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Life History Studies of the Cactus Mealybug, *Spilococcus cactearum* McKenzie (Homoptera: Coccoidea: Pseudococcidae)

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This paper presents the first complete study of the life history, chromosomes, and general habits of the cactus mealybug, *Spilococcus cactearum* McKenzie. Importantly, it contains the first description of the male to be published. Taken in conjunction with Howard L. McKenzie's original description in *Hilgardia,* Vol. 29, No. 15, June 1960, the present work, with its cited references, rounds out a comprehensive record of all the data available thus far. The life stages are described in detail for both sexes, covering their structures and habits. Laboratory rearing experiments in a glasshouse, from egg to adult, are fully recorded, using several constant temperatures in order to determine the optimum range for maximum survival and colonization, as well as the lethal lower and higher temperatures. Chromosome studies for this species are reported for the first time. Reproduction, sex ratio, and mating behavior are described. It was learned that parthenogenesis does not occur; fertilization by the male is essential. One natural enemy was noted: a minute, wasplike, encyrtid parasite that gave effective control. More than 100 acceptable host plants are listed, mostly cacti. The mealybug's feeding habits are given, as are its reactions to various host species and the effects its feeding produces upon them. This insect is considered to be the most important pest of ornamental cacti. The exact place of its origin is a bit uncertain: originally reported from southeast England, it has been taken in France, Italy, California, and New Mexico. Its decided preference for xerophytes and need for moderate temperatures point to a semiarid, desert-type habitat.

THE AUTHORS:

Pichai Manichote, of Bangkok, Thailand, while a student at the University of California, Berkeley, performed much of the experimental work recorded in this paper and produced the original draft of its manuscript, in partial fulfillment of the requirements for the degree of Master of Science. Woodrow W. Middlekauff is Professor of Entomology and Assistant Dean, College of Agricultural Sciences, University of California, Berkeley.

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(Homoptera: Coccoidea: Pseudococcidae)[1]

INTRODUCTION

According to Williams (1962),[2] the mealybug, *Spilococcus cactearum* McKenzie, was first collected at Laindon, Essex, England, in 1928.The first specimens recorded from the United States were taken at Los Angeles in 1941 (McKenzie, 1960). It is considered to be one of the most dangerous pests to ornamental cacti, and is hard to control (Chidamian, 1958; Leese and Leese, 1959; Dodge and Rickett, 1960).

The present paper is the first study of the life history of this mealybug, its general habits, and its chromosomes. It also contains the first description of the male to be published.

HISTORICAL REVIEW

Cactus insects became a major subject of interest to entomologists early in the twentieth century, when several species of prickly pear (*Opuntia*) invaded thousands of acres in Australia. Wilson (1960) stated that 150 to 160 species of insects feeding on cactus were discovered during the period from 1920 to 1939. Of this number, 48 species were introduced into Australia in attempts to control these cacti on about 60 million infested acres. Most of the coccids found on cacti during this period were species of *Dactylopius,* and records of other genera were comparatively few. Hunter, Pratt, and Mitchell (1912) reported on the 5 following species of mealybugs attacking cacti in the United States: *Pseudococcus virgatus* Cockerell, now *Ferrisiana virgata* (Cockerell); *Pseudococcus obscurus* Essig, now *Pseudococcus maritimus* (Ehrhorn); *Pseudococcus longispinus* (Targioni-Tozzetti), now known as *Pseudococcus adonidum* (Linnaeus); an unidentified *Pseudococcus;* and a *Ripersia* species. The cacti in question may have included, at least in part, the same species as those of the invading prickly pears.

TAXONOMY

Spilococcus cactearum, first described by McKenzie (1960), is a member of the family Pseudococcidae, superfamily Coccoidea, order Homoptera. According to Williams (1962), it has often been misidentified as *Coccus* or *Pseudococcus mamillariae* (Bouché). The genus *Spilococcus* was erected by Ferris (1950). Recent keys to North American species of the genus can be found in McKenzie (1962) and Williams (1962).

[1] Submitted for publication June 1, 1966.

[2] See "Literature Cited" for citations, referred to in the text by author and date.

DISTRIBUTION

The distributional records of *Spilococcus cactearum,* enumerated below, are based, in part, on previous reports (McKenzie, 1960; Williams, 1962), and in part on collections made in California by Pichai Manichote, the co-author of this paper.

In California, it has been found in Sonoma, Alameda, San Francisco, Santa Cruz, Contra Costa, Monterey, and Los Angeles counties. Specimens have also been intercepted at the El Cajon, San Diego County, quarantine station, coming from Albuquerque, New Mexico. In Alameda County, it has been collected on cacti in the glasshouse of the Botanical Garden, University of California, Berkeley, and in commercial nurseries in Berkeley and Oakland.

Williams (1962) reported it from England, France, and Italy.

MATERIALS AND METHODS

The laboratory stock culture used in this study was collected in August, 1961, from the glasshouse of the Botanical Garden, University of California, Berkeley. The experimental host plants were grown in clay pots in the glasshouse of the University insectary.

For microscopic study, Canada balsam or Hoyer's solution was used as the mounting medium. Hoyer's solution was preferable for nonpermanent study slides because the insects could be mounted more quickly. Placing the slide on a hot plate for 1 or 2 minutes was sufficient to clear the specimen for study.

More permanent mounts of males and females, using Canada balsam, were prepared as follows: (1) specimens killed in 95 per cent alcohol; (2) bodies of females carefully punctured with fine insect pins (males were too small to be punctured), and both sexes left in a 10 per cent KOH solution at room temperature for 24–48 hours; (3) heated to 60° C. for 10–25 minutes in KOH; (4) stained in an aqueous solution of basic fuchsin for 2–4 hours (females) or for 12–24 hours (males); (5) destained in dilute acetic acid; (6) transferred to 70 and then to 95 per cent alcohol, 30 minutes in each; (7) transferred to xylol for about 10 minutes; (8) transferred to clove oil for clearing for 1 hour or longer; and (9) mounted on slides in xylol-balsam.

The temperature control cabinets used in the life history studies consisted of six 7-c.f. refrigerators, each provided with six 15-w. fluorescent lights. The temperature within the cabinets was thermostatically controlled, and air was circulated by a small fan. The stock cultures of mealybugs used in these trials were reared on *Opuntia microdasys* (Lehm.) Pfeiff.

Certain studies were made in the open insectary glasshouse, where both temperature and humidity fluctuated. A hygro-thermograph was used to monitor these factors. Daily temperatures varied between 21 and 29° C., occasionally reaching 32°. Relative humidities during the day were about 50 per cent, but were somewhat greater during the night.

DESCRIPTION OF LIFE STAGES

The sexes are indistinguishable by external morphology in the first 2 instars. Following these, the female has an additional nymphal instar preceding the adult stage. The male, however, goes into a prepupal and then a pupal stage before final metamorphosis as a winged adult.

Key to the Nondifferentiated and Female Instars

(1) Antennae with 6 segments (first or second instar) .... (2)
Antennae with 7 or 8 segments .... (3)

(2) Tibiae shorter than tarsi; body about 2.5 times as long as antennae (figs. 1–3) .... First instar
Tibiae approximately equal to tarsi; body about 4 times as long as antennae (figs. 4–6) .... Second instar

(3) Antennae with 7 segments; tibiae longer than tarsi (figs 7–9) Third-instar female
Antennae with 8 segments; tibiae longer than tarsi (figs. 10–12) .... Adult female

Eggs. Eggs vary between 321 and 350 μ in length and 175 and 182 μ in width. They are cylindrical in shape, with rounded ends, and are sparsely covered with fine, white, waxy threads. Freshly laid eggs are bright yellow, but as incubation advances, the color turns slightly darker. During the period before hatching, the eyes of the enclosed embryo appear distinctly as minute, reddish-brown spots.

The eggs are laid in an ovisac secreted by ducts and pores at the caudal end of the female's body. From 19 to 176 eggs are laid in each ovisac, with an average of 124.

First nymphal instar, sex not determined (figs. 1–3). Body (on slide) 420–433 μ long, 185–196 μ wide; oblong and flat. The newly hatched insect is translucent yellowish brown. Density of color is somewhat lighter in the anterior and posterior portions than in the middle portion of body. Legs are pale, translucent yellow. As the stage advances, the body becomes covered with a white, waxy exudate.

Dorsally, cerarii appear to be fairly well developed, with 17 pairs present, 7 pairs of which are normally present on the abdomen. Cerarian spines or setae are small and slender. Anal lobe cerarius with 2 slender setae. Dorsal body setae are small and few in number. Six to 8 oral tubular rim ducts are present in a straight row on each abdominal segment except the last. Trilocular pores absent or rarely present.

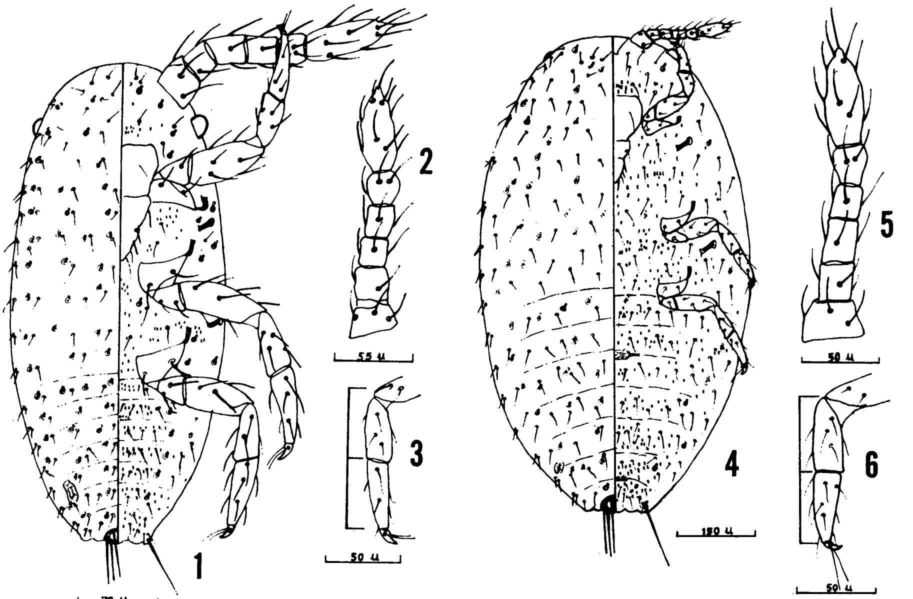
Ventrally, oral tubular rim ducts are the same size as those on dorsum. Normally, 1 is found on each abdominal segment and several on the head and thoracic regions. Ventral body setae are small and few in number, with very small, short, blunt-tipped setae distributed over the venter. Trilocular and multilocular pores are absent or rarely present.

Circulus indistinct. Antennae with 6 segments, 169–176 μ in length, more or less reaching the base of the mesothoracic legs. Labium and legs relatively big and stout compared with body. Tibiae are shorter than the respective tarsi. Average lengths of tibiae and tarsi of front legs (10 specimens), 42 and 48 μ, respectively.

Second nymphal instar, sex not determined (figs. 4–6). Body (on slide) 928–939 μ long, 453–466 μ wide; body outline oval. The living specimen is translucent gray or brown, covered with a white, waxy exudate. Antennae and legs are pale, translucent yellow; the eyes are dark brown.

Dorsally, there appear to be 17 pairs of cerarii, 7 pairs of which are normally on the abdomen. Cerarian spines slender, situated farther apart on head and thoracic regions. Dorsal body setae small, slender, distributed over entire dorsum. Six to 8 oral tubular rim ducts are arranged in a nearly straight row on each abdominal segment, but fewer on each segment of head and thoracic regions. Trilocular pores absent or rarely present.

Ventrally, the oral tubular rim ducts



Figs. 1–6. First and second instars of *Spilococcus cactearum*. (1) First instar, sex not determined. Dorsal view left, ventral view right. (2) Antenna, first instar. (3) Front tibia and tarsus, first instar. (4) Second instar. (5) Antenna, second instar. (6) Front tibia and tarsus, second instar.

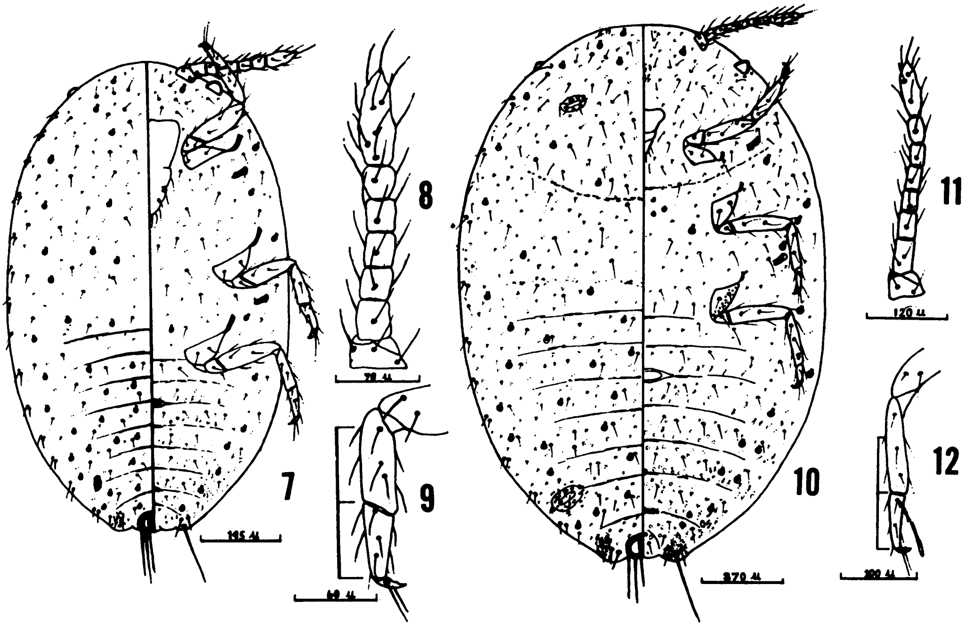
are the same size as those on dorsum, normally 1 on each abdominal segment, several on the head and thoracic regions. Ventral body setae are small and slender. The very small, short, blunt-tipped setae are distributed over venter. Trilocular and multilocular pores are more or less absent.

Circulus oblong. Antennae relatively slender, 6-segmented, not quite reaching base of mid-legs. Labium of medium size compared with that of body. Tibiae approximately equal to tarsi. Average length of front tibiae and tarsi (10 specimens), 50.3 and 51.2 μ, respectively.

Third nymphal instar, female (figs. 7–9). Body (on slide) 1.17–1.69 mm. long, 0.65–0.75 mm. wide; body outline oval. The living specimen is translucent brown, gray, or reddish brown, covered with a white, waxy exudate. Antennae and legs, free of wax, are translucent yellowish brown.

Dorsally, cerarii appear poorly developed, consisting of 7 pairs on the abdomen, but it is difficult to determine the number on the head and thoracic regions because they are very small, slender, and situated farther apart. The total number of cerarii seems to be less than those found in the first and second nymphal instars (approximately 15 or fewer pairs). Anal lobe cerarii have 2 spines. Dorsal body setae are small and slender. Six to 8 oral tubular rim ducts are arranged in a single row on each abdominal segment except the last. Oral tubular rim ducts are fewer on each segment of the head and thoracic regions. Trilocular pores are present, distributed over entire dorsum.

Ventrally, multilocular disc pores are present, usually from the first to the fourth abdominal segment. Tubular ducts of the oral collar type occur in the same region. Normally, 1 oral tubular rim duct of the same size as those on the dorsum occurs on each abdom-



Figs. 7–12. Female *Spilococcus cactearum.* (7) Third instar. (8) Antenna, third instar. (9) Front tibia and tarsus, third instar. (10) Adult. (11) Antenna, adult. (12) Front tibia and tarsus, adult.

inal segment, with a few on the head and thorax. Ventral body setae are more or less slender, but longer than those on dorsum. Trilocular pores are distributed over the venter.

Circulus normally appears circular. Antennae are relatively small, slender, 7-segmented, 269–287 μ long. Labium relatively small. Tibiae longer than tarsi. Average length of front tibiae and tarsi (10 specimens), 78 and 69 μ, respectively.

Adult female (figs. 10–12, 13). Body (on slide) 1.70–3.25 mm. long, 1.74–1.82 mm. wide. Body outline broadly oval. Living specimens are mostly dark gray, except for some individuals that appear to be pale yellow or reddish brown. Covered with a white, waxy exudate, the insect appears to be whitish gray. Antennae and legs, free of waxy covering, are brown. Posterior end of body normally with 2 to 4 short, white pencils of wax. The eyes are dark brown or black.

For recognition characters of the adult female, see McKenzie (1960) and Williams (1962).

Prepupa, male (fig. 14). At this stage, it is clearly distinct from the third nymphal instar female. Body (on slide) 0.92–0.93 mm. long, 0.36 mm. wide; dark brown and free of white, waxy exudate. The eyes are dark brown. Antennae and legs are translucent pale yellow. Antennae with 9 ill-defined segments. Rudimentary wing pads present on the mesothorax. Mouth parts lacking.

Pupa, male (fig. 15). Body elongate (on slide), 1.02–1.24 mm. long, 0.31–0.32 mm. wide. Legs are free, capable of locomotion. Body and simple eyes are dark brown, free of white, waxy exudate. Antennae and legs translucent pale yellow. Head well marked, bearing 3 pairs of darkly pigmented eyes, 1 pair of simple eyes dorsally, 1 pair ventrally, and 1 pair of lateral ocelli. Antennae long, slender, with 10 seg-

Fig. 13. Adult female *Spilococcus cactearum* on *Aeonium haworthii* (x10).

ments, extending posteriorly along margin of body. Antennal segments not clearly distinct, tapering gradually to apex. Mouth parts absent. The mesothorax bears a pair of elongated wing pads, but the halteres have not as yet developed. There are 2 pairs of thoracic spiracles. The anal opening is situated on the dorsal side of the last segment.

Adult male

Until recent years, the taxonomic study of male Pseudococcidae has been neglected, most attention having been given to the female. This has been mainly because of the difficulty in obtaining male specimens (Giliomee, 1961). It was also thought that the male had little significant taxonomic value at the specific level (Ferris, 1957). Recently, Beardsley (1960), in his study of 30 species of the Hawaiian Pseudococcidae, indicated that some of the taxonomic characteristics of male mealybugs may be as important at the specific level as those of females. Giliomee (1961) also established, with complete descriptions, the taxonomically significant characteristics of 3 species of male *Pseudococcus*. Recent reviews of the literature on male coccids may be found in Beardsley (1960) and Giliomee (1961).

General appearance (figs. 16–23). The adult male is a minute fragile insect, with a pair of white, delicate, membranous wings. The halteres are small, with a hooked seta apically. The tip of the abdomen on each side bears a pair of long, white, waxy anal filaments from the glandular plate. The body is dark brown or black, with the excep-

TABLE 1

LENGTH (IN MICRONS) OF ANTENNAL SEGMENTS OF 10 ADULT MALE *SPILOCOCCUS CACTEARUM* REARED IN THE INSECTARY GLASSHOUSE

	Antennal segments									
Number	I	II	III	IV	V	VI	VII	VIII	IX	X
Length (range)	35–45	53–61	81–93	64–77	58–67	61–75	51–61	56–64	51–58	58–63
Average	40	57	88	70	62	66	57	57	55	61

tion of the mesothorax, antennae, and legs, which are translucent pale brown. The simple eyes are reddish brown, dark brown, or black. The following observations were based upon 10 males reared from cacti furnished by the Botanical Garden, University of California, Berkeley.

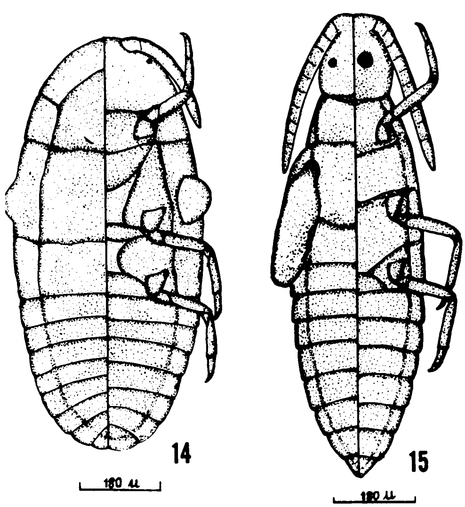
Body. 1.04–1.07 mm. long, 0.30–0.32 mm. wide.

Head (fig. 18). Roughly inverse conical, roundly constricted posteriorly, with a moderately developed midcranial ridge; dorsomedial sclerite not well developed. One pair of simple eyes dorsally, 1 ocellus laterally on each side, and 1 pair of simple eyes ventrally. Dorsal eyes about 20 μ in diameter, widely separated: lateral ocelli small, about 16 μ in diameter; ventral eyes approximately 27 μ in diameter. Functional mouth parts absent.

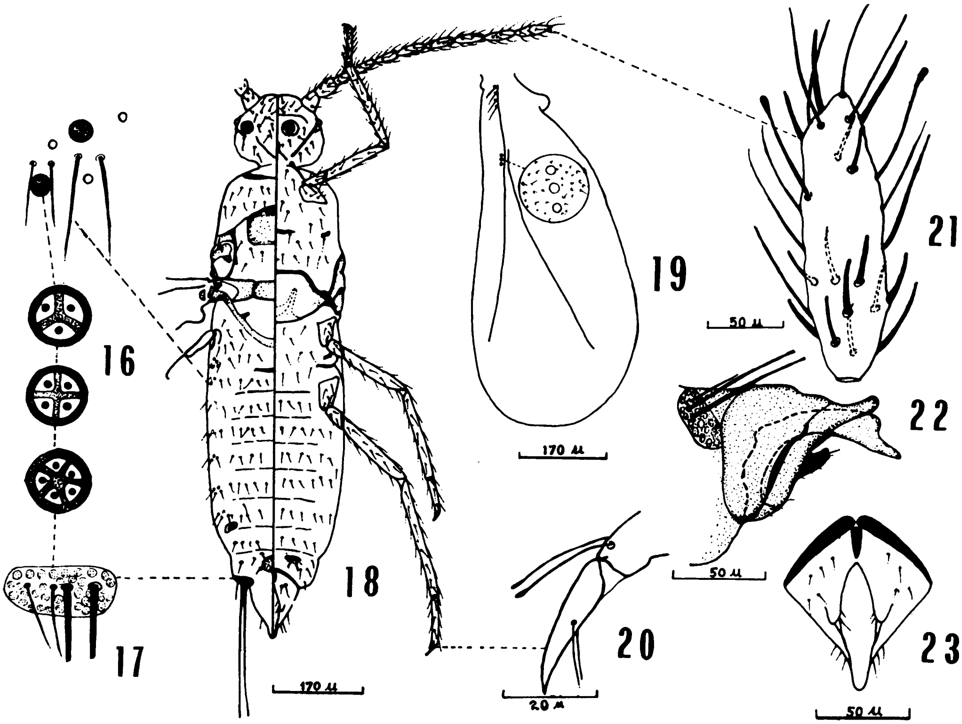
Antennae (figs. 18, 21). Filiform, 10-segmented, inserted on the anterolateral margins of the head close to the preocular ridge. Average length of 10 antennae, 0.61 mm. (table 1). Scape relatively short and thick. Pedicel longer and narrower than scape but thicker than flagellum. Four types of antennal setae are present: stout setae with blunt apex (digitiform), about 12 μ long; thicker specialized sensory hairs of 3 apical segments, about 25 μ long; slender setae (each with a knobbed apex), about 30 μ long; and slender setae (each with an acute apex), about 32 μ long.

Thorax (fig. 18). Convex pronotal angles rounded, separated from the head by a deep cervical groove. A pair of spiracles of equal size ventrally on meso- and metathoracic segments. Prothorax largely unsclerotized. Mesothorax well developed, strongly sclerotized, and strongly humped anteriorly. Postnotum distinct, separated from scutellum by a large, membranous area. A pair of conspicuous postnotal apophyses extend ventrally inward from lateral margin of postnotum. Mesosternum well developed, with internally conspicuous furca. Metathorax externally represented by 2 small suspensorial sclerites, each connected by a sclerotized band to base of halteres.

Wings (fig. 19). Membranous, oblong, 930–970 μ long, 430–445 μ wide; both surfaces covered with microtrichia about 4 or 5 μ long; alar lobe well developed; radius and media veins dis-



Figs. 14, 15. (14) Prepupa of *Spilococcus cactearum,* male. (15) Pupa of *S. cactearum,* male.



Figs. 16–23. Adult male *Spilococcus cactearum*. (16) Dermal discs. (17) Tail-forming pores. (18) Adult. (19) Left wing. (20) Claw of hind leg. (21) Tenth antennal segment. (22) Penis sheath, lateral view. (23) Penis sheath, ventral view.

tinct, but not visibly connected basally. A row of 2 or 3 circular sensoria (fig. 19) is located on the dorsal surface along the radius just above the basal end of the media. A row of 4 slender setae, each about 22 μ long, is located on the leading edge of the radius vein near its base.

Legs (figs. 18, 20). Well developed, elongated, and slender. Front leg shortest, hind leg longest. Coxa is broadly conical, with a basal and apical ridge and well-developed articulating processes. Trochanter subtriangular, anterior and posterior faces each bearing 5 circular sensillae. Femur long, slender, but shorter than corresponding tibia, hind femur about 180 μ in length. Tarsus composed of 2 segments, the basal segment minute. The distal tarsal segment bears a pair of subequal, apically knobbed setae, about as long as the claw (fig. 20). Claw well developed, slightly curved, sharply pointed, about 27 μ long, with a pair of slender, short, setiferous ungual digitules.

Abdomen (fig. 18). Membranous except for the sclerotized apical penis sheath and a small, median, sclerotized patch dorsally and a pair ventrally on segment VIII. Penis sheath (figs. 22, 23) about 100 μ long; a pair of well-developed median lobes, the posterior portion evenly tapered to a rounded apex; about 10 μ wide at a distance of 9 μ before the apex.

Dermal structures (figs. 16, 17). Dermal discs, consisting mostly of 4 peripheral loculi, but occasionally 3 or 5, are distributed along lateral margins of abdominal segments; 1 or 2 discs are found on each side of segments III–VIII; 5 on each side of segment II;

4 or 5 on each side of prothorax; and 2 on anterior part of head between antennae. A tail-forming pore cluster (fig. 17) is located laterally on abdominal segment IX, each cluster consisting of approximately 30–35 pores of the same type as the dermal discs on anterior portion of body. Slender setae are distributed sparsely over the body, mostly 18–20 μ long; digitiform setae absent.

HOST PLANT STUDIES

According to Hamlin (1932) and Wilson (1960), insects found on Cactaceae are mostly restricted to plants in that family. Previous records, as well as field observations by others (McKenzie, 1960), indicated that *Spilococcus cactearum* was restricted to the Cactaceae. In our experiments, *S. cactearum* was tested on many species of cacti, a few succulents, melon seedlings, sugar beets, and potato tubers. It failed to develop colonies on plants other than Cactaceae and succulents. The potato, *Solanum tuberosum* L., which is known to be a very good host for a number of coccids, proved inadequate for *S. cactearum.*

Five ovisacs (about 500 eggs) of the mealybug were placed on potato tubers kept in pint jars covered with linen cloth. Concurrently, 2 other species, *Planococcus citri* (Risso) and *Pseudococcus fragilis* Brain, were also tested by the same method. It was found that the cactus mealybug developed very slowly, with only 9 immature males and 7 immature females resulting. It took the newly hatched nymphs approximately 50 days to develop to the second instar.

As expected, the 2 other species developed well, and formed large colonies on potato.

The accompanying list shows 111 species of cacti and succulents which are suitable host plants for the cactus mealybug; 7 of these records are from McKenzie (1960), and the rest are from our study in the insectary glasshouse, the glasshouse of the University's Botanical Garden, and at local commercial nurseries. Eight plant species in 6 different families on which the cactus mealybug did not develop colonies are given in table 2.

TABLE 2
HOST PLANTS ON WHICH *SPILOCOCCUS CACTEARUM* DID NOT DEVELOP COLONIES

Host species	Plant family
Beta vulgaris L. (sugar beet)	Chenopodiaceae
Citrullus vulgaris Schrad. (watermelon)	Cucurbitaceae
Crassula rosularis Haw.	Crassulaceae
Euphorbia sp.	Euphorbiaceae
Opuntia russelli Br. and R.	Cactaceae
Pereskia aculeata Miller	Cactaceae
Rhipsalis cassytha Gaer.	Cactaceae
Solanum tuberosum L. (potato)	Solanaceae

Host plants upon which *Spilococcus cactearum* developed colonies at Berkeley, California

The 7 species preceded by an asterisk were recorded as hosts by McKenzie (1960).

Family Aizoaceae

Carpobrotus edulis (L.) L. Bol.
Titanopsis calcarea (Marl.) Schw.

Family Crassulaceae

Aeonium haworthii W. & B.
Sedum confusum Hemsl.

Family Cactaceae

Acanthocereus sp.
Ancistrocactus megarhiza (Rose) Br. & R.
Ancistrocactus scheeri (Salm-Dyck) Br. & R.
Aporocactus sp.
Ariocarpus fissuratus (Englm.) K. Schw.
Ariocarpus kotschoubeyanus (Lem.) K. Schum.
Ariocarpus lloydii Rose
Ariocarpus scapharostrus Boed.
Astrophytum capricorne (Dietr.) Br. & R.
Borzicactus samaipatanus (Card.) Kimm.
Cephalocereus sp.
Cereus peruvianus (L.) Mill.
Chamaecereus silvestri (Speg.) Br. & R.

Cochemiea maritima Linds.
Cochemiea setispina (Coult.) Walt.
Coloradoa mesa-verde Boiss. & Davids
Corryocactus brachypetalus (Vaup.) Br. & R.
Deamia testudo (Karw.) Br. & R.
Disocactus biformis (Lindl.) Lindl.
Dolichothele uberiformis (Zucc.) Br. & R.
Echinocactus horizonthalonius Lem.
Echinocereus ehrenbergii (Pfeiff.) Rumpl.
Echinofossulocactus albatus (Dietr.) Br. & R.
Echinofossulocactus densispinus (Tieg.) Schmoll.
Echinofossulocactus lamellosus (Dietr.) Br. & R.
Echinofossulocactus obvallatus (D. C.) Lawr.
Echinofossulocactus pentacanthus (Lem.) Br. & R.
Echinofossulocactus vaupelianus (Werd.) Tieg. & Oehme.
Echinofossulocactus zacatecasensis Br. & R.
**Echinomastus johnsonii* (Parry) Baxt.
Echinopsis ancistrophora Speg.
**Echinopsis* sp.
Encephalocarpus strobiliformis (Werd.) Berg.
Epiphyllum anguliger (Lem.) G. Don
Epithelantha micromeris (Eng.) Weber
Erdisia spiniflora (Phil.) Br. & R.
Escobaria tuberculosa (Eng.) Br. & R.
Eulychnia ritteri Buin.
Ferocactus diguetii (Weber) Br. & R.
Ferocactus rafaelensis (J. A. Purpus) Borg.
Ferocactus schwartzii Linds.
Ferocactus townsendianus Br. & R.
Gymnocalycium netrelianum (Monv.) Br. & R.
**Hamatocactus setispinus* (Eng.) Br. & R.
Heliocereus schrankii (Zucc.) Br. & R.
**Homolocephala texensis* (Hopff.) Br. & R.
Hylocereus calcaratus (Web.) Br. & R.
Hylocereus costaricensis (Web.) Br. & R.
Lobivia lateritia (Gurke) Br. & R.
Loxanthocereus brevispinus Rauh. & Backeb.
Maihuenia poeppigii (Otto) Weber
Mammillaria albicoma Bod.
Mammillaria armillata K. Brand.
Mammillaria blossfeldiana Bod.
Mammillaria fraileana (Br. & R.) Bod.
**Mammillaria macdougalii* Rose
Mammillaria microhelia Werd.
Mammillaria moellendorffiana Schurly
Mammillaria multidigitata Linds.
Mammillaria napina J. A. Purpus
Mammillaria neopalmeri Craig
Mammillaria rubida Back.
Mammillaria scrippsiana (Br. & R.)
Mammillaria sempervivi (D. C.)
Mammillaria tamayonis Schnee
Mammillaria tetrancistra Englm.
Mammillaria woburnensis Scheer
Mammillaria zeilmanniana Bod.
Mammillaria zephyranthoides Scheidw.
Mediocactus sp.
Mila caespitosa Br. & R.
**Myrtillocactus geometrizans* (Mart.) Cons.
Navajoa peeblesiana Croiz.
Neolloydia ceratites (Quehl.) Br. & R.
Neolloydia horripila (Lem.) Br. & R.
Nyctocereus guatemalensis Br. & R.
Nyctocereus oaxacensis Br. & R.
Obregonia denegri Fric
Opuntia macbridei Br. & R.
Opuntia microdasys (Lehm.) Pfeiff
Opuntia vestita Salm-Dyck
Ortegocactus macdougallii Alex.
Pilosocereus alencis (Weber) Byles & Rowl.
Pilosocereus collinsii (Br. & R.) Byles & Rowl.
Rebutia duursmaiana Backeb.
Rebutia spegazziniana Backeb.
Sclerocactus polyancistrus (Eng. & Big.) Br. & R.
Sclerocactus whipplei (Eng. & Big.) Br. & R.
Selenicereus maxonii Rose
Selenicereus spinulosus (D. C.) Br. & R.
Strombocactus pseudomacrohele Backeb.
Thelocactus bicolor bolansis (Runge) Knuth
Thelocactus conothelos (Reg. & Klein) Knuth
Thelocactus hastifer (Werd. & Bod.) Knuth
Thelocactus leucacanthus (Zucc.) Br. & R.
Thelocactus phymatothelos (Pos.) Br. & R.
Toumeya lophophoroides (Wurd.) Bravo & Marsh.
Trichocereus andalgalensis Web.
Trichocereus spachianus (Lem.) Ricc.
Turbinicarpus pseudomacrochele (Backeb.) Buxb.
Turbinicarpus schwartzii (Schurly) Backeb.
Utahia sileri (Eng.) Br. & R.
Weberocereus tunilla (Web.) Br. & R.
Weingartia neumaniana (Backeb.) Werd.
Wilcoxia schmollii (Weing.) Backeb.
Wilcoxia viperina (Web.) Br. & R.
**Wilcoxia* sp.

Habitat preference

The cactus mealybug can thrive in various kinds of glasshouse environments under variable temperature and humidity conditions. Heavy infestations or well-established colonies on *Opuntia microdasys* (Lehm.) Pfeiff., *Maihuenia poeppigii* (Otto) Weber, *Selenicereus spinulosus* (D. C.) Br. & R., *Mammillaria albicoma* Bod., *Opuntia vestita* Salm-Dyck, *Chamaecereus silvestri* (Speg.) Br. & R., *Nyctocereus oaxacensis* Br. & R., and *Weberocereus tunilla* (Web.) Br. & R. were found locally during November and Febru-

TABLE 3
LENGTH OF 8 ADULT FEMALES OF *SPILOCOCCUS CACTEARUM* REARED ON 2 DIFFERENT HOST PLANTS

Host plant	Length of 8 mealybugs (mm.)								Average
	1	2	3	4	5	6	7	8	
Sedum confusum........	1.76	1.88	1.79	1.90	1.92	2.01	1.81	1.70	1.85
Maihuenia poeppigii....	2.57	2.51	2.60	2.72	2.65	2.68	2.56	2.45	2.59

ary, at which time the temperature in the glasshouse was about 21° C. and the relative humidity was about 50 per cent. Colonies were less well developed in these houses during April and June, when the temperature varied between 10 and 38° C. and the relative humidity was between 30 and 90 per cent. Generally, mealybugs developing in glasshouses are more robust than those developing in warm, dry, outdoor situations.

The cactus mealybug usually infests stems, but occasionally the crowns, roots, and flowers. The distribution of the insects on the host plant is presumably based upon the physical environment and the nature of the plant. On *Weberocereus tunilla* (Web.) Br. & R., a soft-skinned and spineless cactus, under presumably favorable conditions, the mealybug tends to aggregate in colonies on the ventral side of the stem of the young plant. In *Hamatocactus setispinus* (Eng.) Br. & R., a hard-skinned species with large spines, colonies are formed mostly around the growing parts of the plant or on new shoots. In *Opuntia microdasys* (Lehm.) Pfeiff., which has small, densely spaced spines with tiny setae on the surface, they are never found in groups, but are commonly scattered all over the surface of the plant. In certain species of succulents, such as *Aeonium haworthii* W. & B., which has true leaves and stems, the mealybugs are mostly found on the stems, leaves, and bases of the leaves. As to the infestation on shaded and unshaded areas of the same kind of plant, no apparent preference has been noted.

Effects of host plants upon the cactus mealybug

Normally, the shape and general appearance of the mealybug are not influenced by the host plant. Experimental results showed that egg production varied on different hosts. It was also observed that almost every species of susceptible cactus, during its propagation period when it had no roots, produced smaller-sized mealybugs than did a rooted plant of the same species.

Size. Sixty eggs of the cactus mealybug were placed on each of 2 species of young plants, 1 succulent and 1 cactus, allowed to hatch, and grown to maturity. Fully mature females with initial ovisacs were then measured. Results from each of 8 specimens showed that the average lengths of the insects reared on *Sedum confusum* Hemsl. and *Maihuenia poeppigii* (Otto) Weber were about 1.86 and 2.59 mm., respectively (table 3).

Egg production. Based on counts of eggs and empty egg shells in ovisacs, it was shown that the average numbers of eggs from groups of 5 cactus mealybugs reared on the same two hosts were 55.6 and 127.8, respectively (table 4).

Reactions of host plants to infestation

As a result of mealybug infestation, 3 distinct types of plant response were

TABLE 4

NUMBER OF EGGS FROM 5 FEMALE *SPILOCOCCUS CACTEARUM* REARED ON 2 DIFFERENT HOST PLANTS

Host plant	Number of eggs from 5 mealybugs					Average
	1	2	3	4	5	
Sedum confusum	45	63	56	43	71	55.6
Maihuenia poeppigii	135	127	118	136	123	127.8

TABLE 5

EGG INCUBATION TIME AND PER CENT SURVIVAL OF *SPILOCOCCUS CACTEARUM* CRAWLERS 24 HOURS AFTER HATCHING UNDER CONSTANT TEMPERATURE CONDITIONS

Temperature (°C.)	Number of eggs	Incubation time		Per cent survival 24 hours after hatching
		Range	Average	
		days		
16	73	22–29	25.1	100.0
20	43	19–25	21.1	100.0
25	198	8–15	12.8	100.0
28	67	9–13	10.1	83.6
30	271	4–11	7.1	42.1
35	171	3–7	5.6	0.0

noted. Large numbers feeding on *Mammillaria albicoma* Bod. caused a pink or reddish discoloration in the grooves of the host plant, followed by tissue necrosis in that area. If the growing point was also infested, often the host would die.

Plant deformation was noted in many species where infestations were heavy. *Opuntia macbridei* Br. & R., *Echinocereus ehrenbergii* (Pfeiff.) Rumpl., and an *Echinopsis* species were among those which became distorted.

The third type of response occurred in every heavily infested plant, and to a degree which depended on the plant species. For example, *Opuntia microdasys* (Lehm.) Pfeiff., which in severe infestations never showed any initial sign of injury, gradually turned from yellowish green to yellow, then completely stopped growing, began to dry from the top, and soon died. No studies were made on the etiology of these effects.

LIFE HISTORY STUDIES

Development at constant temperatures

Experiments to determine the incubation period of eggs under constant temperatures were conducted at 16, 20, 25, 28, 30, and 35° C., respectively. Newly laid eggs were put into small vials, which were in turn placed in the cabinets. At 16, 20, 25, and 28° C., all eggs hatched. At 30° C., most of the eggs hatched, but a few of them did not. At 35° C., very few hatched, and those which did had difficulty in breaking off from the egg chorion and usually died in 1 or 2 hours. The period of incubation varied inversely with the temperature. Incubation data and percentage of crawlers left after 24 hours are given in table 5.

An experiment in the settling of crawlers was conducted at 20, 25, 28, 30, and 35° C. Thirty newly hatched mealybugs from the stock culture were placed on *Sedum confusum* Hemsl. in each cabinet. The mealybugs present were counted 3 days later. Results showed that different temperatures influenced the settling of crawlers. The number remaining was found to be highest at 20°, with none at 35° C. (table 6).

An experiment to determine the development time of both females and males from egg to adult was conducted at 20, 25, 28, 30, and 35° C. Five potted *Opuntia microdasys* (Lehm.) Pfeiff. were put in each cabinet, and 10 newly hatched mealybugs were placed on each plant and examined twice daily. Results are tabulated in tables 7 and 8.

It was impossible to rear newly hatched crawlers to adulthood at 30 and 35° C., but both older nymphs and adults from the stock culture could live for a number of days if placed on plants and held at these temperatures.

Development was most rapid between 25 and 28° C., with the optimum falling somewhere between these two temperatures. Colonies were established at 20 and 25° C., but not at 28° C. or above. Although they could become adults at 28° C., they did not establish colonies at this temperature.

Development and habits under glasshouse conditions

Five newly hatched crawlers were put on each of 10 *Opuntia microdasys* (Lehm.) Pfeiff. After the first molt, only 1 insect was retained on each plant and the rest were discarded. Daily examination of the nymphs was made to ascertain the time of molting of each individual insect. When once the molts occurred, the exuviae were removed. Individual records of each mealybug were kept until they had become fully developed adults.

TABLE 6

NUMBER OF CRAWLERS REMAINING ON *SEDUM CONFUSUM* AFTER 3 DAYS*

Temperature (°C.)	Crawlers remaining on host	
	Number	Per cent
20	17	56.7
25	12	40.0
28	5	16.7
30	2	6.7
35	0	0.0

* Temperatures were kept constant during each 3-day period. Thirty crawlers were used at each temperature.

First nymphal instar of nondifferentiated male and female. Hatching occurs by rupturing the anterior end of the egg chorion. After freeing itself, the newly hatched nymph or crawler is comparatively inactive, remaining in the ovisac for a period of 1 to 5 days. The white, waxy covering of the body gradually increases for approximately 24 hours after hatching.

After leaving the ovisac, the crawlers move around, searching for a feeding place. This is the most active stage. When on a suitable host, they start feeding after 1 to 6 hours. The average duration of the instar was 13.1 days in this experiment.

Second nymphal instar of nondifferentiated female. At this stage, the nymphs tend to be sedentary in habit, with only occasional movements, but will move quite rapidly for a short distance if disturbed. The average duration of this instar was also 13.1 days.

Third nymphal instar female. At this stage, the insects tend to be relatively inactive. They move only when there is a marked change in the physical environment or when they start to molt. The average duration was 11.1 days.

TABLE 7

DEVELOPMENTAL TIME OF IMMATURE FEMALES OF *SPILOCOCCUS CACTEARUM* AT DIFFERENT CONSTANT TEMPERATURES*

Temperature (°C.)	First instar			Second instar			Third instar		
	Number surviving†	Developmental time		Number surviving†	Developmental time		Number surviving†	Developmental time	
		Range	Average		Range	Average		Range	Average
		days			*days*			*days*	
20	16	32–35	32.9	7	21–23	21.7	5	28–29	28.4
25	12	25–29	27.8	7	10–17	13.7	5	12–17	15.6
28	7	11–20	14.6	3	8–9	8.7	3	9–10	9.3
30	2	10–12	11.0	0	...	...	0	...	...
35	0	...	...	0	...	...	0	...	...

* Fifty specimens were used at each temperature.
† After each molt.

TABLE 8

DEVELOPMENTAL TIME OF IMMATURE MALES OF *SPILOCOCCUS CACTEARUM* AT DIFFERENT CONSTANT TEMPERATURES*

Temp. (°C.)	First instar			Second instar			Third instar (prepupa)			Fourth instar (pupa)		
	Number surviving†	Developmental time		Number surviving†	Developmental time		Number surviving†	Developmental time		Number surviving†	Developmental time	
		Range	Average		Range	Average		Range	Average		Range	Average
		days			*days*			*days*			*days*	
20	16	32–35	32.9	4	22–24	22.0	4	7–9	7.5	4	7–8	7.3
25	12	25–29	27.8	5	14–20	15.6	5	4–5	4.6	5	4–6	5.0
28	7	11–20	14.6	2	12–17	14.5	2	4–5	4.5	2	3–5	4.0
30	0	...	...	0	...	...	0	...	...	0	...	...
35	0	...	...	0	...	...	0	...	...	0	...	...

* Fifty specimens were used at each temperature.
† After each molt.

Adult female. Adults are relatively sedentary, but will move from time to time in search of a new place to feed or to form ovisacs. Several females with ovisacs were found about 3 feet away from the host plants. Most females that moved from the host normally formed ovisacs on soil surface debris or in the soil near the crown or roots of host plants. In a presumably favorable environment, females typically aggregate to form a colony and to construct closely knitted ovisacs. They form a cottony mass in which 10 to 20 females can be found.

Females will mate at any time after becoming mature. Normally, the inseminated female starts to form an ovisac 2 to 4 days after mating, and completes it 1 to 2 days before laying the first egg. The average preoviposition time is slightly over 25 days. The oviposition period varied from 14 to 18 days in the glasshouse. The average number of eggs laid per day per female is shown in figure 24. The incubation period varied from 10 to 16 days, with an average of 12.2 days.

The female dies soon after egg-laying terminates. The empty body of the dead

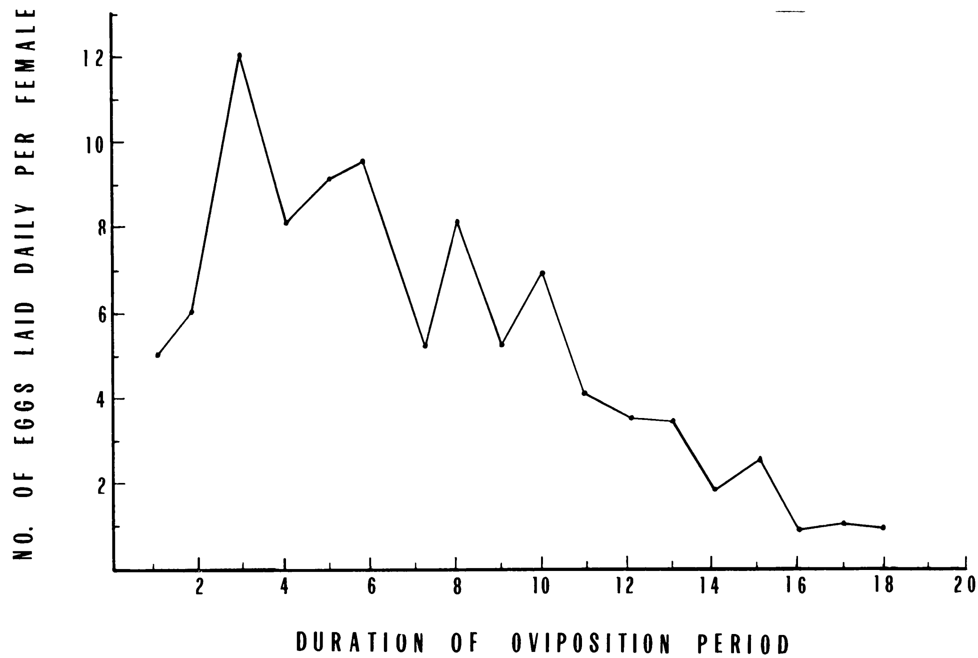


Fig. 24. Average number of eggs laid daily per female *Spilococcus cactearum,* and duration of oviposition period.

female then rises to a vertical position, and is anchored by the mouth bristles to the plant. The average life of a mated adult female was 43 days.

Unmated females live much longer than mated ones, but do not lay eggs or form ovisacs. The average total life of 8 unmated females was 137.9 days.

Second nymphal instar male. The newly formed second nymphal instar male is similar to the second nymphal instar of the female, but becomes distinguishable near the end of this stage when the males begin constructing their cocoons of fine, white, waxy threads. Here the males remain quiescent. The exuviae are pushed to the end of the cocoon after each subsequent molt. The average duration of this instar was 12.4 days.

Prepupa male. At this stage, the insect is quiescent within the cocoon. If removed, however, it can move and will reform a new cocoon, but a prepupa so treated never becomes an adult. The average duration of the prepupal stage was 4.4 days.

Pupa. Here, again, the pupa is quiescent within the cocoon, but can also move if disturbed. If the cocoon is removed, the pupa can still become an adult. The average duration of this stage was 6.3 days.

Adult male. The adult male normally remains in the cocoon for 2 to 7 days before emergence. The newly emerged males are quite sedentary, seldom flying about. The average total life span after molting from the pupal stage was 7.9 days.

The place of cocoon formation varied, some being found on the spines of cacti; in the female colony; in the soil surface debris or within the soil; on the bottoms of clay pots where the host plants were grown; and sometimes as much as 3 or 4 feet away from the host plant.

The cactus mealybug appears to de-

TABLE 9

SUMMARY OF THE LIFE CYCLE OF *SPILOCOCCUS CACTEARUM* GROWN ON *OPUNTIA MICRODASYS* IN THE INSECTARY GLASSHOUSE

FEMALES

Stage	Number of specimens	Minimum	Maximum	Average
		days		
Egg	135	10	16	12.2
First instar	35	9	16	13.1
Second instar	31	10	18	13.1
Third instar	28	9	13	11.1
Preoviposition period (mated females)	10	21	33	25.4
Adult life span	10	35	51	43.0
Total		94	147	117.9

MALES

Stage	Number of specimens	Minimum	Maximum	Average
		days		
Egg	135	10	16	12.2
First instar	14	10	16	13.1
Second instar	12	9	14	12.4
Prepupa	12	3	7	4.4
Pupa	12	4	9	6.3
Adult life span	12	3	12	7.9
Total		39	74	56.3

velop faster and more vigorously at variable temperatures in the glasshouse, with temperatures averaging 20° C. or slightly above (table 9). Under these conditions, females averaged 37.3 days from hatching to adult, while males averaged 36.2 days.

The cactus mealybug produces honeydew in very small amounts, mostly during the period of its rapid growth. This honeydew does not appear to cause injury to the plant. In relatively large colonies of these mealybugs, 5 to 12 drops of honeydew were found on the spines or on the surface of the cactus near the colony. This exudate was not attractive to ants, but on several occasions psocids were found, presumably utilizing the honeydew.

Development out of doors

While *Spilococcus cactearum* is quite common in glasshouses in the San Francisco Bay area, it is not normally found out of doors. Several experiments during the fall, winter, and spring demonstrated that outdoor survival of a colony would be unlikely in this area.

At Berkeley, well-developed colonies of *S. cactearum* reared in the glasshouse on *Opuntia microdasys* (Lehm.) Pfeiff. and *Echinocereus ehrenbergii* (Pfeiff.) Rumpl. were placed outdoors on 3 occasions, September 9, September 27, and October 4, 1961. All continued to develop until the middle of October, after which time the number of mealybugs gradually declined through the rest of October. No eggs were found by the end of October. In November, all adult females disappeared and only 11 in the early instars were left. Males were not seen. Three plants out of 6 died during this time. During the winter months, the remaining 11 immature mealybugs continued to develop and would move when disturbed. In March, there was but 1 mature female remaining, at which time she was mated with a male from the glasshouse, produced one ovisac with 19 eggs, and died in May.

Eggs placed outdoors in mid-February on *Opuntia* began to hatch about 75 days later, in May. From 60 of these hatched eggs, only 4 females matured in July, and again no males were found.

During this same period, thriving colonies in all stages of development could be found in a nearby glasshouse.

CHROMOSOME STUDIES

Except for the genus *Puto*, all species of mealybugs in the Pseudococcidae (including *Spilococcus cactearum*) which have been studied have the lecanoid chromosome system. This chromosome system, first discovered by Schrader (1921) in the mealybug *Pseudococcus nipae* (Mask.), is characterized by one haploid set of chromosomes becoming heterochromatic and excluded from the genetic continuum at spermatogenesis in the male, but otherwise the chromosomes of the two sexes are not distinguishable.

The method employed in the study of chromosomes follows, briefly. Gravid females (2 to 4 days after mating) were stained and squashed in acetocarmine following fixation in Bradley-Carnoy (4 parts by volume of chloroform, 3 of absolute alcohol, 1 of glacial acetic) (Bradley, 1948), with a very small amount of a saturated solution of ferric acetate in propionic acid added as mordant.

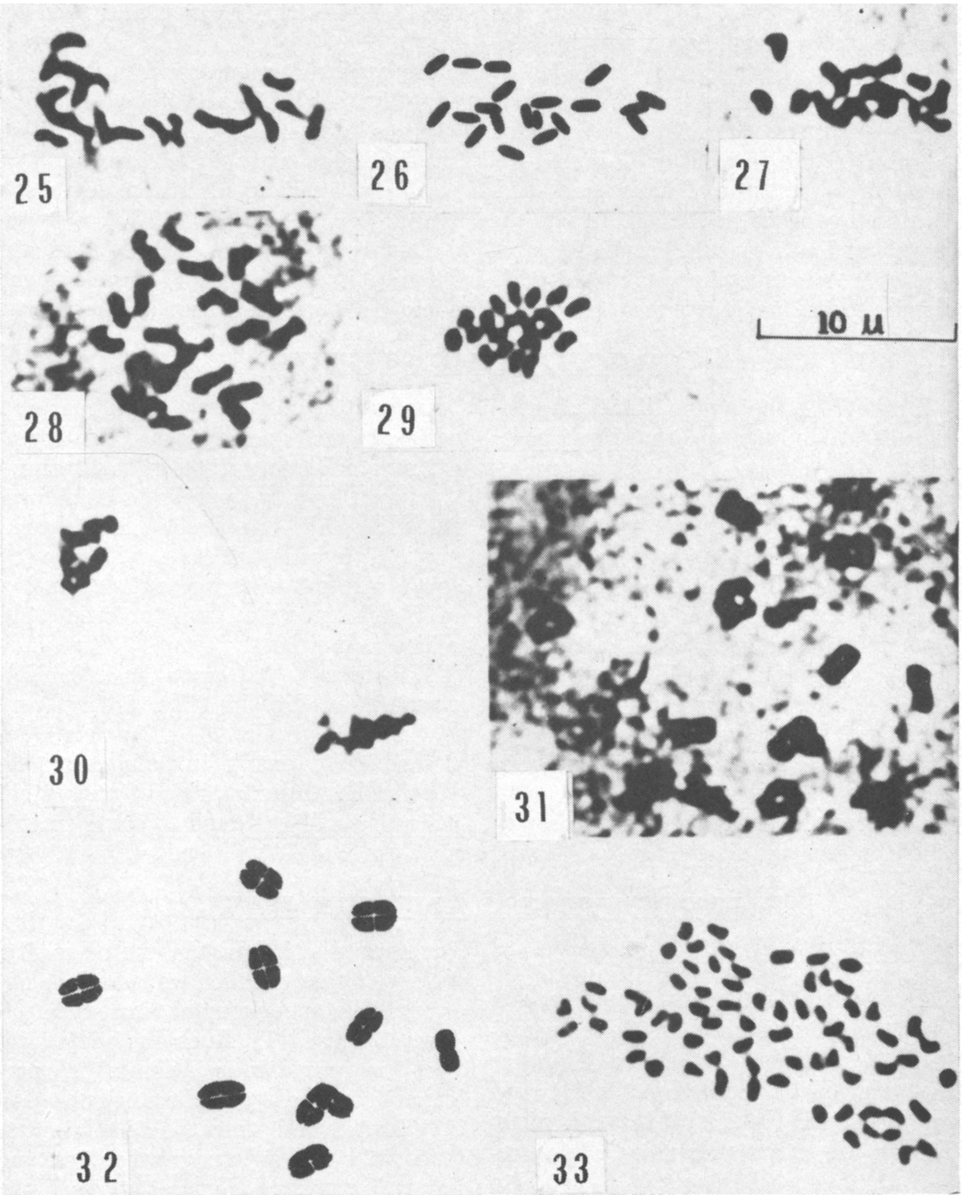
Spilococcus cactearum has 20 chromosomes in diploid (figs. 25–27) and 10 in haploid (fig. 31). As has been described by many investigators, e.g. Hughes-Schrader (1948), polyploid cells also will be found to occur in this species (fig. 33).

REPRODUCTION AND SEX RATIO

Reproduction

It appears that sexual reproduction is the normal method in those mealybugs where males are present. This was first shown by Schrader (1923) and later by Sutherland (1932), both working on the citrus mealybug, *Planococcus* (=*Pseudococcus*) *citri* (Risso). Ito (1938) also showed this to be the situation with the pineapple mealybug, *Pseudococcus brevipes* (Cockerell). Uichanco and Villanueva (1932), when studying the pink mealybug of sugar cane, *Trionymus sacchari* (Cockerell), stated that both sexual and asexual reproduction occur in that species.

The present study has shown conclusively that fertilization is necessary for reproduction in the cactus mealybug, and that parthenogenesis does not occur. The experimental procedure follows, briefly. (1) Each individual insect was reared in isolation after emergence from the egg in the stock colonies. (2) Mated and unmated females were fixed in Bradley-Carnoy's fixative, and later 5 unmated females aged 75–90 days were dissected, with only a few eggs being found. There were no sperm bundles. Upon dissecting 5 mated females initiating ovisac formation, numerous sperm bundles were present in the spermatheca and oviduct of every female. Spermatozoa were also found. Eight unmated adult females remained alive for 97–165 days, but none of them laid eggs.



Figs. 25–33. Chromosomes of *Spilococcus cactearum*. (25–27) Somatic metaphase. (28) Oögonial premetaphase. (29) Oögonial metaphase. (30) Oögonial telophase. (31, 32) First metaphase. (33) Polyploid cell showing 70 chromosomes.

Sex ratio

The sex ratio of the total progeny may vary widely among females, influenced in part by maternal age at the time of mating and by environmental conditions. James (1937, 1938) studied the effects of environmental influences on the sex ratio in *Planococcus* (=*Pseudococcus*) *citri* (Risso); while Nelson-Rees (1960), in a more recent paper on the same species, studied the effect of maternal age upon the sex ratio of progeny.

The procedure used in the study of the sex ratio of the cactus mealybug follows. Eggs were collected on the fourth and sometimes up to the seventh day after oviposition. These were stained with aceto-carmine following fixation in the Bradley-Carnoy fixative, and a few drops of ferric acetate in propionic acid were added (Brown and Nelson-Rees, 1961). Male and female embryos were counted by dissection. From the total of 1,242 embryos from females reared on many species of cacti and succulents in the glasshouse in November, 1961, 665 were females and 577 were males. The sex ratio was close to 1:1. It is to be noted, however, that normally in nature there seems to be great variation in the ratio of the males and females from brood to brood.

MATING BEHAVIOR

Mating is rarely seen in nature, but can easily be observed in the laboratory. Males 2 to 4 days old were isolated in small vials for 1 to 3 days. They were then put into similar vials containing females of different ages. As a rule, these active males were anxious to mate. Mating took place immediately whenever an adult female was found. It was noted that only adult females mated. Males seemed to have poor recognition of the location of the female genitalia. Many of the attempts at copulation seemed to be on a trial-and-error basis, with the male trying to insert the copulatory stylets into other parts of the female's body, as, for example, the head and thoracic regions. In many cases, the antennae of females moved, but older females tended to remain motionless during the mating period.

When mating occurs, the male lies on the female in such a way that the anterior part of his body is placed upon the posterior part of the female's abdomen, which is grasped firmly by his legs. The female raises her abdomen, bending it forward to bring her genitalia closer to the male copulatory stylets. During copulation, the male remains motionless, while the female may walk around or remain motionless. In some cases, especially in younger females, a peristalsis-like movement occurs in the abdomen. The duration of copulation from 10 observed matings varied from 3 to 15 minutes, with an average of 8.2 minutes.

Double and even triple coitus, as described by Nelson-Rees (1959) in *Planococcus citri* (Risso), also occurred with confined *Spilococcus cactearum*. As a rule, when 2 or more males were put into the mating vial with an excess number of females, 2 or sometimes 3 males competed to mate with 1 female. The mating capacity of males was 2 to 6 times for the 8 males observed, with an average of 4 times over a 6-hour period. One female could be mated several times under these conditions. James (1937) reported males of *Planococcus citri* (Risso) mating an average of 9.1 times, with a maximum of 23 times by a single male.

NATURAL ENEMIES

The senior author found an encyrtid parasite, *Pseudaphycus* sp., attacking *Spilococcus cactearum* in the insectary glasshouse on July 3, 1962. According to Dr. Richard L. Doutt, of the Division of Biological Control, University of California, Berkeley, who identified the parasite, this species is near *P. angelicus* (Howard), a highly variable form which has been reared from a number of different mealybugs in California. He believed it to be the same as, or very close to, *P. angelicus,* differing from it by being slightly larger.

Various motile stages of the mealybug were attacked by this wasp. Parasitized pupae were also found. The number of parasites from each parasitized mealybug varied from 1 to 4. The dead mealybugs were swollen (mummified), and were usually covered with white, waxy threads (ovisac-like). In the insectary glasshouse situation, the parasite effectively controlled the mealybug population.

An experiment was conducted with another encyrtid wasp, *Leptomastix dactylopii* (Howard), a parasite of *Planococcus citri* (Risso), furnished by Dr. Doutt. It was tested many times, but did not attack *Spilococcus cactearum.*

SUMMARY

1. This work was undertaken to determine the details of the life history of the cactus mealybug, *Spilococcus cactearum* McKenzie.

2. A description of every stage is given (including the first description published to date of the adult male), plus a key to the different stages of the female. In the study of this mealybug, the following structures were of value in identifying stages: antennae; the proportion of tibia to tarsus; the length of the body; and the number, arrangement, and form of the ducts and pores.

3. In our study, we found the cactus mealybug able to form colonies on many species of Cactaceae and a few succulents in the Aizoaceae and Crassulaceae. It did *not* form colonies on sugar beet, watermelon, potato; on one species each of Crassulaceae and Euphorbiaceae; or on *Opuntia russellii* Br. & R., *Pereskia aculeata* Miller, and *Rhipsalis cassytha* Gaer. (Cactaceae).

4. The nature of injury to the host plant is described.

5. In the glasshouse, the average duration of the life cycle of *Spilococcus cactearum* from egg to death was about 118 days in mated females and 56 days in males. At different constant temperatures, colonies of the mealybugs were established at 20 and 25° C. At 28° C., the rate of development of the nymphal instars was very close to that of the others reared under the favorable glasshouse temperatures, but was several degrees too high to permit colony development. Temperatures above 30° C. were lethal.

6. Chromosome studies, reproduction, sex ratio, and mating behavior are discussed.

7. An encyrtid parasite, *Pseudaphycus* sp., effectively controlled the mealybug in one glasshouse under observation.

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141

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