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Bionomics of *Comadia redtenbacheri* (Hammerschmidt, 1847) (Lepidoptera: Cossidae)

C. Llanderal-Cázares, R. Castro-Torres & K. Miranda-Perkins

Abstract

Boring insects feed on the internal tissues of their hosts, and their activity is detected only after a severe damage to the host has occurred; therefore, studying their biology in the wild is difficult. The objective of the study was to complement knowledge about the biology, ecology and taxonomic position of *Comadia redtenbacheri* (Hammerschmidt, 1847), an agave borer with a long lifecycle. Laboratory observations were made on life stages obtained from larvae collected in Hidalgo, Mexico, which were induced to pupate in tubes with vermiculite and soil. Emerged adults were placed in cloth bags where they mated and laid eggs. Larvae that emerged from these eggs were raised on an artificial diet. Field observations were made in some localities of the State of Mexico; for this, external leaves and rhizomes of *Agave* plants were examined to look for eggs and larvae. Eggs and larvae were found in *Agave salmiana* Otto ex Salm-Dyck and *Agave applanata* Lem. ex Jacobi. Eggs are brown; they are found mainly at the base of external leaves. Neonate larvae bore a hole in the chorion and feed on it for a few days; they are gregarious and migrate towards the rhizome as they mature; last instar larvae are aposematic and release a volatile odoriferous secretion; their development is not uniform and can last more than a year. Pupation takes place in a silken cocoon under the soil. Adults are nocturnal; female calling starts one hour after the start of the scotophase, and can last until 5:30 am; oviposition happens a few hours after mating. The parasitoids *Lissonota fascipennis* Townes, 1978 (Hymenoptera: Ichneumonidae), and *Acantholespesia texana* (Aldrich & Webber, 1924) (Diptera: Tachinidae) and fungal and bacterial pathogens are commonly found in larvae. Predators of larvae and adults include ants, rodents and birds.

KEY WORDS: Lepidoptera, Cossidae, *Agave*, ecology, life cycle, nomenclature, Mexico.

Bionomía de *Comadia redtenbacheri* (Hammerschmidt, 1847) (Lepidoptera: Cossidae)

Resumen

Los insectos barrenadores se alimentan de los tejidos internos de su hospedero, y su actividad es detectada sólo hasta que existe un gran daño en el hospedero, lo que complica su estudio en la naturaleza. El objetivo del estudio fue complementar el conocimiento de la biología, ecología y taxonomía de *Comadia redtenbacheri* (Hammerschmidt, 1847), un barrenador de *Agaves* con un ciclo de vida largo. Las observaciones en laboratorio se hicieron a partir de diferentes estados biológicos obtenidos de larvas colectadas en Hidalgo, México, las cuales se indujeron a pupar en tubos con vermiculita y suelo; los adultos emergidos se colocaban en bolsas de tela donde se apareaban y ovipositaban; las larvas obtenidas se criaron en dieta artificial. Las observaciones en campo se hicieron en diferentes localidades del Estado de México; para esto, se revisaron las pencas y rizomas de *Agave* para buscar larvas y huevos. Se encontraron huevos y larvas en *Agave salmiana* Otto ex Salm-Dyck y *Agave applanata* Lem. ex Jacobi. Los huevos son café; se encuentran principalmente en la base de pencas externas secas. Las larvas neonatas perforan el corion y permanecen alimentándose de él por algunos días; son gregarias y migran hacia el rizoma a medida que maduran; los últimos instares son aposemáticos y liberan una secreción odorífera volátil. La pupación ocurre en un capullo de seda bajo el suelo. Los adultos son nocturnos; la hembra inicia el llamado una hora después del inicio de

la escotofase y éste se puede prolongar hasta las 5:30 horas am; la oviposición se da algunas horas después del apareamiento. Los parasitoides *Lissonota fascipennis* Townes, 1978 (Hymenoptera: Ichneumonidae) y *Acantholespesia texana* (Aldrich & Webber, 1924) (Diptera: Tachinidae), y varios hongos y bacterias patógenas se encuentran en las larvas. Los depredadores de larvas y adultos son hormigas, roedores y aves.

PALABRAS CLAVE: Lepidoptera, Cossidae, *Agave*, ecología, ciclo de vida, nomenclatura, México.

Introduction

Boring insects feed on the internal tissues of their hosts, and their activity is detected only after serious damage has occurred, which makes their study difficult (NIELSEN, 1981); moreover, the adults are rarely observed, except when they are reared on their hosts or collected with light traps (DREES *et al.*, 2008). *Comadia redtenbacheri* (Hammerschmidt, 1847) is an edible insect that bores into *Agave* plants during its larval stage. Its life cycle lasts a year or more, but the adults live only between three and five days (LLANDERAL *et al.*, 2007). In the original description of the species, HAMMERSCHMIDT (1847) mentions that its development could last up to 12 months like in other species of Cossidae. Studies about its biology, life cycle and ecology are scarce, probably due to the complexity and time necessary to obtain results, as it is the case in other lepidopteran borers.

Most edible insects are collected from the wild, and the impact that their overexploitation has on the vegetation, fauna and ecology is unknown. Several measures have been proposed for their conservation, like the development of protocols for their protection and the use of flagship species to preserve their habitats, because unregulated collection from the wild, loss of habitat and an increase of their demand have become a threat to their survival (YEN, 2009). Efforts have been made in some countries to rear those insects as a starting point for their conservation and management, but it is vital to take into account the biology, distribution and population dynamics of the species (YEN, 2012; VAN HUIS *et al.*, 2013), as well as the knowledge from local people (KUHNLEIN & RECEVEUR, 1996; PAOLETTI & DREON, 2005). Due to this, the objective of the study was to complement knowledge about the biology and ecology of the *Agave* red worm.

Materials and methods

The observations of larvae from the third to the seventh instar were made on specimens collected from 2012 to 2015 in *Agave* plants in the state of Hidalgo, Mexico. Larvae with a weight of <0.3 g were kept in leaves of *Agave salmiana* Otto ex Salm-Dyck (Agavaceae) cut in pieces of approximately 5-9 cm wide, which were changed every time fungi were observed growing on the surface. Larvae with a weight of ≥0.3 g were placed in plastic trays with tubes half-filled with soil to allow them to dig and pupate. The technique is described in detail in MIRANDA-PERKINS *et al.* (2013). From these specimens we obtained pupae, adults, eggs and first and second instar larvae. When the adults emerged, they were transferred to cloth bags, which allow air circulation, to let them mate and oviposit. The eggs were collected two or three times a week, and they were placed in Petri dishes covered with Agribón® (Polymer Group Inc., Charlotte, NC). Newly-hatched larvae were placed in rearing trays of 32 cavities (C - D International, Pitman, NJ) where they were reared on artificial diet for lepidopterans (Southland Products Inc®, Lake Village, AR).

To study larvae in their natural habitat, several *Agave* plants were inspected in the municipalities Santiago Zacualuca (19° 42' 07.8" N, 98° 54' 58.3" W) and Hueypoxtla (20° 00' 45" N, 99° 02' 34" W), in the State of Mexico. The external leaves were separated to look for eggs and larvae; afterwards, the whole plant was dug out and the rhizomes inspected. If larvae were found, the plant was collected and taken to the laboratory for further analysis.

To observe the external surface of the eggs and antennae, these were fixed in 3% glutaraldehyde for 24 h and washed three times with 0.1 M Sorensen's phosphate buffer at a pH of 7.2, placing the samples in the buffer for five minutes at each change. Afterwards, the tissues were dehydrated in ascending concentrations of ethanol; first they were placed in solutions of 30, 40, 50, 60 and 70%

ethanol for 45 min at each concentration and then they were placed in 80, 90, 100 and 100% ethanol for 1 h at each concentration. The specimens were critical-point dried in CO₂, mounted on SEM stubs on an adhesive carbon tape, and sputter-coated with gold (Ion Sputter JFC-1100, Jeol, Japan). The observations were made with a SEM microscope model JSM-6390 (Jeol, Japan).

The images were taken with a digital Single Lens Reflex camera (D7000, Nikon, Japan), and the images were processed with Adobe Photoshop CC (v. 14.0, Adobe Systems Inc.).

Results and discussion

The first description of the species was made by HAMMERSCHMIDT (1847), who classifies this insect as *Zeuzera* (*Cossus*) *redtenbacheri*. After that, in 1870 in his work "Insectos del maguey", BLÁSQUEZ (1870) names the species *Bombyx agavis*, without realizing that it had already been described. DYAR (1910) reclassifies it as *Hypopta chilodora* from a few specimens collected in central Mexico. ANCONA (1931) renames *H. chilodora* as *Hypopta agavis*, but DYAR (1937) decides both species are synonyms of *Hypopta redtenbacheri*. BROWN (1975) makes an ample revision of the genus *Comadia* and considers that the morphology of *H. redtenbacheri* fits the genus *Comadia*, and thus reclassifies it as *Comadia redtenbacheri*. In the extensive revision of Cossidae, SCHOORL (1990) validates the taxonomic and phylogenetic position of the insect after comparing the morphological characters of a large number of genera. More recently, CASTRO-TORRES & LLANDERAL-CÁZARES (2016) confirm that the morphological characteristics make this insect part of the genus *Comadia*.

The larvae were found in *A. salmiana* and in plants of the complex *Agave applanata* Lemaire ex Jacobi, a species that had not been reported as host of the *Agave* red worm, and that is used as a source of fiber and as an ornamental plant (Fig. 1a). *A. applanata* is medium-sized; the leaves are broad, rigid, lanceolate and blue-green in color; the lateral thorns are prominent, dark and slightly curved at the margins; the apical thorns are long and rigid; the rhizome is softer than *A. salmiana*, which may make it easier for the larvae to exit the tissue after they are fully mature. The only reported hosts for the species are in the genus *Agave* Linnaeus, especially *A. salmiana*, *Agave atrovirens* Karwin and *Agave mapisaga* Trelease (RAMOS-ELORDUY *et al.*, 2011). It is interesting to note that many species of *Agave*, if not all, have bundles of raphides in their tissues as a means of defense (WATTENDORF, 1976; ISHII, 1991; BLUNDEN, *et al.*, 2008), so we believe that the larvae of *C. redtenbacheri* must have anatomical or biochemical adaptations, or even symbiotic relationships with microorganisms that allow them to feed on these plants.

LIFE CYCLE AND ECOLOGY

Egg: They are white, about 12 mm long. The surface of the chorion shows a reticulated pattern that gives them a rough aspect. The female lays the eggs in masses, and covers them with a brown secretion from the accessory glands, which are prominent and with a reservoir to store the secretion (Fig. 1b) (RAMÍREZ-CRUZ & LLANDERAL-CÁZARES, 2015). The secretion has a porous appearance under Scanning Electron Microscopy (Figs. 1c, 1d). The number of eggs laid may appear to be related to the number of males that are in contact with the female (MIRANDA-PERKINS *et al.*, 2016).

The aggregation of eggs has been considered as a response to the structure of the host plant, and in butterflies it seems to be related to the aposematic coloration of some of the development stages and to the gregarious behavior of the larvae. In some lepidopterans, it has been determined that oviposition in masses, especially when these are formed by several layers, protects the eggs from desiccation, cannibalism and predation of neonate larvae, and increases the hatching rate compared with eggs laid singly; in other species it could be a strategy of the females to save time and energy when searching for oviposition sites (STAMP, 1980; CLARK & FAETH, 1998; FIGUEIREDO *et al.*, 2016). In laboratory at room temperature, eggs hatch after two months on average. During this time, some lose humidity and

collapse, but become hydrated after being sprayed with water. When the larvae are about to hatch, the dark heads of the larvae can be seen through the chorion. In the field the eggs are found mainly on plants with a height of around 60 cm, from the first week of January until May. The eggs are laid on the base of the external leaves, often on dry ones, but that remain moist enough at the base; these leaves can be easily separated from the inner leaves, and they show frequently some degree of decomposition. As with other borers, the preferred hosts are those that show certain degree of weakening, and thus can be considered as secondary invaders (NIELSEN, 1981). The color and the texture of the eggs resemble those of dry leaves, which could help with the camouflage, as can be seen in Fig. 1b. When the females do not mate, they still lay between a couple of eggs to more than 40, all which are unviable. Some females lay their eggs on plants that have already been infested in previous cycles.

Larva: Newly-hatched larvae are approximately 2 mm long. The head is partially retracted into the thorax, and the body is slightly flattened dorsoventrally. The first instars are white, and from the third or fourth instar they start to acquire a pinkish coloration that progressively intensifies until an intense red tone is reached (Fig. 1e). A distinctive characteristic of the larvae is the presence of a dark thorn on the dorsum of the tenth abdominal segment (DAMPF, 1927; CASTRO-TORRES & LLANDERAL-CÁZARES, 2015).

Neonate larvae use their mandibles to bore a hole in the chorion, and afterwards they knit a silken net that protects them. The silk gives the eggs a cottony appearance. After hatching, the larvae remain under the silk for two or three days feeding on the chorion; when most of the larvae have hatched, they bore through the leaf and enter it as a group. The leaves with larvae in this stadium are dark at the base and with a decaying appearance, but their odor is similar to that of mature compost.

All the instars of the larvae are gregarious, and according to STAMP (1980), the gregarious behavior of phytophagous insects is the result of the oviposition in masses. From the first instar, the larvae can build silken tunnels through which they move as a group; this is similar to other species like *Yponomeuta cagnagellus* (Hübner, [1813]) (Lepidoptera: Yponomeutidae), a gregarious lepidopteran whose larvae follow trails of silken threads by touch to orient themselves and find their congeners, although chemical cues may also be involved (ROESSING, 1989). As the *Agave* red worm larvae grow, they migrate to the rhizome, where they can molt up to six times and reach 4 cm in length. Although BLÁSQUEZ (1870) and ANCONA (1931) mention between three and four molts, HERNÁNDEZ-LIVERA *et al.* (2005) reported seven instars. The development of the larvae is not uniform, and in the same plant larvae in different development stages can be found. This is similar to what was observed by DELGADO-TEJEDA (personal communication) after artificially infesting plants with first instar larvae, and then isolating the plants with cloth screens; after checking the rhizomes the next year, she found larvae of different sizes and even pupae. Due to this we think that the duration of the larval stage in this species is variable, ranging from eight months to more than 12, as in other species of *Comadia* (RIVERS, 1897). The molting behavior has never been observed in the field; in the laboratory, the larvae that are about to molt exit the piece of leaf, remain almost motionless for a day or two until they molt, and then introduce themselves again into the leaf. As they grow, the coloration becomes more intense and they start secreting a characteristic odor that remains on the surfaces that are in contact with the larvae. The aposematic coloration in the larval stage seems to be common to several species of Cossidae belonging to subfamilies as diverse as Cossinae, Zeuzerinae and Chilecomadiinae (sensu Schoorl) (CARTER, 1984; OLIVARES & ANGULO, 1992; ZONG *et al.*, 2006; TIAN *et al.*, 2010; VEERANNA & REMADEVI, 2011), but while in *C. redtenbacheri* the color appears progressively and in the fully developed larvae it is the most intense, in some other species of the family the color appears at the beginning of the larval stage and disappears towards the last instars. The variation of the coloration could be correlated with the period where the insects are more exposed to predators; in this species that period occurs when the mature larvae go out of the rhizome in large numbers to find a place to pupate (BLÁSQUEZ, 1870; DAMPF, 1931). The bright colors of several species have been considered as a defensive mechanism (PINHEIRO *et al.*, 2015). Some aposematic species are also gregarious, which makes their presence more obvious and emphasizes their defenses, thus dissuading predation (GAGLIARDO & GUILFORD, 1993); however, from an evolutionary point

of view, aposematism and gregarism may not be interdependent (RUXTON & SHERRATT, 2006). The larvae of some cossids also secrete a mixture of volatile fatty acids of relatively high molecular weights, which may serve a defensive function (TRAVERE *et al.*, 1960; BERGMANN *et al.*, 2007). During September and October, the larvae go out of the rhizome and dig into the soil to a depth of 3 cm. There they build a cocoon with silk and particles of the substrate (Fig. 1f). The larvae curve themselves either dorsally, ventrally, or laterally.

Pupa: They are adecticous and obtect, where the mandibles are immobile and the appendages are adhered to the body. At the beginning they are white, and they get a creamy hue as they mature, until a dark brown is reached towards the emergence of the adults. The head has two black chitinous projections, one on the vertex and the other near the clypeal region. The abdomen presents several rows of spines on the pleural and dorsal region. The number of rows of spines can be used to distinguish the sexes (CASTRO-TORRES & LLANDERAL-CÁZARES, 2016). Males can also be separated from females by the presence of a pair of tubercles present on the ventral surface of the ninth abdominal segment (Fig. 1g, 1h).

After forming the cocoon, the larvae stay inside for five months and a half on average, but they remain as larvae for up to half of that period, as prepupae for up to 1.5 months, and as pupae for about a month (MIRANDA-PERKINS *et al.*, 2013). The larval stage inside the cocoon is easily reactivated in the presence of light. During the prepupal stage they start losing color until they reach a creamy white hue. The pupae make a hole in the cocoon and emerge from the substrate with the aid of the chitinous projections on the head and the rows of spines. The last abdominal segment often remains in the substrate, which gives the adult a point of support. In laboratory, adults emerge during the whole day, but mainly in the afternoon.

Adult: They exhibit a cryptic coloration; they are light brown with rows of dark brown scales together with whitish scales (Fig. 2a). The thorax is covered by a number of filiform scales. Males are dark; the antennae are bipectinate (Fig. 2b) and the body length is about 1.3 cm. Females are paler than males; the antennae are serrate (Fig. 2c) and the body length is 1.6 cm on average.

Pheromone emission and mating happen the first or second day after emergence. Females start calling about an hour after the start of the scotophase, and they can continue until 5:30 am uninterrupted. This is different to what LLANDERAL-CÁZARES *et al.* (2007) report; they mention that the calling period extends only until 23:00. The difference may be the presence of light, which can affect the calling behavior (DELISLE & MCNEIL, 1986). SOLOMON & NEEL (1972) mention that males of *Prionoxystus robiniae* (Peck, 1818) (Lepidoptera: Cossidae) can respond to the calling between midday and dusk, but they mainly respond during the afternoon. During the calling, the female extends the last abdominal segments and the ovipositor (Fig. 2d) and sometimes it moves rhythmically, which according to SOLOMON *et al.* (1972), serves to regulate the release and dispersion of the sexual pheromone in *P. robiniae*. Mating can occur at any time during the night. Females emerge with most of the oocytes ready to be fertilized and oviposited in a few hours, which is similar to other lepidopterans with short adult lifespans and non-feeding adults (CHAPMAN, 2013). The weight of the ovaries could explain the fact that females are not as mobile as males. Males are able to fly shortly after their emergence. SOLOMON & NEEL (1972) observed something similar in *P. robiniae*. In this species, females remain on the host plant, about a meter from the site of their emergence, while males exhibit a rapid flight in zigzag.

Oviposition takes place a few hours after mating and starts with a searching behavior where the female repeatedly probes the surface with the ovipositor until it finds a suitable site, which normally includes crevices or rough textures. In cloth bags, oviposition occurs mainly between tighter folds, or between the coxae or wings of dead individuals. If the ovipositor of a female during the searching behavior was gently pressed between the folds of the bag, the female immediately stopped searching and started ovipositing; when the folds were released, the female started the searching behavior again. This shows that a mechanical stimulus alone is enough to trigger oviposition. At the tip of the ovipositor there are several types of trichoid sensilla, which have been associated to mechanoreception, that probably are important to find suitable substrates for oviposition. Females can lay 33 eggs on

average, although some females can lay more than 160. Although eggs can be laid singly, most of them are laid in masses. According to HEBERT (1983), this behavior occurs in species with non-feeding adults because it helps the individuals save energy and use it to lay eggs. RAMÍREZ-CRUZ & LLANDERAL-CÁZARES (2015) report that the average potential fecundity (APF) in this species is 104; however, the number of eggs laid was less than 50% of the APF on average. The huge difference between APF and real fecundity is influenced by female size, the balance between oviposited eggs and their size (LAMBERT, 2008), and the quality of host plants in pro-ovigenic species (AWMACK & LEATHER, 2002). In our study, the larvae were extracted from their host plant and forced to pupate probably before they were fully developed, which may have diminished the nutrients available to the adults; therefore, it is necessary to analyze the real fecundity in adults that emerge from larvae that had pupated naturally. In laboratory, adults emerge from March to May, which is similar to what BROWN (1975) reported for Texas, but in the field the flight period goes from December to May (JIMÉNEZ-VÁSQUEZ & LLANDERAL-CÁZARES, 2015: 38).

NATURAL ENEMIES

Parasitoids: The larvae are parasitized by *Lissonota fascipennis* Townes (Hymenoptera: Ichneumonidae) (Fig. 2e, 2f) and *Acantholespesia texana* (Aldrich & Webber) (Diptera: Tachinidae) (Fig. 2g). A single larva can carry a single ichneumonid larva and up to five tachinids. In laboratory, *L. fascipennis* emerges from the cocoons from March to May, but in the field, parasitized larvae from fourth to sixth instar were found in August and September. Parasitized larvae can bear small brown spots with a small perforation that marks the point of entrance of the ovipositor of *L. fascipennis*, generally on the back of the body (ZETINA *et al.*, 2009; ZETINA *et al.*, 2012; ZETINA & LLANDERAL, 2014). Larvae and pupae of moths are the main hosts of Ichneumonidae, which are specific in several cases. The parasitoids can oviposit inside, on or near their hosts and the immature stages develop as endoparasites, with the life cycles of both organisms interrelated (NICHOLLS, 2008). The stage where parasitization of the *Agave* red worm larvae takes place and how the larvae are found by *L. fascipennis* females remain unknown. Some ichneumonid species that parasitize subterranean pupae have a hardened cuticle that allows them to move through the soil (THOMAS & ELMES, 1993). The adults of *A. texana* emerge from the cocoons of *C. redtenbacheri*. In specimens collected in the field, ZETINA *et al.* (2012) found fifth and sixth instar larvae of *C. redtenbacheri* parasitized by the dipteran in August and September, and the adult dipterans in November and December. Most female tachinids lay their eggs on the surface of the integument of their host, and newly hatched larvae bore through the cuticle and enter the body cavity. Once inside, the parasitoid larvae connect their spiracles to the entrance hole or to the tracheal trunks. After the third instar, the larvae exit the body of the host and form a cylindrical puparium that breaks through the anterior pole during the emergence of the adult (O'HARA, 2008; CHAPMAN, 2013). Lesions caused by *A. texana* can be found in any part of the body of the host, and they consist of a brown, tunnel-shaped melanized structure with a conspicuous hole caused by the entrance of the parasitoid. When the parasitoid larvae are in the last instar, the tissues of the host have already been completely consumed (ZETINA & LLANDERAL, 2014).

Microorganisms: Most of the larvae that were placed in plastic trays died. In some cases it was due to infection by *Beauveria bassiana* (Balsamo) Vuillemin (Fungi: Hypomycetes); this fungus hardens the tissues of the host and covers the integument with white mycelium. Other individuals were infected by bacteria, which produce wet rots and foul odor in the hosts. MIRANDA-PERKINS *et al.* (2013) reported that *B. bassiana* can infect up to 39.6% of the larvae still active inside the cocoons in laboratory. ZETINA & LLANDERAL (2014) observed that infections by bacteria, viruses and fungi cause changes in the color and consistence of the body of the host (Fig. 2i). HERNÁNDEZ-FLORES *et al.* (2015) found nine genera of bacteria associated with *C. redtenbacheri*, none of which were pathogenic to insects or humans.

Predators: All the stages of the insect are preyed by ants, rodents and birds. The latter can find the cocoons that are below the ground, and destroy the prepupae, but they do not feed on them, possibly

due to the volatile compounds that the larvae secrete (Fig. 2h); however, the adults are easily spotted and devoured when they are resting on the leaves of the *Agave*. It is possible that the larvae are protected by their aposematic coloration and their secretion, while the adults rely on their camouflage to escape predation. The adults of some Cossidae produce a clicking sound when they flex their wings before flying, and this may be a defensive strategy against predators (MINET & SURLYKKE, 2003), but this behavior has not been observed in *C. redtenbacheri*.

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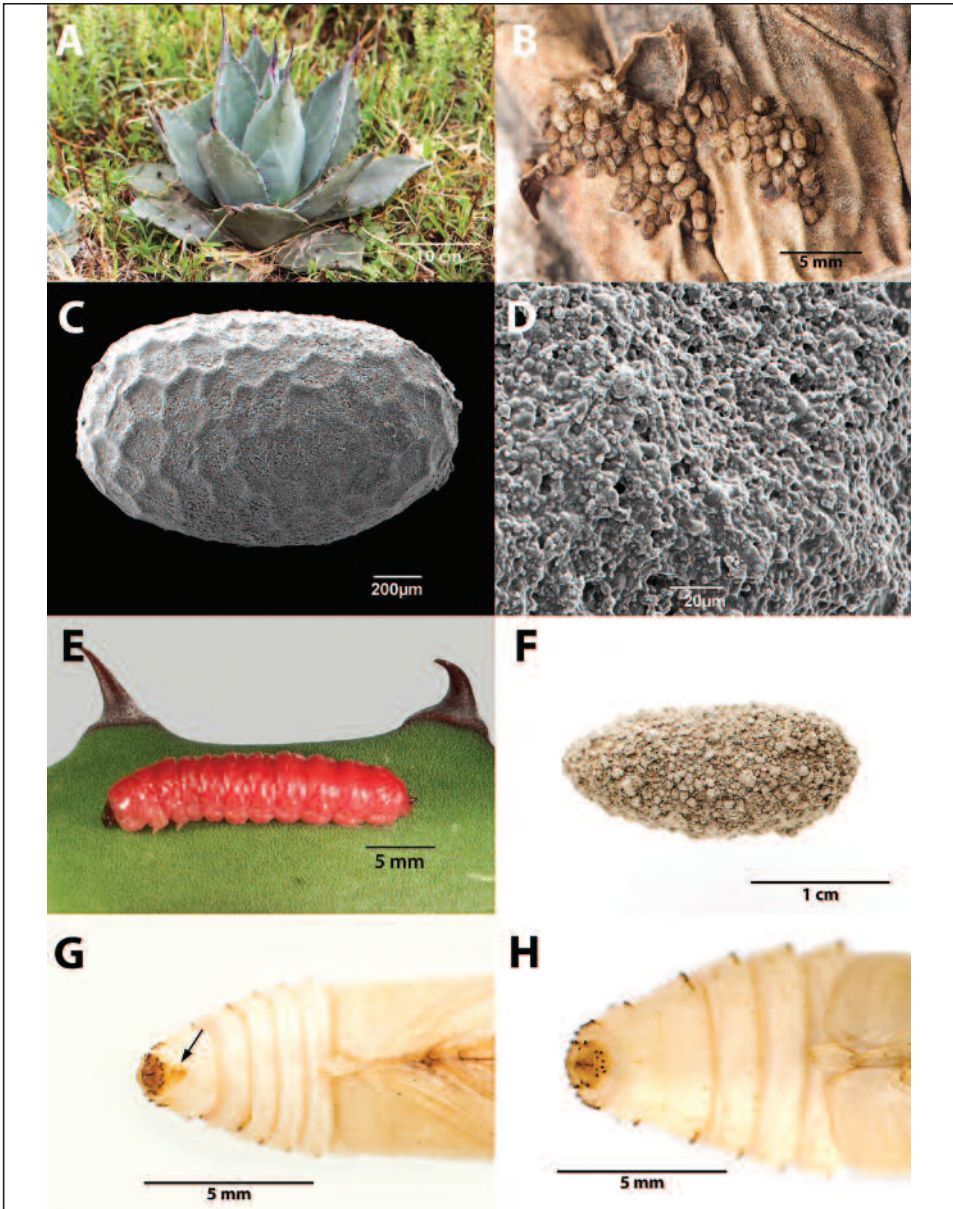


Fig. 1.– A. *Agave applanata*. B. Eggs of *Comadia redtenbacheri* on a dry leaf. C. SEM of the egg of *Comadia redtenbacheri* covered by a secretion from the accessory glands. D. Detail of the secretion of the accessory glands. E. Mature larva of *Comadia redtenbacheri*. F. Cocoon of *Comadia redtenbacheri*. G. Distal segments of a male pupa of *Comadia redtenbacheri* showing small tubercles (arrow). H. Distal segments of a female pupa of *Comadia redtenbacheri*. No tubercles are present.

