs at both ends of the gall. Scale bars: 5 mm (b), 200  $\mu$ m (c), 5  $\mu$ m (d), 1 mm (e), 2.5 mm (f).

sucked-out remains of a last-instar *S. viridis* nymph (Figures 18(a) and 18(b)). Nymphs with pipunculid larvae in the abdomen were also observed (Figure 18(c)). One male and three female adult flies were reared in the laboratory (Figure 18(d)).

**4.9.3. Hymenoptera: Trichogrammatidae.** Among egg parasitoids of *S. viridis*, an undescribed *Aphelinoidea* sp. (Hymenoptera, Trichogrammatidae), 0.5–0.8 mm in length, kills the largest proportion of eggs. In August 2011 among 50 sampled galls containing a total of 7,152 fully developed

summer-generation eggs, the mean percentage of parasitized eggs per gall was 43.0% (range, 0.0–98.2%). From such galls we reared 181 female and 171 male *Aphelinoidea* sp. The anterior poles of parasitized eggs become dark (Figure 19(a)) and their posterior poles become filled with an orange substance, apparently the meconium excreted by the wasp larva prior to pupation. The emerging wasp chews an exit hole next to the egg's anterior pole on the inner surface of the gall wall (Figure 19(b)). A number of emerged wasps were found inside the galls, and one instance of mating was observed there. During the same period, in August



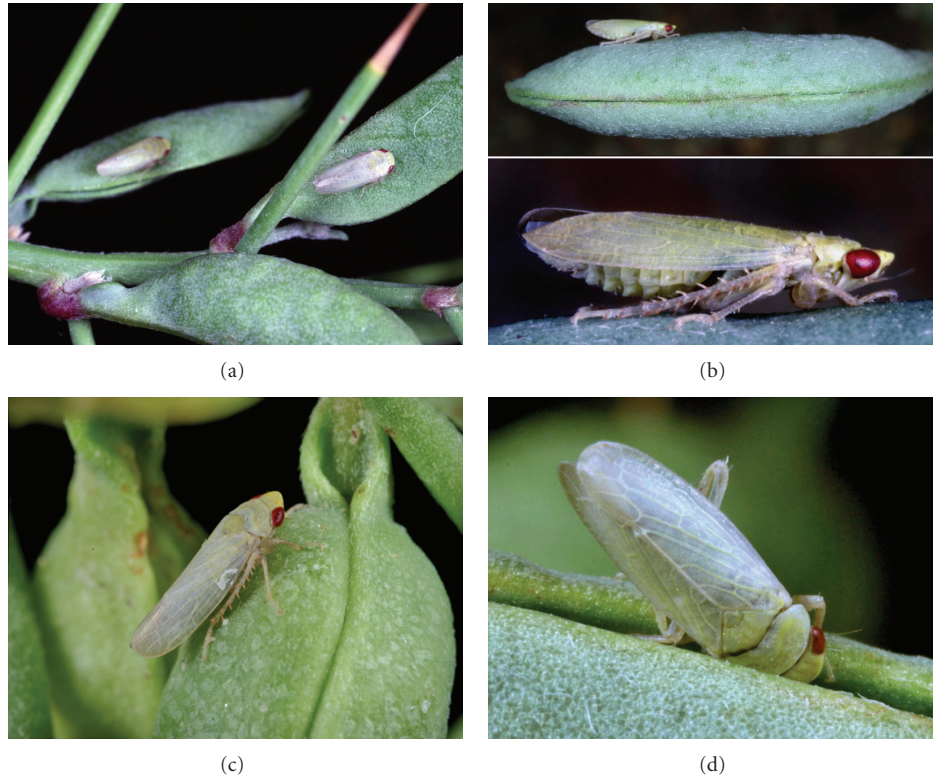


FIGURE 13: Premating behavior of males of *Scenergates viridis*. ((a)–(c)) Males “waiting” on the outside of female galls. (d) A male squeezing into a female’s gall.

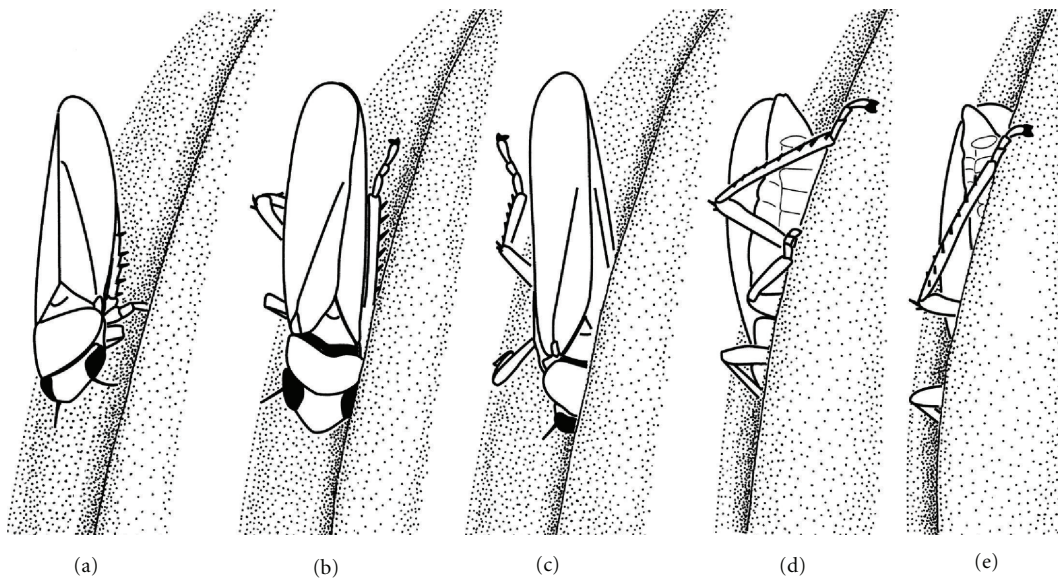


FIGURE 14: A male *Scenergates viridis* squeezing into a female’s gall. ((a)–(e)) Successive stages, based on a video recording. The stages (d) and (e) were observed from the ventral side.

2011, we observed female *Aphelinoidea* sp. running on the outsides of the galls containing females just beginning to lay eggs of the overwintering generation, apparently looking for a way in. Some such galls contained dead *Aphelinoidea* sp. females stuck in the excrement plugs (Figure 12(e)). In

September 2010, 21 of 88 examined galls with overwintering-generation eggs contained between 1 and 10 (average, 2.2) dead *Aphelinoidea* sp. females (but no males) stuck in the excrement plugs. From nine dry overwintering galls collected in December 2010 (Figure 7(a)), five male and nine female

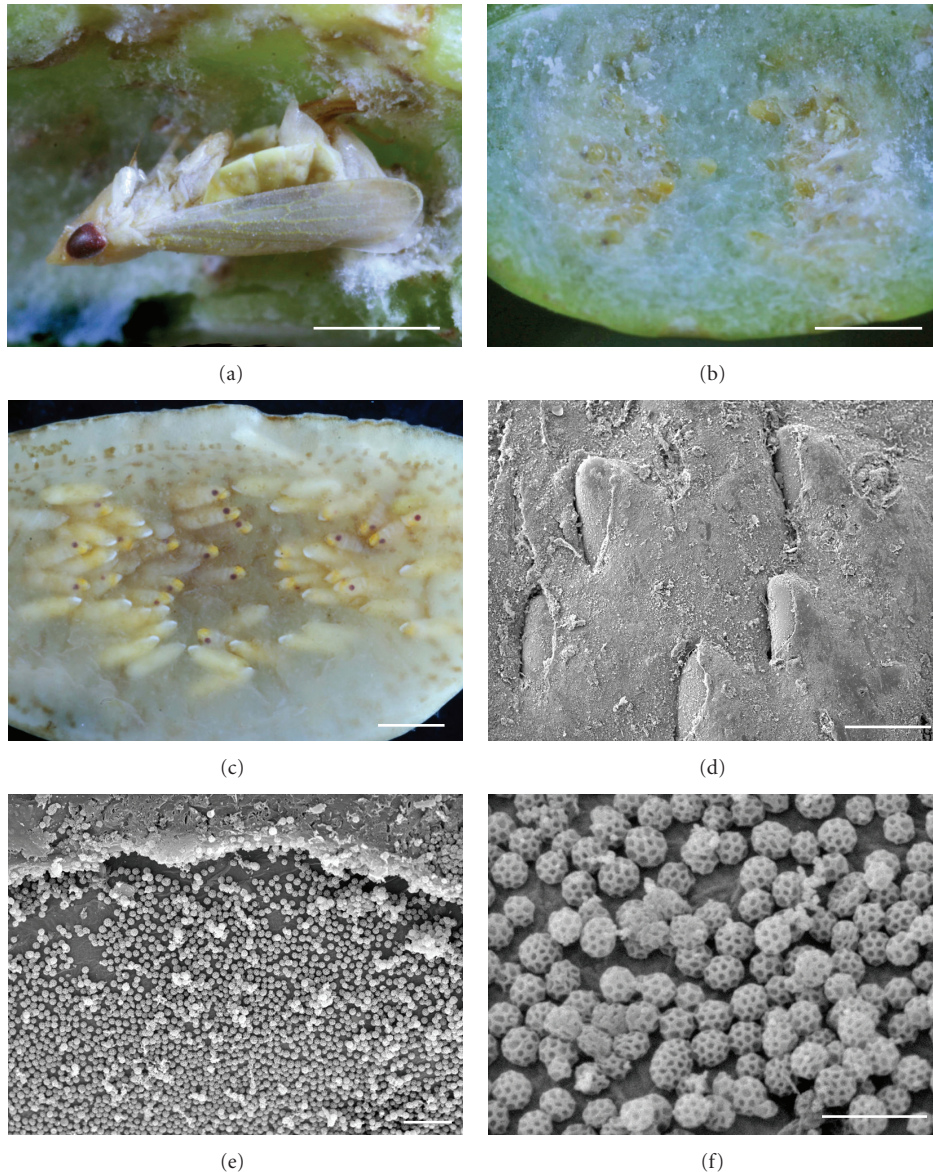


FIGURE 15: Oviposition and eggs of *Scenergates viridis*. (a) Remnants of a female that died in the course of egg laying with her ovipositor inserted under the gall's inner epidermis. (b) The inner surface of an intact gall valve with yellow eggs partially visible under the plant epidermis; note the conspicuous whitish pruinosity (brochosomes) on the latter. (c) The inner surface of a gall valve soaked in ethanol, with eggs visible underneath the epidermis; note that only some of the embryos have already developed their eyes. (d) The inner surface of a gall valve showing anterior poles of the eggs protruding from oviposition slits. (e) Closeup of an egg tip (lower part of the photo) protruding from under the epidermis (upper part of the photo). (f) Brochosomes on the egg surface. Scale bars: 1 mm ((a)–(c)), 200  $\mu$ m (d), 5  $\mu$ m (e), 2  $\mu$ m (f).

*Aphelinoidea* sp. were reared next May. The first of these wasps emerged a month later than the first leafhopper hatchlings, by that time most leafhopper nymphs had already hatched out.

The second species of Trichogrammatidae, *Paracentrobia* sp., apparently also emerges from the gall's inner surface. Only eight females and four males were reared from galls containing summer-generation eggs in August 2011. No details on the appearance of the eggs parasitized by this species or the rate of parasitization are available.

**4.9.4. Hymenoptera: Mymaridae.** Unlike *Aphelinoidea* sp., an undescribed *Gonatocerus* sp. (Hymenoptera, Mymaridae), 0.8–1.1 mm in length, parasitizes eggs of *S. viridis* through the gall's outer epidermis. Consequently, adult wasps emerge by chewing exit holes in the gall's outer surface (Figures 19(c) and 19(d)). As in *Aphelinoidea* sp., the larvae of *Gonatocerus* sp. excrete a bright orange substance from their rear end, but since the two parasitoids have opposite orientations within the host eggs, those containing *Gonatocerus* sp. are easily recognizable (Figure 19(a)). In August 2011, among 50



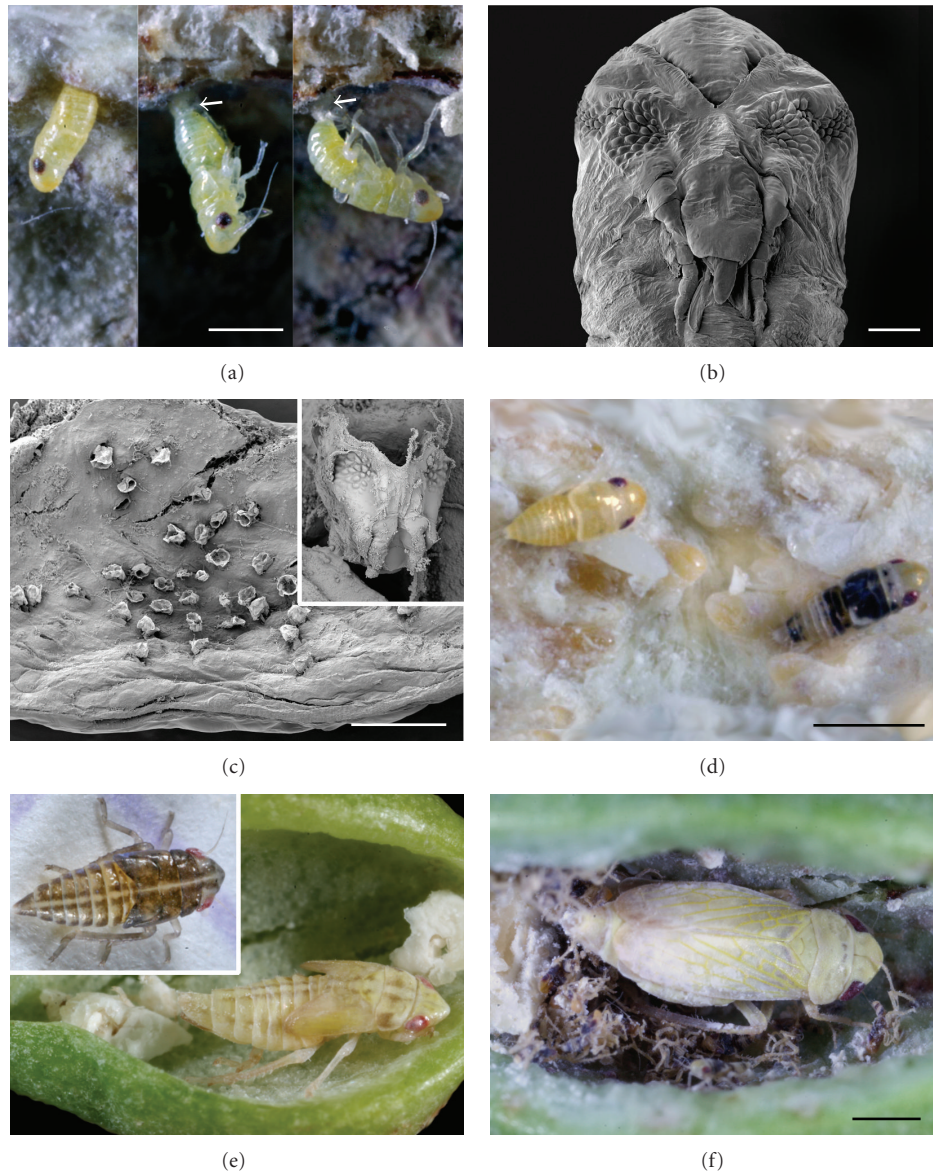


FIGURE 16: Eclosion and immatures of *Scenergates viridis*. (a) Three stages of hatching: arrow points to the pronymphal exuvia. (b) The anterior end of a pronymph in ventral view, with the first-instar nymph's head emerging from the V-shaped rupture at the apex. (c) The inner surface of a dry overwintered gall after the nymphs have hatched out, with numerous pronymphal exuviae attached to eclosion slits; one exuvia is magnified (inset). (d) Two differently colored first-instar nymphs from the same brood. (e) Female (below) and male (inset) last-instar nymphs; the nymphal gall was opened artificially. (f) A gall which failed to open, here opened artificially to expose the dead female atop the mass of dead hatchlings. Scale bars: 0.5 mm ((a), (d)), 50  $\mu$ m (b), 1 mm (c), 1 mm (f).

ethanol-preserved galls containing fully developed summer-generation eggs, the mean percentage of parasitized eggs per gall was 1.5% (range, 0–7.7%). Fifty-two females and 33 males were reared from such galls. During the same period we recorded on video two female *Gonatocerus* sp. probing the outer surface of a gall with their ovipositors.

**4.10. Other Associates.** In one area we observed a group of camelthorn shrubs with galls containing summer-generation immatures of *S. viridis* and covered externally with unidentified apterous aphids tended by the *Tapinoma karavaievi*

Emery ants (Hymenoptera, Formicidae) (Figures 20(a)–20(c)). A few open galls were both covered and filled with aphids (Figure 20(d)). Remarkably, except for a few individuals that were dispersing, other parts of the plants, including normal leaves, were free of aphids.

Besides trichogrammatids, the gall excrement plugs often contained trapped unidentified mites and adult and immature thrips from the families Thripidae and Phloeothripidae (Thysanoptera). Since these were observed both in galls that contained and those that did not contain eggs of *S. viridis*, they were probably inquilines feeding on the gall tissue rather than the leafhopper eggs.

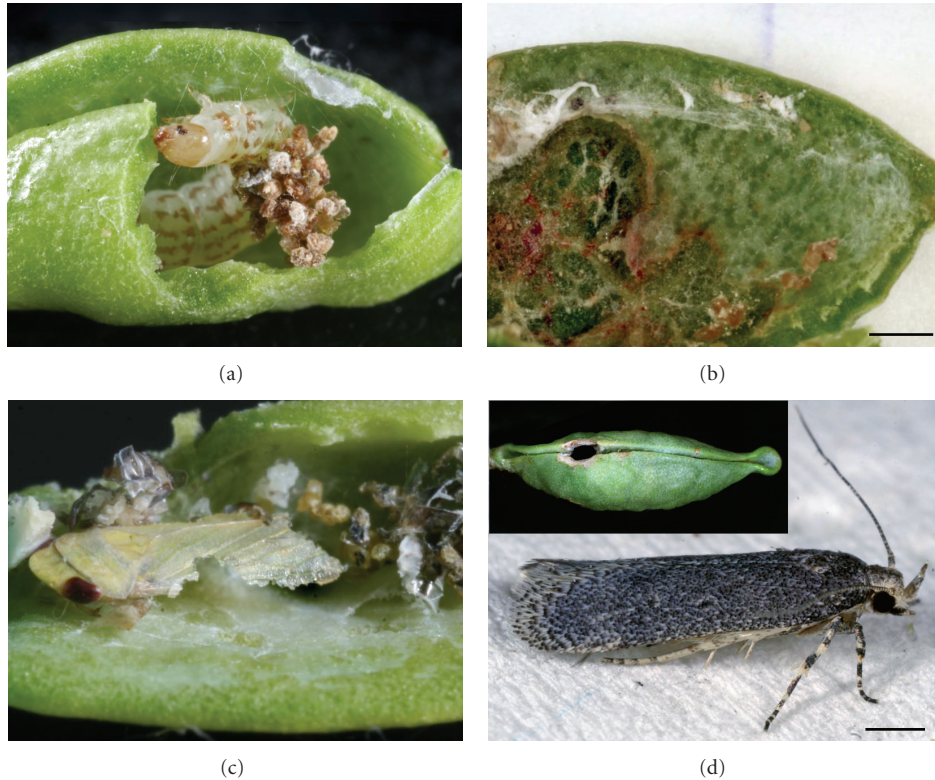


FIGURE 17: *Filatima* sp. moth (Gelechiidae), a predator of the galls of *Scenergates viridis*. (a) A gall broken open to expose the caterpillar; note the caterpillar's frass and silk netting. (b) The inner surface of a gall valve, partially eaten (in the lower left area) by a caterpillar. (c) Remnants of a partially eaten *S. viridis* next to caterpillar frass; note also the silk netting. (d) A reared female moth and a gall with a caterpillar's exit hole (inset). Scale bars: 1 mm ((b), (d)).

## 5. Discussion

**5.1. Key Galling Traits of *Scenergates*.** The cameltorn gall leafhopper is an accomplished gall maker and displays a number of related adaptations (reviewed below). This is particularly striking given the lack of any known galling prowess in other Auchenorrhyncha. It is worth noting, however, that these adaptations coexist in *S. viridis* with the general appearance, morphology, and behaviors typical of free-living leafhoppers, such as jumping and the presence of wings in both sexes.

**5.1.1. Control over Leaf Growth and Movement.** The nymphs of *S. viridis* induce profound modifications of *Alhagi* leaves. The following three aspects of their control over leaf growth and movement may each potentially involve a separate mechanism.

**(1) Triggering of the Initial Folding of the Leaf.** The fact that we were unable to find incompletely formed galls or exposed nymphs suggests that initial folding of the young leaf is too rapid to involve growth of the tissue. Such folding may instead result entirely from the changed turgor pressure within the leaf, as in nastic movements. Nascent cameltorn leaves are longitudinally folded, and as they gradually unfold, they pass through a boat-shaped stage resembling a partially

open pod. Hypothetically, some galls may be initiated at this stage, thus limiting the parasite's task to merely reclosing the pod. However, it appears that many young leaves passing through this stage are too small for the nymph to squeeze in.

**(2) Modifying Further Growth of the Leaf.** The galls are similar to normal leaves in length but their surface area is significantly larger, indicating increased lateral growth of the leaf lamina. Moreover, the gall valves are thicker than normal leaves, the egg-containing female galls being particularly succulent (Figure 10(a)). Measurements demonstrated that the walls of female galls begin swelling prior to oviposition, with the difference in wall thickness between male and female galls becoming noticeable during the last nymphal instar (Figure 10(b)). In similarly shaped leaf galls induced by Psyllidae, swelling of the walls results mostly from cell proliferation and to a lesser degree from an increase in cell volume [23].

The increased thickness of the female galls of *S. viridis* is likely an adaptation to their special role in reproduction. A thick wall may protect the eggs from desiccation, particularly during winter months when the galls dry out. It may additionally act as a barrier against *Gonatocerus* sp. wasps, which reach leafhopper eggs from outside the gall. Given that the wasps' ovipositors range in length between



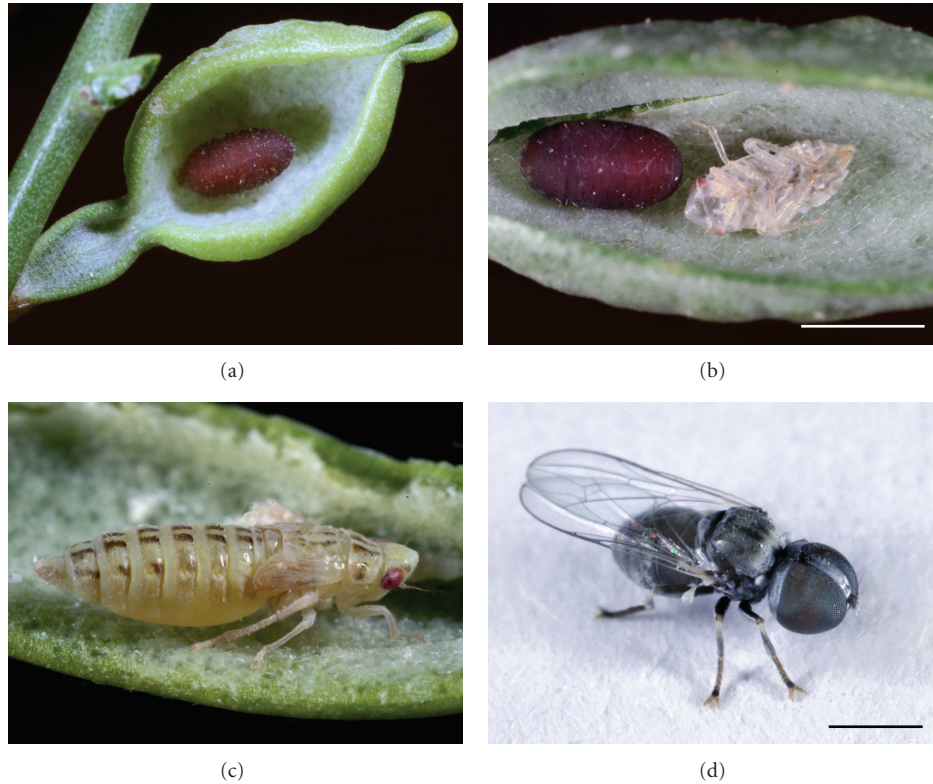


FIGURE 18: *Tomosvaryella argyrata* (Pipunculidae), a parasitoid of *Scenergates viridis*. (a) A puparium glued to the inner surface of a gall; note that the gall has fully opened. (b) A puparium next to sucked-out remains of a last-instar immature *S. viridis*. (c) A last-instar female nymph of *S. viridis* with a pipunculid larva inside its swollen abdomen (compare with an unparasitized nymph in Figure 16(e)). (d) An adult *T. argyrata* reared from *S. viridis*. Scale bars: 2 mm (b), 1 mm (d).

approximately 0.55 and 0.65 mm (*S. Triapitsyn*, personal communication) and that leafhopper eggs lie close to the wall's inner surface, the average maximum wall thickness of 1.6 mm (Figure 10(b): G6-7) puts the eggs well out of the wasps' reach. Although the gall walls are not uniformly thick, the swelling may contribute to the considerably lower rate of parasitization by *Gonatocerus* sp. than that by *Aphelinoidea* sp. Lastly, thick walls may be essential for accommodating a large number of leafhopper eggs without killing the gall.

(3) *Maintenance of the Closed State of the Gall.* While opening of dry overwintering galls is a trivial result of their shriveling (Figure 7(a)), opening of summer-generation galls when the progeny is ready to hatch out (Figure 9(c)) requires a mechanism. We hypothesize that the closed state (Figure 9(b)) is maintained by the leafhopper's feeding inside the gall, accompanied by injecting the plant with certain chemicals contained in the saliva, while cessation of feeding leads to the opening of the gall. This hypothesis explains the fact that male galls become broadly open after the males leave them (Figure 9(d)) and so do the galls of nymphs killed by pipunculids (Figures 18(a) and 18(b)). At the same time, the galls damaged by caterpillars stay closed (Figure 17(d): inset), which may be a consequence of the fleshy inner part of their valves being destroyed (Figure 17(b)).

#### 5.1.2. Safe Waste Disposal and Protection against Intruders

(1) *Use of Brochosomes as Lining of the Gall Chamber.* Brochosomes form hydrophobic coats on the integuments of Cicadellidae [19]. Adults and, in many subfamilies including Deltoccephalinae, immatures use their legs to actively spread brochosomes over their body and appendages. The hypothetical primary role of the brochosomal coats is repellence of the liquid excrement produced by leafhoppers. Coating of plant surfaces with brochosomes is unknown among free-living leafhoppers, except in one group of genera in which females powder the plant epidermis above their eggs with specialized brochosomes, which are produced exclusively by gravid females [24] and apparently provide protection against egg parasitoids [25]. We could not observe *S. viridis* coating the gall chamber surface with brochosomes, but this is most likely done by scraping the secretion off the body with the legs during grooming. The galls of young nymphs already displayed numerous brochosomes on their inner surface. Together with wax platelets produced by the plant epidermis, such lining (Figures 11(c) and 11(d)) is likely to contribute to the higher hydrophobicity and "nonstickiness" of that surface (Figure 11(f)). These properties are essential to prevent contamination of the gall with the sticky honeydew produced by the phloem-feeding leafhopper. The interiors of the galls are indeed strikingly clean (Figure 12(a)). The

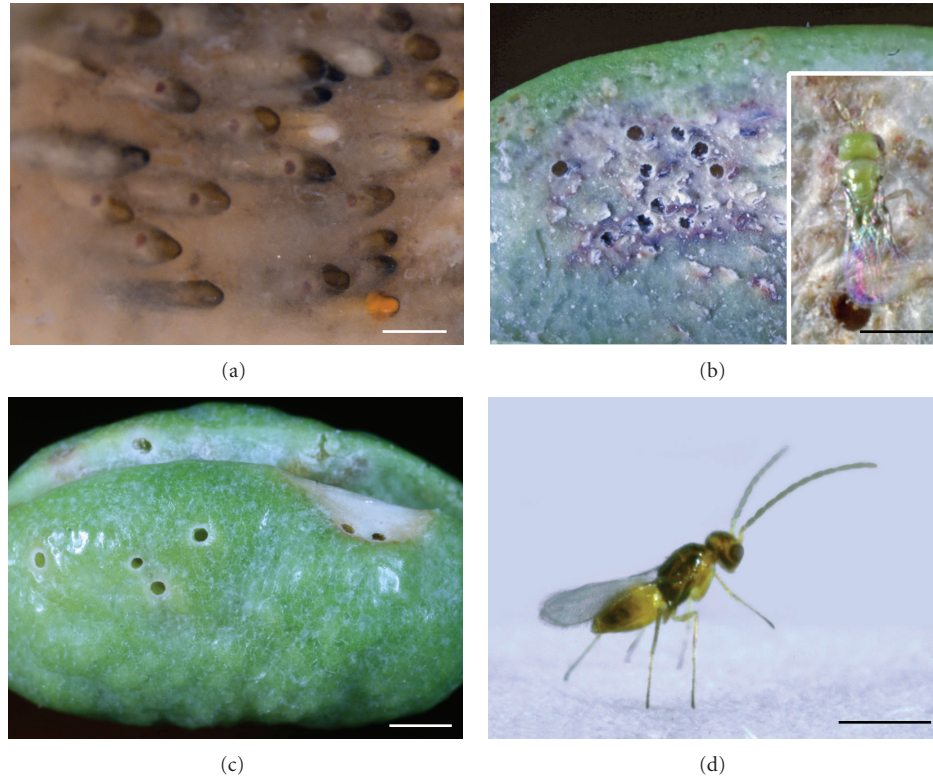


FIGURE 19: Egg parasitoids of *Scenergates viridis*. (a) The inner surface of a gall soaked in ethanol, with eggs of *S. viridis* visible underneath the epidermis; those with dark apices have been parasitized by *Aphelinoidea* sp. (Trichogrammatidae), and the egg with an orange apex has been parasitized by *Gonatocerus* sp. (Mymaridae). (b) *Aphelinoidea* sp. Exit holes on the inner surface of a gall and an adult female next to the hole (inset). (c) Exit holes of *Gonatocerus* sp. on the outer surface of a gall; note that one hole is on the commissural area of a valve. (d) An adult male *Gonatocerus* sp. reared from galls of *S. viridis*. Scale bars: 0.5 mm ((a), (d)), 1 mm ((b), (c)).

female galls containing eggs appear most heavily coated with brochosomes (Figures 15(b), 15(e) and 15(f)); the latter may to some extent deter trichogrammatid egg parasitoids.

(2) “Excrement Plugs.” The excrement plugs appear to be an ingenious way to simultaneously dispose of the dangerous liquid waste within the narrow space of the gall and utilize it to protect the gall from intruders. They act as mechanical barriers which block larger intruders from entering the chamber through the orifices at the basal and apical ends of the gall. Because the leafhopper moistens the plugs by excreting new honeydew, they may also act as sticky traps for the smallest intruders such as thrips, mites, and trichogrammatid wasps, all of which we found trapped in the plugs (Figure 12(e)). It is likely that the leafhoppers, particularly postoviposition females, can use their hindlegs to actively push the intruder into the sticky plug.

It is not clear how exactly the plugs are formed. Most probably, prior to excreting the next droplet of honeydew, the leafhopper moves to one end of the chamber and deposits it there. Crushed exuviae also become incorporated into the plugs (Figure 12(c)). The crushing behavior, unknown in any free-living auchenorrhynchs, apparently serves to maintain the gall chamber clean and unobstructed. Crushing was not observed directly, but is most likely performed

with the powerful hindlegs. It is remarkable that males, which leave the galls after they reach adulthood, “do not bother” or do not have time to dispose of their last-instar exuvia (Figure 12(f)) while the females, confined to the galls, process their last-instar exuvia like those from the younger instars. Plugging of gall orifices with exuviae is known in galling scale insects [3].

Our observation that the excrement plugs become mouldy in moist conditions suggests that extreme aridity of climate is a prerequisite for the galling behavior of this leafhopper. Thus, if gall formation occurs among other species of Auchenorrhyncha, such cases are more likely to be found in arid habitats.

**5.1.3. Exiting and Entering Galls.** The ability to squeeze through narrow slits, as observed in males of *S. viridis* (Figures 13(d) and 14), is another derived behavior not known among free-living leafhoppers. The process is obviously facilitated by the flattened body shape and particularly by the anteriorly flattened head (Figure 13(b)). Both traits occur in many free-living leafhopper species, apparently serving as camouflaging features. Penetration between closed gall valves is a strenuous task. It is remarkable in this respect that the few observed penetrations took place when the outdoor temperature reached its maximum. It is possible that males



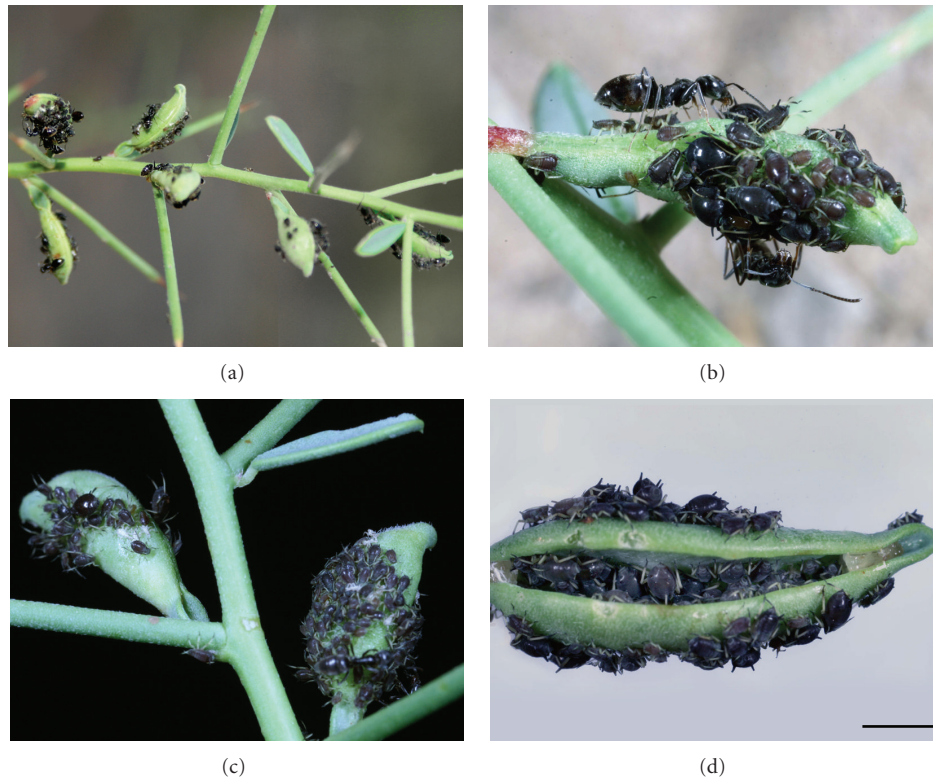


FIGURE 20: Unidentified aphids feeding on the surface of galls of *Scenergates viridis*. ((a)–(c)) Closed galls covered with aphids tended by *Tapinoma karavaievi* ants (Hymenoptera, Formicidae). (d) An open gall with aphids both outside and inside. Scale bars: 2 mm (d).

standing on the outside of female galls (Figures 13(a)–13(c)) wait for the rising temperature to decrease turgor pressure in the gall valves or perhaps just warm up their muscles for the intrusion. Exiting galls is easier and faster because the valves offer less resistance when pushed from the inside.

**5.1.4. Maternal Guarding.** Among Auchenorrhyncha, maternal guarding behavior is known only in the treehopper families Membracidae and Aetalionidae. In these two families, females stand by and protect their single egg batches from predators and parasitoids [26]. Other species produce multiple egg batches or scattered eggs and leave them unattended. Female *S. viridis* stay with their eggs inside the gall, and in the case of the overwintering generation, even until their offspring hatch (Figure 6(a)). Indirect evidence indicates that such females continue feeding and, at a decreased rate, laying eggs. It is most likely that they also actively protect the gall from intruders, including predators and parasitoids of eggs. Presumably, the females can kick and push these intruders out of the gall or into the excrement plugs with their hindlegs. The damaged hindlegs of postoviposition females (Figure 6(b)) may result from such activity.

**5.2. Natural Enemies and Associates.** The abundance of galls containing all life stages of *S. viridis* at the study site enabled us to identify major natural enemies and associates of this leafhopper within the narrow time limits of the study.

The galls are subject to predation by *Filatima* sp. moth larvae. According to Alexei Bidzilya (personal communication), this Holarctic genus includes up to 15 described and some undescribed Palearctic species that occur mostly in steppes and semideserts. Many Gelechiidae are leaf miners or gall inducers [27], while some facultatively feed on galls induced by other insects [28]. Whether *Filatima* sp. is a specialist predator of the galls of *S. viridis* remains to be found out. The caterpillars found by Dubovskii and Sulaimanov [14] in seven of the 100 examined galls probably belonged to this species.

The complex of parasitoids of *S. viridis*, including trichogrammatid and mymarid egg parasitoids and pipunculid parasitoids of larvae, is typical of Cicadellidae. The chalcidoid wasp genera *Gonatocerus*, *Aphelinoidea*, and *Paracentrobia* and the pipunculid fly genus *Tomosvaryella* all contain known parasitoids of free-living Cicadellidae [29, 30].

Among the parasitoids of *S. viridis* only *T. argyrata* has hitherto been described taxonomically, based on a series of males collected in Israel but with no information on the hosts (Christian Kehlmaier, personal communication). The type locality of *T. argyrata* is, therefore, outside the known distribution range of *S. viridis* (Figure 2) but within the range of *Alhagi maurorum*. It is possible that the range of *S. viridis* is wider than is currently known. Since pipunculids inject their eggs directly into immature auchenorrhynchs [31], the most likely targets in the case of *S. viridis* are the first-instar nymphs during the period between leaving their

mother's gall and forming their own gall. We suggest that this time frame is short. Thus, the attack tactics of the fly are an intriguing subject for future investigation. The eventual opening up of the galls of pipunculized nymphs (Figures 18(a) and 18(b)) appears to be crucial for the fly's exit.

The reared new species of trichogrammatid and mymarid wasps will be taxonomically described elsewhere. These species are likely to be adapted to the galling life style of their host. In particular, *Aphelinoidea* sp. are capable of locating and penetrating egg-containing galls, and *Gonatocerus* sp. can locate both such galls and the eggs lying deeply underneath the epidermis. One potential drawback of host specialization for egg parasitoids could be the absence of host eggs during a certain part of the year. It is worth noting in this respect the broad overlap between two generations of *S. viridis* during the late summer (Figure 4) which may facilitate continuity in the life cycle of the parasitoids.

It is known that the phloem sap of some aphid-induced galls contains more nutrients than ungalled plant parts [32]. The observed concentration of unidentified aphids on camelthorn galls (Figure 20) may indicate an increased nutritional quality of the phloem sap produced in these leafhopper-induced galls. A similar case, also observed in Middle Asian deserts, has been reported previously: the aphid *Brachyunguis* (*Xerophilaphis*) *saxaulica* (Aphididae) feeds both on and under the scales of cone-shaped bud galls induced on *Haloxylon* by the jumping plant lice of the genus *Caillardia* (Psyllidae) [33]. This aphid is so intimately associated with the psyllid galls—it rarely occurs on ungalled parts of the plant—that it has been mistaken for their inducer. The fact that the aphid often feeds on the exposed gall surface has been interpreted as an indication that it not merely uses the gall as a shelter, but that the phloem sap produced in the gall is particularly nutritious [33]. The same authors reported that *B. saxaulica* is tended by several ant species, including *T. karavajevi*.

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