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**BIOSYSTEMATICS OF THE FAMILY DACTYLOPIIDAE (HOMOPTERA:
COCCINEA) WITH EMPHASIS ON THE LIFE CYCLE OF DACTYLOPIUS
COCCUS COSTA**

by

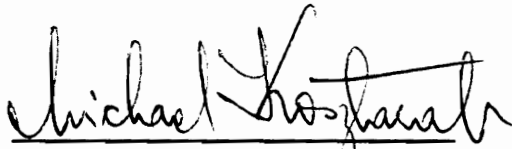
Gema Maria del Carmen Pérez Guerra

Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
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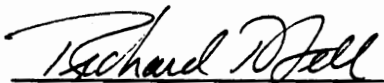
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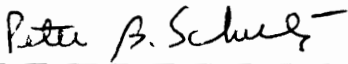
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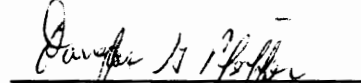
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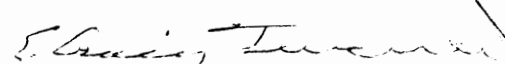
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Committee Chairman: Michael Kosztarab

ENTOMOLOGY

(ABSTRACT)

The cochineal insects include nine species assigned to the genus *Dactylopius* Costa, 1835, the only genus in the family Dactylopiidae. The present research is a comprehensive review of all the species in the family Dactylopiidae, with special emphasis on the life cycle of the type species *Dactylopius coccus* Costa. The adult females of the nine species have been redescribed and illustrated in detail, with a discussion on their morphological affinities and relationships. Their hosts, natural enemies, distribution, etymology, and role as biological control agents are discussed. For several species many new distribution and host records are given. Also, new types have been designated for some of the species. These included designation of one neotype and three paratypes for *Dactylopius coccus* Costa, one neotype for *D. tomentosus* (Lamarck), and designation of eight new topotypes for *D. opuntiae* (Cockerell).

Methods are given on collecting, preservation and slide mounting, also on measurements and on preparation of illustrations. Cuticular ultrastructure is shown in scanning electron micrographs. All developmental stages of the type species *D. coccus* are described. The life cycles under two temperatures and

relative humidities, for both males and females are discussed. Aspects of reproduction in *D. coccus*, its dispersal methods, factors affecting development, and its economic importance are also included.

A separate chapter deals with the host-plants of Dactylopiidae. This includes data on host plant suitability and host plant resistance.

Three identification keys are presented: one to the suborders of Homoptera, the other to the superfamilies and families of Coccinea, and another one for the determination of the species of *Dactylopius*.

The phylogenetic relationships of the family Dactylopiidae with respect to all the Coccinea families is discussed. A phylogenetic tree for the *Dactylopius* species is proposed.

I dedicate this thesis to
FELIPE PEREZ MARRERO, my father
and to
JOSEFA GUERRA VIERA, my mother
for letting me pursue life as I have wanted.

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I knew that to pursue a Ph. D. is a difficult task, and this difficulty increases when the student is not in his/her country with his/her people, language, and culture. Here, in America, it would be almost impossible without the support of many friends and colleagues who made me feel like being at home.

I would like to thank Dr. Michael Kosztarab, my major advisor, for his assistance with this study and for his suggestions during the preparation of this manuscript, also to the members of my advisory committee , Dr. Richard D. Fell, Dr. Douglas G. Pfeiffer, Dr. Peter B. Schultz, and Dr. Craig E. Turner, Jr. for their assistance and recommendations.

I want to thank the curators of the different Coccinea collections for providing information and specimens for this study. Their names are given under "Abbreviations".

I am also indebted to my friends, Harlan Hendricks, for cheering me up and help me with my work all these years; also to Colleen Cannon who always was close to support me whenever I needed; to Imre Foldi who showed enthusiasm in my work and helped me with suggestions. I thank my fellow graduate students, all those who provided me with valuable assistance. My thanks goes also to A. Carnero and O. Saavedra in Tenerife (Canary Islands) for their help in the laboratory and in the field.

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CHAPTER 1

INTRODUCTION

The species in the family Dactylopiidae are known as cochineal insects. They are unique among the scale insects serving first as a source of carmine dye, and second as biological control agents of certain species of *Opuntia* weeds. They have been considered a difficult group of insects to study because of the confusion about their identities. In some cases, the identification of some of their host plants is still not sufficiently clear due to hybridization in the field.

The *Dactylopius* species were recognized very early in history. When the Spaniards conquered Mexico in the early 1500's they learned that the Indians had had a well established dye industry for centuries. The Indians also differentiated between two forms of insects: the "true cochineal" and the "wild cochineal". The first was the largest species of *Dactylopius* and contained twice the amount of pigment as any of the other species. Since that time, this species has been cultivated and protected by man because of its economic importance. The second form or "wild cochineals" include the remaining species in the family. They also contain the pigment, but in lesser quantities because of their smaller size.

In order to establish the cochineal industry in other countries, the Spaniards introduced both the host plants and the insects in parts of Central and South America, as well as in Spain. During the 16th Century and part of the 17th, the Spaniards protected their monopoly of the carmine industry and introduced severe penalties for those who tried to smuggle living samples into other countries that were not under their control. However, species of cochineal were

later introduced into other countries: Australia, India, South Africa, Sri Lanka, etc. Introduction was primarily as part of an extensive biological control campaign against some species of prickly pear or *Opuntia* cactus which are considered as noxious weeds. In some countries the insects were successfully established, but in many others they did not survive.

During the last part of the Nineteenth Century, entomologists realized that the "wild cochineal" was made up of a complex of species, very similar in external appearance. Also, more than one species can often be found on the same host in the same region. Thus, many synonyms were created which has led to frequent misidentifications. These problems have given to this group a reputation of being taxonomically difficult.

The family Dactylopiidae includes only the genus *Dactylopius*. This genus can be separated from the genera in other families because it has characteristics such as: the red pigment contained in the body, and their specialization to Cactaceae plants. Morphological characters can also be used. *Dactylopius* has thick setae with truncate or rounded apices, clusters of quinquelocular pores, which may or may not be associated with tubular ducts, and lack the association of the anal ring with setae and/or pores in all instars.

The first *Dactylopius* was named by Linnaeus (1758) as *Coccus cacti* referring to the commercial species that the Spaniards had discovered in the New World. Costa (1835) placed them in the genus *Dactylopius*. Green (1912) retained all the species in the family under the genus *Coccus* based on descriptions of certain structures such as the length of the body, antennae, eyes, and legs; which currently do not have taxonomic value for this group of insects. Ferris (1955) recognized only four species from North America which were

illustrated and briefly described. Mann (1969) recognized seven species, but some of these were later found by other workers to be members of the same species. He gave distribution and host plant records for each one, but no illustrations. De Lotto (1974) included a total of nine species in the family Dactylopiidae. He recognized five from among the previously described species and named four new species which were illustrated and concisely described.

The present work is the first comprehensive biosystematic study of the family Dactylopiidae. Nine species have been redescribed and illustrated in detail, because workers found it difficult to separate the species.

After the description and illustration of each species, diagnostic characters are presented and discussed, revealing similarities and differences among the species. In addition, host and distribution records, etymology, and natural enemies are given. The potential of each species as a biological control agent is also discussed.

A separate chapter deals with the biology of the type species of the genus, *Dactylopius coccus* Costa. It discusses the life cycle under two temperature and relative humidity conditions for both males and females. The nymphal stages for both sexes of *D. coccus* are also described and illustrated. Some aspects of reproduction of the type species are discussed in the same chapter, as well as the methods used for artificial and natural dispersal. In addition some of the factors affecting development and economic importance are also given.

An attempt was made to prepare practical keys to assist users with species identification. Based on this goal, three keys were prepared, one to the suborders of Homoptera, other to the superfamilies and families of Coccinea, and

one to the species of *Dactylopius*. The usefulness of these keys depends on the quality of slide-mounted specimens.

The relationships of the *Dactylopius* species with their host plants is also taken into account in another chapter. The phylogenetic relationships both with respect to the other families of Coccinea, and among the species within the Dactylopiidae, is also considered.

CHAPTER 2

MATERIALS AND METHODS

Most of the specimens used in this study were borrowed from a number of institutions in the United States and other countries. These institutions are listed under "Collections providing specimens for this study" and are recognized in the "Acknowledgements" section. Some additional materials were also collected and the specimens mounted on slides.

Collection and preservation. All the members of the Dactylopiidae occur on species of Cactaceae and are easily recognized because they are more or less completely concealed in white cottony wax. *Dactylopius coccus* Costa is an exception because it is covered with white powdery wax. These insects may be found either singly or in small groups. All stages were collected from infested plants and placed into 70% ethanol in glass vials. Some insect colonies were kept on cladodes (green flattened stem resembling a foliage leaf). The cladodes were grown in sandy soil contained in pots and maintained in a greenhouse where temperature and humidity were regulated.

Adult males are easily recognized because they have wings. Males were collected with a fine brush from around the female colonies. They were preserved in a fixative/preservative liquid made from: 4 parts of chloroform + 3 parts of 95% ethanol + 1 part of glacial acetic acid.

Preparation of material for study. All specimens were slide-mounted to allow for detailed morphological studies under a phase contrast microscope. Fresh,

dry, and alcohol-preserved specimens were all found to be suitable for slide-mounting. The slide mounting procedure used in our laboratory is modified from Wilkey's method (1962) as follows:

1. If the insect is alive, kill and fix in 70% Ethanol (preferably warm). Leave it in alcohol for at least 2 hours.

2. If the insect is dead (dried on leafpads or stored in alcohol), place it in 10% KOH in a small glass dish for at least 2 hours, then test to see if the body contents are soft by gently pressing the body with a spatula. If body fluid does not come out easily, leave the specimen in the KOH for a longer period or heat it (do not boil) for a few minutes over an electric hotplate, and check again.

3. When the body is soft, while still in the KOH, press out the body contents with a spatula. This is more easily performed under a dissecting microscope and it may need to cut a slit on the body margin for the expelling the body contents. The specimen should be clear (transparent, or nearly so) before transferring it into 70% ethanol for about 10 minutes.

4. The specimens are placed in Essig's Aphid Fluid and 2 drops of Wilkey's Double Stain are added. Leave the specimens in the stain for 2 hours and check for the intensity of staining by removing the specimens to 70% alcohol. If they are not sufficiently stained, put them back in the stain longer. Old adult females usually require almost 24 hours of staining.

5. Transfer stained specimens into 70% ethanol for 10 minutes to remove excess stain.

6. Transfer the insect from the 70% ethanol to 95% ethanol and leave it for 5-10 minutes.

7. Transfer to clove oil for further clearing, the specimens should remain for about 20 minutes. If needed, the insects can be stored in this liquid for weeks.

8. To prepare a slide, place a thin drop of Canada balsam diluted with xylene on the center of a slide and place the specimen in the center of the drop with head down. Press it to the bottom of the balsam to keep it from drifting when the cover slip is added. Place a cover slip (12, 15 or 18 mm in diameter) over the specimen and transfer the slide to a drying oven for 2 weeks at 40^o C. The slide should be labeled with insect and host plant name, locality of collection, date of collection, collector, and determiner's name.

Measurements and counts. All measurements given in descriptions are in microns, except for those specified as millimeters (mm). An ocular micrometer and a Zeiss RA phase contrast microscope were used for measurements. Normally, 10 specimens were described and measured for each species. When possible, the specimens were selected from the type material or from same host and geographical areas from which they were described. The range for measurements and quantitative data is based on selected and measured specimens, while the descriptions are usually based on all of the examined

specimens. Length and width were measured at the longest and widest points for each morphological structure.

The numbers given in the descriptions for clusters, pores, and setae refer to the number counted on half of the body, as represented in the illustrations.

Material examined. For each species the material studied are listed under "Material examined". The records are arranged alphabetically first by country, and after by host, then by locality, date, collector(s), the number of slides and specimens available and the institution where the material is deposited.

Terminology. The terminology used for the descriptions of adult females is that used by Ferris (1955), Karny (1972), and De Lotto (1974).

Preparation of plates. The body outlines of adult females, larval stages, and male were drawn from slide-mounted specimens using a Leitz Prado 500 microslide projector. Details and enlargements of morphological structures were illustrated using a Zeiss RA phase contrast microscope with an attached drawing tube. For each species, a central drawing is divided to show the entire body, the left half represents the dorsal surface and the right half the ventral surface.

The proportions for enlargement of morphological structures within the same plate or from plate to plate are not uniform, so the measurements given in the description should be used for identifications.

The specimen(s) used for the illustration are marked with an asterisk (*) in the section "Type material studied" and/or in "Material studied".

ABBREVIATIONS

Collections providing specimens for this study Names of curators appear in parenthesis.

BM British Museum of Natural History (J. Cox)

CDA California Department of Agriculture,
Sacramento (R. J. Gill)

MNHN Museum National D'Histoire Naturelle,
Entomologie, Paris, France
(D. Matile-Ferrero)

PPRI Plant Protection Research Institute,
Pretoria, South Africa (I. M. Millar)

UCD University of California, Davis (R. O.
Schuster)

USNM United States National Museum of Natural
History, Washington D. C., and
Beltsville, MD. (D. R. Miller)

VPI Virginia Polytechnic Institute and State
University, Blacksburg (M. Kosztarab)

Other abbreviations

Aug.	August
C	Centigrade or Celsius
Co.	County
coll.	Collector (s)
Dec.	December
E	East
elev.	elevation
Feb.	February
fig.(s)	figure(s)
Hwy.	Highway
GPG	Gema Pérez-Guerra
Jan.	January
junct.	junction
KOH	potassium hydroxide
mi.	miles
min.	minutes
Mt.(s)	Mount or mountain(s)
N	North
Natl.	National
NE	northeast
Nº	number
Nov.	November
Oct.	October

Pl.	plate
Rd.	Road
ref.	reference
Rt.	Route
S	South
Sep.	September
St.	Street
Univ.	University
W	West

Selected literature. The selected literature included the original species descriptions, and selected major references on each species of *Dactylopius*. Some articles of lesser importance are also listed for completeness in the "Selected literature and synonymy" lists. The page number is given in the citation after the author and year, when the literature was seen by the author.

CHAPTER 3 THE FAMILY DACTYLOPIIDAE

GENERAL MORPHOLOGY OF ADULT FEMALES. Plates 1, 2, 3

Body Form (PI. 1). Live females may be oval or globous in shape. The shape or outline and the color, are affected by the age of the specimen and whether or not the female is gravid. The body is covered with either a white waxy powder as in *Dactylopius coccus* or with long wax filaments that partially or entirely cover the whole insect as in the other *Dactylopius* species. When the wax is removed the insect body appears dark, purple-red or red-purple.

When mounted on microscope slides, females vary from nearly circular in outline to oval or elliptical in shape.

Derm. The derm is membranous with sclerotized mouthparts, legs, spiracles, and parts of the anal ring.

Segmentation. The head and thorax are fused and there are no distinct segments to distinguish the segmental limits. However, on the ventral side of the prothorax, just under or slightly behind the labium and between the first coxae, is a small sclerotized sternal apophysis which terminates on each side in a large knob. In some specimens, the prothoracic apophysis is not visible. Another apophysis can be observed on both the meso and metathorax; the latter usually with more distinctly separated branches (PI. 1).

The segmentation is well defined on the abdomen and, as in other scale insects, the vulva opens in the ventral intersegmental membrane between the segments VIII and IX. The anal ring is located dorsally on the abdominal segment X (PI. 1 & 2).

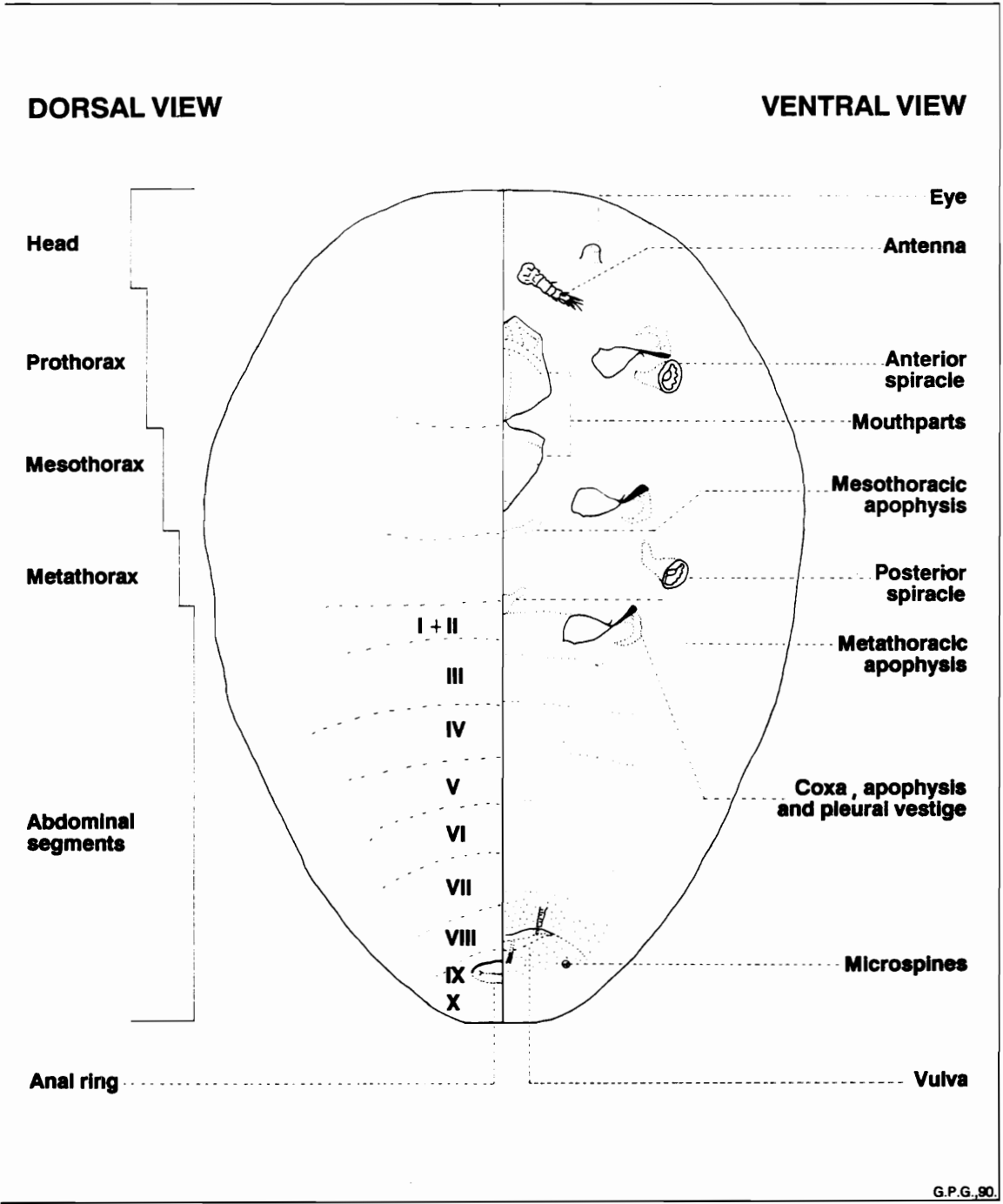
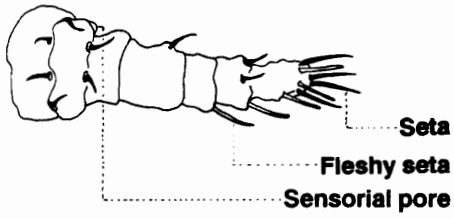
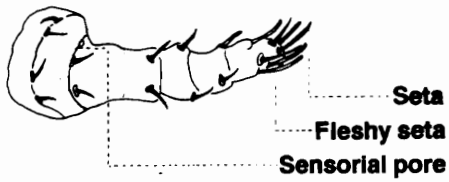


Plate 1. GENERAL MORPHOLOGY OF DACTYLOPIIDAE

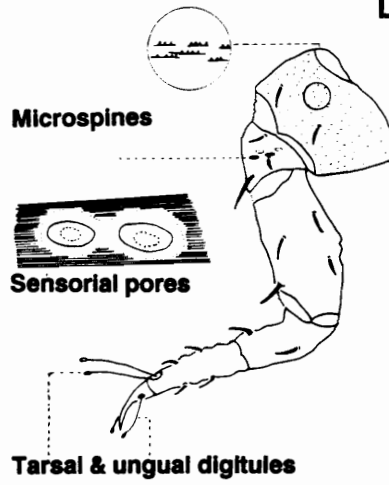
ANTENNA 7-segmented



ANTENNA 6-segmented



LEG



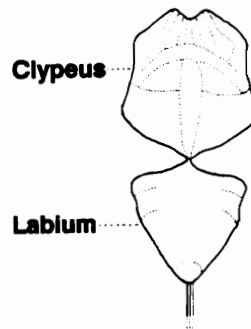
SPIRACLE



SPIRACLE



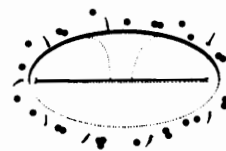
MOUTHPARTS



VULVAR AREA



ANAL RING



G.P.G.,90.

Plate 2. MORPHOLOGICAL DETAILS OF DACTYLOPIIDAE

DORSAL SURFACE

Pores (PI. 3). The structure and distribution of the different types of pores provide one of the basis for identification of the female species in this family. All of the pores are of quinquelocular type, and pentagonal in shape, with five loculi of the same size. According to De Lotto (1974), these are of two types:

a) Narrow-rimmed pores (**Fig. B**) with a narrow non-sclerotized rim.

b) Wide-rimmed pores (**Figs. C₁, C₂, C₃, C₄, C_N**) with a wide sclerotized rim which is represented in the figure by an thick black ring out of the pore.

Wide-rimmed pores normally are distributed on the dorsum and on lateral and sublateral areas of the venter, although exception is found in a few species. They can be found isolated, but usually form clusters from two to more than 30, depending on the species and the body region. The largest clusters are frequently found on the last abdominal segments, particularly on the margins. Normally these formations contain one or more tubular ducts which open at various places inside the cluster.

Narrow-rimmed pores are distributed only on the median areas of the venter. They can be found singly or in clusters, especially on the last abdominal segments where they are more numerous. Sometimes tubular ducts open into them, but the ducts never form part of the whole structure as is found with the wide-rimmed pores.

Setae (PI. 3). The shape and length of the setae are variable. They can range from an almost cylindrical shape with a truncate (**Fig. D₁**) or rounded (**Fig. D₂**)

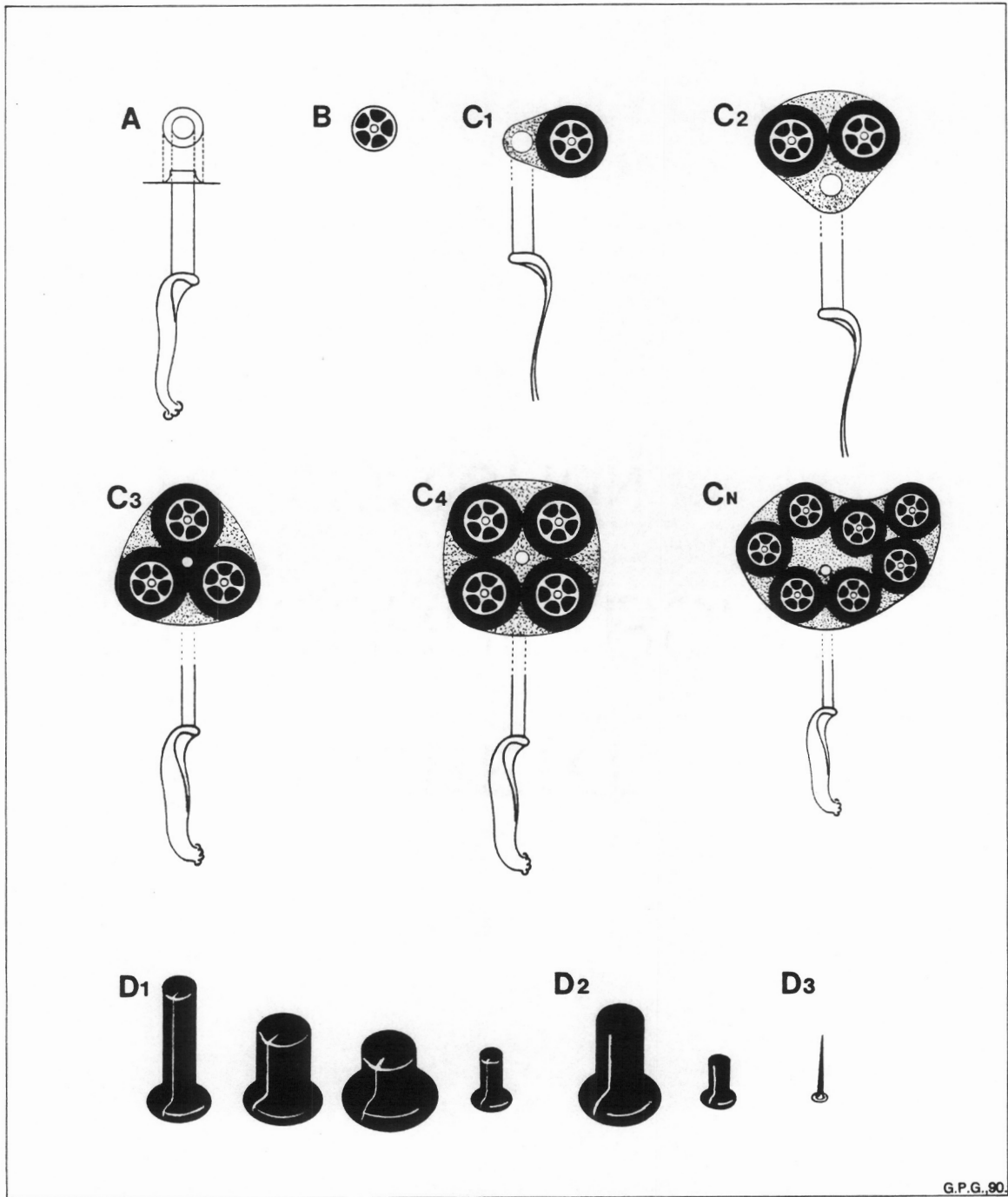


Plate 3. TEGUMENTAL STRUCTURES IN SPECIES OF DACTYLOPIIDAE

A. Tubular duct; **B.** Ventral narrow-rimmed pore; **C₁.** wide-rimmed pore and tubular duct; **C₂.** Cluster with two wide-rimmed pores and tubular duct; **C₃.** Cluster with three wide-rimmed pores and tubular duct; **C₄.** Cluster with four wide-rimmed pores and tubular duct; **C_N.** Cluster with five or more wide-rimmed pores with tubular duct; **D₁.** group of setae with truncate apex; **D₂.** group of setae with rounded apex; **D₃.** hairlike seta.

apex to hairlike setae (**Fig. D₃**) with a slender apex. These setae are located on the dorsum and in the lateral and sublateral areas of the venter. In some species (e.g. *D. zimmermanni*) two or three setae of different sizes are arranged in groups or in longitudinal rows; in others (e.g. *D. coccus*), the setae are quite uniform. In general, setae become smaller toward the head, but in some species (e.g. *D. opuntiae*) setae are very uniform in size. In the family Dactylopiidae, the form and distribution of the body setae are also used as taxonomic characters for species differentiation.

Anal ring (Pls. 1 & 2). The anal opening is located dorsally on abdominal segment X, just slightly anterior of apex of the abdomen. The anterior part is enclosed in a narrow band that can be sclerotized; the posterior part is reduced and not as sclerotized as the anterior. Inside the anal ring the anal opening is found at the end of an internal, funnel-shaped dermal, invagination. The anal ring is obvious in all species except *D. tomentosus*.

VENTRAL SURFACE

Eyes (Pl. 1). These are located on the ventral side, and are simple, conically-truncate, quite large and prominent on a sclerotized base. No ocelli are present.

Antennae (Pls. 1 & 2). In general the antennae are short, with six or seven segments. The terminal segment tapers toward the apex. Sometimes antennal differences can be found within the same species, especially when the segmentation between some antennal articles, usually third and fourth, is unclear

or incomplete (e.g. *D. coccus*). Antennal segments have setae and the distal segments also have fleshy-setae. In all species a sensorial pore is found in the membrane between the second and third antennal segments.

Mouthparts (Pl. 1 & 2). The sclerotized mouthparts are located ventrally, just anterior to the first coxae. The clypeus is usually large with a wide pentagonally shaped base. This structure forms the base for the mandibles and maxillae. The labium is always three-segmented, triangular with rounded vertices. It bears nine pairs of short hairlike setae.

Legs (Pl. 2). The legs are well developed and present throughout all of the immature instars. In the adults they are reduced and strongly sclerotized. All of the specimens examined had a well-developed, sclerotized apophysis and pleural vestige for each leg.

The coxae bear small spinelike projections or microspines, but in some species (e.g. *D. salmianus*) the procoxae do not have these. Microspines are found on the ventral derm of the thorax and along the segments on the abdomen.

The trochanters bear four (two each on dorsal and ventral surfaces) clear sensorial pores near the anterior margin. The femora are large bearing some setae joined basally with the trochanter and distally with the tibia by membranes. Tibiae and tarsi are shorter than femora and without articulation between them.

The claws generally lack teeth, although in some species, such as *D. confertus*, individuals may have a tiny tooth-like process on some of the claws or in all of them.

The apex of the tarsus and the apex of the claw bear digitules which are large and slender setae knobbed apically (i.e. with an enlargement in the distal part). Digitules arise basally, one on each on the dorsal and ventral surfaces of the tarsus (tarsal digitules) and from the claw (ungual digitules). Digitules of the specimens examined apparently have no taxonomic significance.

Spiracles (Pls. 1 & 2). Both anterior and posterior spiracles are large and sclerotized. These characters have taxonomic value, since the operculum which closes the atrial orifice can have the lateral margins smooth or rough.

Ducts (Pl. 3, Fig. A). The ducts are integumental tubules invaginated into the body. The pore or outer part of the duct is circular with a high thick ring toward the outside. The duct is a long cylinder with the proximal end invaginated into a ladle-like shape. A filamentous prolongation or ductule arises from the proximal end and at one side. The ductule opens into a gland reservoir that has a truncate border or in a festoon shape.

Ducts can be found associated with dorsal and ventral clusters of pores or alone in the ventral median area of head, thorax, and abdomen.

Vulvar area (Pl. 1 & 2). The vulva is the female genital opening and is present on the ventral side of the abdomen of mature specimens only. The vulva forms a transverse slit surrounded by dermal folds. On each anterior lateral side there is a large sclerotized process and a small process on each posterior margin. These four processes or apophyses are present in all species; the two anterior ones are

larger than the two posterior. In the family Dactylopiidae the vulva is surrounded by narrow-rimmed pores and some setae.

Distribution. The family includes one genus, *Dactylopius* Costa (defined by Ferris, 1955) and is represented by nine species (De Lotto, 1974), all originating in the Neotropical region. They have been introduced by human activities to other parts of the world.

CLASSIFICATION OF THE DACTYLOPIIDAE

In the suborder *Coccinea*, approximately 6,000 species of scale insects have been described, 20% of these occur in the United States. They had been classified in about 800 genera around the world. The key to the suborders of Homoptera presented here has been adopted from Kosztarab and Kozár (1988). It is based on adults of both sexes, unless stated otherwise.

Key to suborders of Homoptera

1. Tarsi 3-segmented; antennae short and bristle-like; legs well-developed, often adapted for jumping; beak arises from posterior part of head (cicadas and hoppers)..... **Auchenorrhyncha**
- Tarsi 1- or 2-segmented; antennae normally long and filiform, rarely reduced or absent; legs moderately developed or often reduced, not adapted for jumping (except in *Psyllinea*); beak when present, arises between front coxae..... 2

- 2. Tarsi 2-segmented, with 2 claws; adult females normally winged and with well-developed legs except in some aphids; male (when winged) always with 2 pairs of wings; without prepupal and pupal stage (psyllids, whiteflies, aphids)..... **Sternorrhyncha**
- Tarsi 1-segmented (rarely 2-segmented in males and some female margarodids), with only 1 claw; adult females always wingless; rarely legless (Diaspididae, Asterolecaniidae); males normally winged and with only 1 pair functional; male development includes prepupal and pupal stages (scale insects) **Coccinea**

Key to superfamilies and families of Coccinea

This key is adopted with some modifications from the pictorial key to the North American families of scale insects from Howell & Williams (1975). The key is based on external morphological characters of the adult females and the structures mentioned are illustrated. The structures are also defined in the "Glossary" provided at the end of the key. The definitions are adopted from the glossary of Entomology from Torre-Bueno (1990).

- 1. Abdominal spiracles present (Superfamily Orthezioidea) 2
- Abdominal spiracles absent (Superfamily Coccoidea) 3

- 2. Anal ring distinct, with numerous pores and 6 long setae; eyes usually stalked; antennae 3-8 segmented..... **Ortheziidae**

- Anal ring reduced, with no pores or setae; eyes rarely stalked; antennae 1-13 segmented..... **Margarodidae**

- 3(1). A large dorsal spine present near center of abdomen; anterior spiracles much larger than posterior; brachial plates present on dorsum near spiracles..... **Kerriidae**
- No large dorsal spine near center of abdomen; spiracles about equal in size; brachial plates absent 4
- 4. Anal opening covered with 2 triangular anal plates which form an operculum (except 1 plate in the genus *Physokermes*); abdomen with a well-developed anal cleft..... **Coccidae**
- Never more than 1 anal plate covering anal opening (though sclerotized plates laterad of anal opening may be present); anal cleft, if present, usually not as well-developed as in Coccidae 5

- 5. A triangular or oval anal plate covering anal opening; furrows or ridges present on caudal margin; usually found under leaf sheaths of grasses
..... **Aclerididae**
- No anal plate covering anal opening; furrows or ridges not present on caudal margin; habitat and host variable..... 6

- 6. Cluster pore plate present just below each posterior thoracic spiracle; anal ring surrounded by short, stout setae **Cryptococcidae**
- Cluster pore plate absent; anal ring not surrounded by short, stout setae ...
..... 7

- 7. 8-shaped pores present on dorsum..... 8
- 8-shaped pores absent from dorsum; 8-shaped tubular ducts rare, when present derm always with small irregularities..... 11

- 8. 8-shaped pores on dorsum and in a submarginal band on venter; ventral tubular ducts scattered over entire body; antennae 1-9 segmented; on various hosts..... 9
- 8-shaped pores restricted to dorsum; ventral tubular ducts form a submarginal band around body margin; antennae 5-segmented; on *Fagaceae* only **Kermesidae** (in part)

- 9. Antennae 1-9 segmented; ventral bilocular pores and sclerotized anal plate present..... 10
- Antennae 1-segmented; ventral bilocular pores and sclerotized anal plate absent..... **Asterolecaniidae**

- 10. Antennae 1-segmented, with an associated cluster of 5-7 locular pores; triangular, sclerotized plate lying over anal opening..... **Cerococcidae**
- Antennae 7-9 segmented; without an associated cluster of 5-7 locular pores; sclerotized plate lying over anal opening not triangular, much wider than long **Lecanodiaspididae**

- 11(7) Clusters of wide-rimmed pores scattered over dorsum, these may or may be not associated with one or more ducts; body setae range from almost

- cylindrical with truncate or rounded apex to hairlike; anal opening appears as a transverse slit; on Cactaceae only **Dactylopiidae**
- Pores not arranged in clusters and setae not truncate as above; anal opening variable; on various hosts..... 12
12. Terminal abdominal segments fused into a pygidium or pygidium-like compound area; anal opening simple; body covered by a thin shield-like scale or test..... 13
- Terminal abdominal segments not fused to form a pygidium; anal opening often setiferous; body not covered by thin shield-like scale or test 14
13. Beak 1-segmented; legs usually absent or reduced to remnants; antennae 1-segmented; multilocular pores absent; dorsal ocellar eyespots absent; scale covering includes at least the 1st exuviae **Diaspididae**
- Beak 2-segmented; legs present; antennae 3 or 4 segmented; multilocular pores present; dorsal ocellar eye spots present; scale covering not containing the shed exuviae of earlier molts **Conchaspidae**
- 14(12) Small irregularities on derm; legs absent; 8-shaped tubular ducts occur on dorsum and venter (very small and hard to see without high power magnification); anal ring simple, with 0-2 setae and no pores; often associated with palms **Phoenicococcidae**
- Dermal irregularities absent; legs usually present; 8-shaped tubular ducts absent; anal ring variable; on a variety of hosts..... 15

15. Dorsal ostioles, cerarii, and ventral circuli usually present; normally with 1-18 pairs of cerarii; anal ring with inner and outer layer of pores; tubular ducts not invaginated.....**Pseudococcidae**
- Without dorsal ostioles, cerarii, and ventral circuli; anal ring variable; with invaginated tubular ducts 16
16. Tubular ducts, when present, scattered over venter; anal ring usually with pores and setae; microtubular ducts present; usually with protruding anal lobes; on a variety of hosts..... **Eriococcidae**
- Tubular ducts arranged in a ventral submarginal band; anal ring simple, without pores and setae; microtubular ducts absent; without distinctly protruding anal lobes; associated with *Fagaceae* **Kermesidae**

GLOSSARY

The definitions of some of the technical terms that appear in the key are listed alphabetically. These are primarily found in the families indicated in parenthesis.

Brachial plates. A pair of lobes on thoracic dorsum laterad of spiracles (Kerriidae).

Cerarii. Clusters of trilocular pores and stout setae located dorsolaterally on body, often on a sclerotized surface (Pseudococcidae).

Circulus. An adhesive organ, either as a ring or an hourglasslike structure between the fourth and fifth or on the fourth sternite of the abdomen (Pseudococcidae).

Cluster pore plate. Plate with pores on venter, just posterior to hind spiracles, apparently resulting from the reduction of the hind legs (Cryptococcidae).

Eight-shaped (or 8-shaped) pores. Flat, oval structure composed of two adjacent rings giving the appearance of a number "8" (Asterolecaniidae).

Operculum. The anal plates combined or singly forming one single lid over the anal opening (Coccidae).

Ostioles. Small dermal invaginations on dorsal submarginal area of prothorax and on terminal abdominal segments (Pseudococcidae).

Pygidium. A strongly sclerotized, unsegmented region terminating the abdomen, following the first four abdominal segments (Diaspididae).

CHAPTER 4

HOST PLANT RELATIONS

Host plants. The species of the Dactylopiidae are plant pests of Cactaceae (Cactus family). Bailey & Bailey (1978) mentioned that this plant family includes about 50-220 genera and 800-2,000 species of mostly spiny, succulent, perennial herbs, shrubs, vines, or small trees. According to one of the most widely accepted theories, the plants are almost exclusively native to Central America (Gulf of Mexico and Caribbean area) from where they migrated to North and South America. Some botanists believe that the Cactaceae is a family of recent phylogenetic origin. This assumption is based on a lack of fossils, the great variability of species, and the large number of reproductive forms (seeds, pieces of plant, new stems).

The cochineal insects can be found mainly on two genera of cacti: *Opuntia* and *Nopalea*, the latter includes eight or nine species, the former over 200. Since the Sixteenth Century when the cochineal insects were discovered by the Spaniards, many species of cacti have been introduced to different countries for both the propagation of the insects and as ornamental plants.

According to Piña-Luján (1977), Linnaeus classified the Mexican host plant for *Coccus cacti* (= *Dactylopius coccus*) as *Cactus cochinillifera*. Müller called the host plant *Opuntia cochenillifera*, and Salm-Dyck referred to it as *Nopalea cochenillifera* (in Piña-Luján, 1977). However, several authors agreed that this was not the host plant for the cochineal in Mexico, but rather *Opuntia ficus-indica*, also known as "Nopal de Castilla", and *Opuntia tomentosa* or "Nopal de San Gabriel". Piña-Luján (1977) also cited *Opuntia pilifera* (commonly called in Mexico: "Nopal

Pluma or Nopal Castarrita") as a host plant for some of the wild species of cochineals.

In the Canary Islands, Spain, where *D. coccus* was introduced one hundred years ago and has been cultivated since, *Opuntia ficus-indica* is the most common host plant today, and is found only in cultivation. The insects also feed on other *Opuntia* spp. but those insects decrease its size and fertility.

The genus *Opuntia* is also known as "prickly pear" or "Indian fig" and, according to Fernald (1950), they are branching plants with the segments or internodes separated by joints or articulations. The plants are flattened to terete and bear the flowers along the margins of the new shoots. Some species of *Opuntia* have been used since pre-Colombian times by the natives of Central America, not only for the cochineal cultivation, but also as a food source. They consume the fruits and new stems of the plants while the older stems are used for feeding livestock.

Opuntia ficus-indica (L.) Miller has been also known as *Cactus ficus-indica* L., and *Opuntia ficus-barbarica* Berger. These plants have also been cultivated for the edible fruit, to decorate gardens, and for use as hedges because they grow from 1 to 5 m high. The stems are ovoid, 30-50 cm long, fleshy with flattened joints; the areoles are small, spineless; and the flowers are bright yellow, 7-9 cm in diameter. They grow where the winters are mild. According to Uphof (1968), the fruit is known as tunas, Indian figs or prickly pears. They are highly valued by Mexicans and are shipped in large quantities to the United States. They have high nutritional value and are eaten fresh, dried or prepared in various ways.

For each species of *Dactylopius*, under "Material studied" and "Additional hosts", the host plants are listed from which specimens have been collected.

Host plant suitability and host plant resistance. In the Canary Islands, in the field, the suitability of host plants for *D. coccus* was correlated with the rate of development of the insects. The host plants on which the cochineals developed fastest were considered as the most suitable hosts. *D. coccus* developed faster on *Opuntia ficus-indica* than on *O. tomentosa*. The fine large hairlike spines found on this species of cactus make it difficult for the crawler to settle down. The observations were made outdoors at fluctuating temperatures during June, July and August. When the temperature rises a couple of degrees (from 24 to 26°C), the development of the insects was very affected. The optimum development temperature of *D. coccus* was 25-26°C on *O. ficus-indica*.

In order to test the host preference for the insects, fresh cladodes or new stems from different host plants were offered to the crawlers or first instar stage of *D. coccus*, which is the active phase of the insect. They preferred to settle on the different hosts in this order: *Nopalea cochinellifera*, *O. ficus-indica*, and *O. tomentosa*. *Nopalea cochinellifera* (L.) is an ornamental plant in the Canary Islands that can reach 3-4 m high. It is easily infested with *D. coccus* and the colonies develop rapidly. However, there are two problems in using this plant as a host: 1) because of its height, it is inconvenient to harvest the insects, and 2) the plant does not develop well in windy areas, where most of the *D. coccus* cultivation occurs.

All the host plants manifest resistance to the insects' attack by slowing down the developmental rate. As a result of this slower rate of development, the plant causes the insect to extend its range of the host plant search for other host plant on which to develop.

To date *D. coccus* has not been listed from host plants other than those already known. However, Karny (1972) mentioned from South Africa an extension of host plant range for "species P" (= *D. opuntiae*). This species successfully attacks some spineless cactus varieties that initially were thought to be resistant to the attack of cochineal insects.

CHAPTER 5

GENERAL BIOLOGY OF DACTYLOPIUS COCCUS COSTA.

LIFE HISTORY

All the species of *Dactylopius* appear to have somewhat similar life history patterns. The female has four developmental stages: egg, first nymphal instar (crawler), second nymphal instar, and adult. The male has six stages: egg, first instar nymph, second instar nymph, prepupa, pupa, and adult.

The study of the life cycle of *D. coccus* Costa was completed in the Canary Islands (Spain) during the summer of 1986. All observations were made in the laboratory.

1) **Material-** The host plant, *Opuntia ficus-indica*, and the insects were collected in Las Chumberas, Geneto, Tenerife.

2) **Infestation-** The new colonies were initiated by placing some gravid females on fresh cladodes during their oviposition period. These plants were infested as follows:

A) Two cladodes with a total of 200 crawlers

B) Ten cladodes with a total of 140 crawlers

3) **Temperature and humidity-** Two tests were carried out under constant temperature and humidity conditions. The temperature and relative humidity in the rearing room were checked regularly with a hygrothermograph and the temperature fluctuation did not exceed 1^o C. One was 24^o C and 65% R.H.; and other was 26^o C and 60% R.H. Both temperature and relative humidities

correspond to the mean from two areas of production of *D. coccus* in the Canary Islands.

DEVELOPMENTAL STAGES OF D. COCCUS COSTA

EGGS

Description. Eggs are light red, oval with a smooth shiny surface; about 0.7 mm long and 0.3 mm wide.

Incubation. None of the females observed gave birth to crawlers. The eggs hatched immediately or sometime during the first 30 minutes after being laid. The rapid hatch gives the impression that the females are viviparous, thus some authors have erroneously described them as such.

Hatching. Shortly before hatching, the crawler can be observed through the egg chorion. The egg breaks along a dorsoventral longitudinal line which starts at the head and continues almost half the length of the egg. The crawler requires from four to over twenty minutes to emerge through the gap in the chorion. At first, the legs, antennae, and mouthparts are glued to the body, but after one or two minutes the insect frees these parts. The discarded chorion is white and remains close to the mother.

FIRST INSTAR FEMALE AND MALE OF D. COCCUS COSTA

Plate 4

Description. The first instar is also called a "crawler" during its active phase. It is oval, about 1.0 mm long and 0.5 mm wide, with a bright red color and well-developed legs and antennae. The antennae are six-segmented with the third segment the longest. The eyes are dark, and easy to discern. Setae with a rounded and truncate apex (Pl.3; Fig. D₁ & D₂) are located singly in two longitudinal medial and submedial rows and in groups of two or three along the body margins. Some hairlike setae are found on the ventral side and on the last segments of the dorsum. Across the head there is a transverse row of four setae on each side. Small clusters of wide-rimmed pores (Photo 1) are close to the marginal setae, primarily on the abdominal segments.

Gunn (1979) stated that cochineal-insect crawlers are larger and live longer than other coccoid crawlers. The settled first instar nymphs differ from the crawlers in their larger size and by the increased formation of white powdery wax.

Behavior. After emerging, the crawlers stay for a few minutes in the protective wax on their mother's body. The crawler then begins to move away from its mother to another cladode of the same or a different host plant. Usually crawlers walk to the top of the host plant where they can find fresh cladodes. This is also the period in the life cycle when wind and air currents play an important role in the dispersal of the insects.

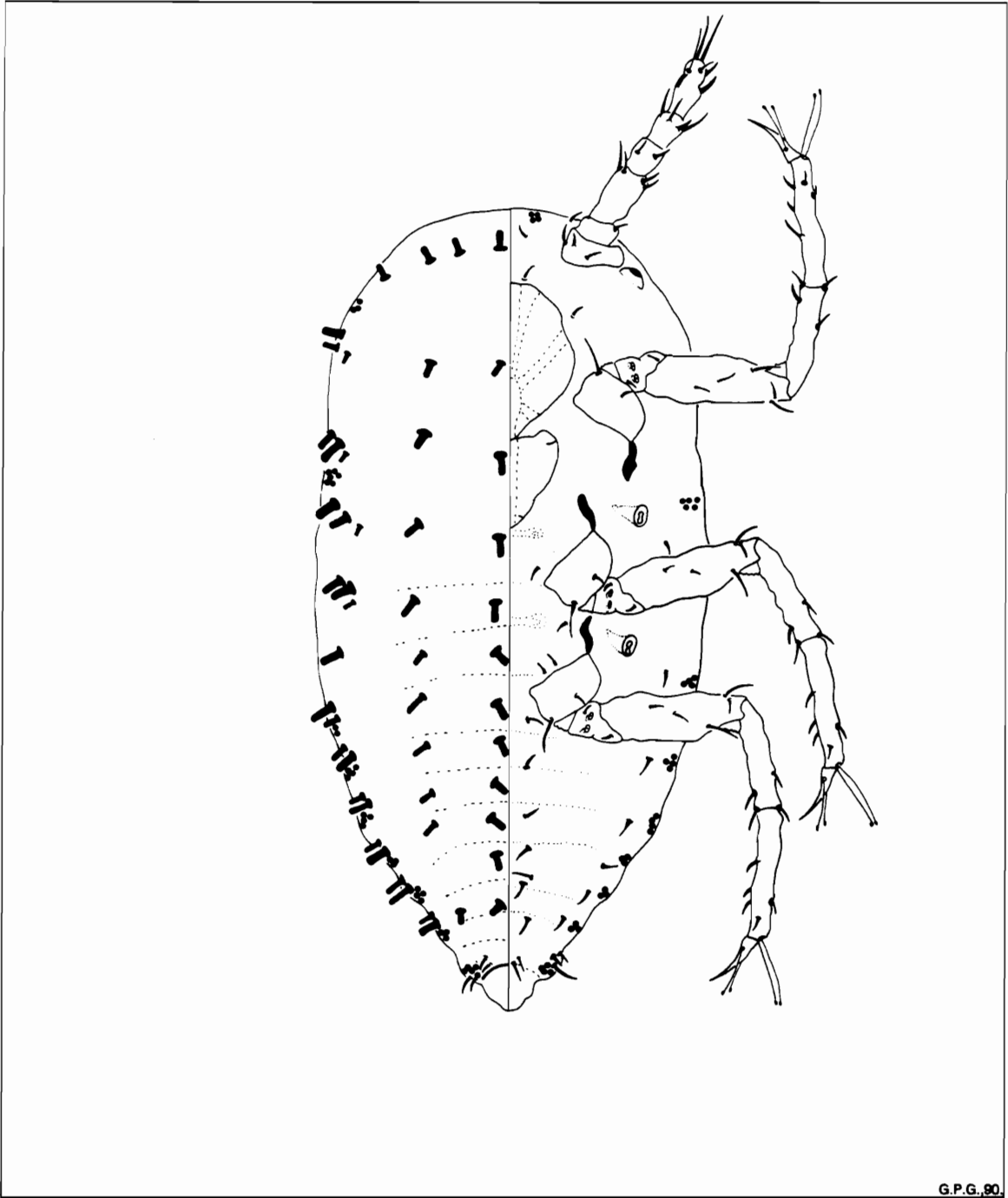


Plate 4. First instar female and male of *Dactylopius coccus* Costa



Photo 1. Ventral view of the first instar of *Dactylopius coccus* Costa showing small lateral clusters of wide-rimmed pores and setae. (Scanning electron micrograph).

The young nymph can search for almost two days for a place to settle. Typically it attempts to insert its mouthparts into the plant tissue. Young cladodes that are still non-turgid are preferred. The insects exhibit a thigmotactic behavior, preferring to settle at spine bases or irregularities in plant surfaces. The crawlers appear to be negatively phototactic and therefore show a sensitivity to sunlight. They are usually found on the side of the stem which is not exposed to direct light. Once the crawler is established, it will not move again. Most of the crawlers which settle close to their mother are males, while those that settle further away are females.

Wax secretion. The secretion of wax starts within an hour after hatching. First, small white dots appear on dorsal side of the abdomen, and later on thorax. After a few hours the crawler appears dusted with white powder, and the first short waxy threads can be observed. These threads are produced from glands under the base of the large dorsal setae. The threads of wax grow straight up increasing continually in length. By the time the insect completes the first instar, the threads of wax are longer than the body. These threads are brittle and break easily, but are used as sails to aid in the dispersal of the insects by air currents to other plants.

The newly hatched crawlers do not show sexual dimorphism, but as they start to produce the wax threads, the males and females can be separated. In general, male crawlers have shorter wax filaments than the females and the filaments develop only on the abdominal segments, while females have longer filaments and these are on the head, thorax, and abdomen. Sexual dimorphism in the wax threads of first instar of *D. coccus* Costa is similar to that of *D. austrinus* De Lotto as described by Gunn (1978).

the wax threads of first instar of *D. coccus* Costa is similar to that of *D. austrinus* De Lotto as described by Gunn (1978).

The first molt. The first molt took place 35-38 days after hatching at 24^o C, 65% R.H., and after 25-27 days at 26^o C, 60% R.H.

The old cuticle of the first instar opens dorsally on the cephalothorax to allow the insect to escape. The insect slowly pushes the cuticle back requiring about 20 minutes to complete. The exuviae are almost triangular, white, and remain attached to the posterior part of the insect until it is dislodged by the wind. The soft new cuticle of the nymph is carmine in color.

SECOND INSTAR FEMALE OF D. COCCUS COSTA

Plate 5

Description. Second instar nymphs are oval, about 1.1 mm long and 0.6 mm wide. The body setae are not as long as in the first nymphal stage. Clusters of 20 or more wide-rimmed pores, which are very loose and look like islands (Photo 2), are mainly found on the body margins. The antennae are six-segmented. The mouthparts are large. The legs are well-developed but non-functional. The spiracles are also large with a smooth opercular opening. The anal ring is well-developed with a sclerotized narrow bar at the anterior margin.

Behavior. After molting, the insect must re-attach herself to the host plant. They usually remain in close proximity to resettle but some move and will not attach successfully.

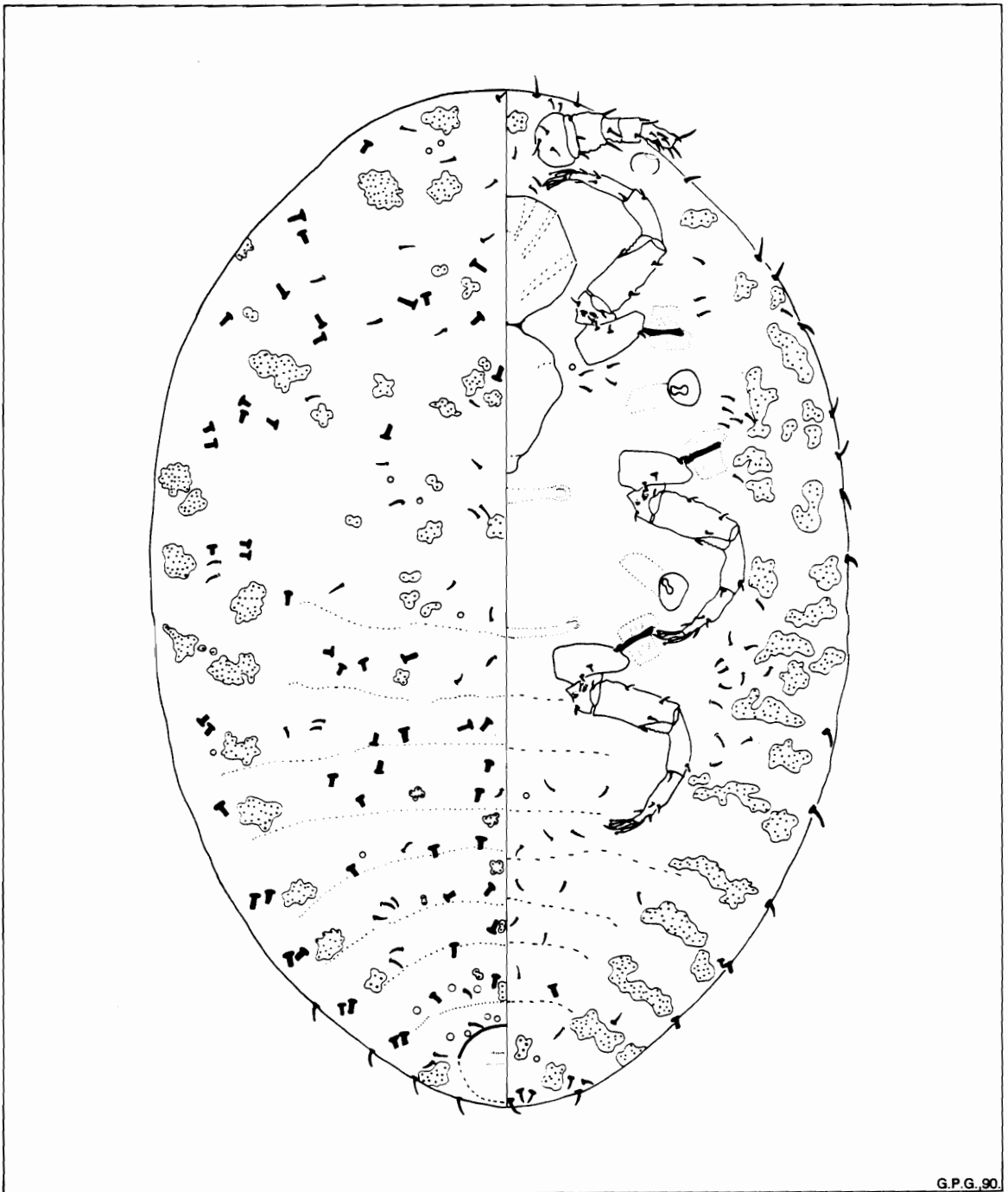


Plate 5. Second instar female of *Dactylopius coccus* Costa



Photo 2. Ventral view of the second instar female of *Dactylopius coccus* Costa showing lateral clusters of wide-rimmed pores and setae. (Scanning electron micrograph).

Wax secretion. After molting nymphs are shiny brownish-red, but their bodies are rapidly covered with white powdery wax while the segments are clearly visible. The second instars do not have the long wax threads as in the first nymphal stage.

The second molt. The second molt occurred 20-23 days after the first molt at 24^o C, 65% R.H., and 11-15 days after the first molt at 26^o C, 60% R.H.

The molting process was the same as described for the first molt, but the exuviae is larger, also triangular, and remains attached to the caudal end of the insect for a longer period.

ADULT FEMALE OF D. COCCUS COSTA

Plate 12

At 24^o C, 65% R.H. the nymphs became adults 23 days after the second molt, and at 26^o C, 60% R.H. the nymphs only needed 11 days.

Morphology. The adult female of *Dactylopius coccus* Costa is described in Chapter 6.

Wax secretion. A few hours after the second molt, the insect starts to produce white powdery wax. The wax is somewhat more dense than on the second instar and covers both the dorsal and ventral sides.

Pre-oviposition period. The pre-oviposition period extends from the last molt until the production of eggs. The insects at 24^o C, 65% R.H. required 35-37 days, while at 26^o C, 60% R.H. they needed 32-35 days.

The total time required to reach sexual maturity in females, from the egg stage through the pre-oviposition period was 93-98 days at 24^o C, 65% R.H., and 68-77 days at 26^o C, 60% R.H. These results show that the insects reared at 26^o C developed faster than those reared at 24^o C.

Oviposition. After copulation, the size of adult females increased. The eggs were laid mainly at the night. Often, during their first day of oviposition, females laid a few eggs which were isolated in space and time; but soon reached a peak in the oviposition rate. At this time, the eggs were produced in a chain-like sequence, glued together at the extremes. Toward the end of the oviposition period, females become wrinkled and decreased in size, until they died. The post-oviposition period is about 10-20 days. If the females are separated from the host plant, they continue egg-laying. The largest detached females had longer oviposition periods, so they could be used for infesting new plants. The oviposition period lasted 30-50 days.

Fecundity. The average number of eggs per female was 430; the range was 275-600. Females which did not lay any eggs lived for a longer period.

Moran & Cobby (1979) showed that for *D. austrinus* De Lotto, fecundity is dependent upon female density on the plant and on the condition of the host plant. They also observed that the mean crawler production per female

decreased as the female cochineal density increased but increased when the cladodes were rotten or dead.

DEVELOPMENT OF MALE DACTYLOPIUS COCCUS COSTA

The life-history of male *Dactylopius coccus* Costa resembles that of holometabolous insects which pass through a complete metamorphosis and in which the nymph is morphologically very different from the adult.

The first instar male was discussed together with the first instar female because of their similarities. The main differences were related to their behavior and wax secretion. The primary behavioral difference, as previously explained, is related to migration; the male crawlers did not migrate far from their mother. The other difference is related to wax secretion; the large filaments of wax in male nymphs are shorter and less numerous than that of female nymphs.

SECOND INSTAR MALE OF DACTYLOPIUS COCCUS COSTA

Plate 6

Description. The second instar of the male can be differentiated from the second instar female mainly by size. It is slightly larger and narrower, 1.3 mm long and 0.3 mm wide. They also have a large number of tubular ducts on venter as well as on dorsum. All the setae are hairlike, these being numerous and scattered over the entire body. Wide-rimmed pores are present dorsally as well as ventrally. They may be found singly or in small groups on the body margin.

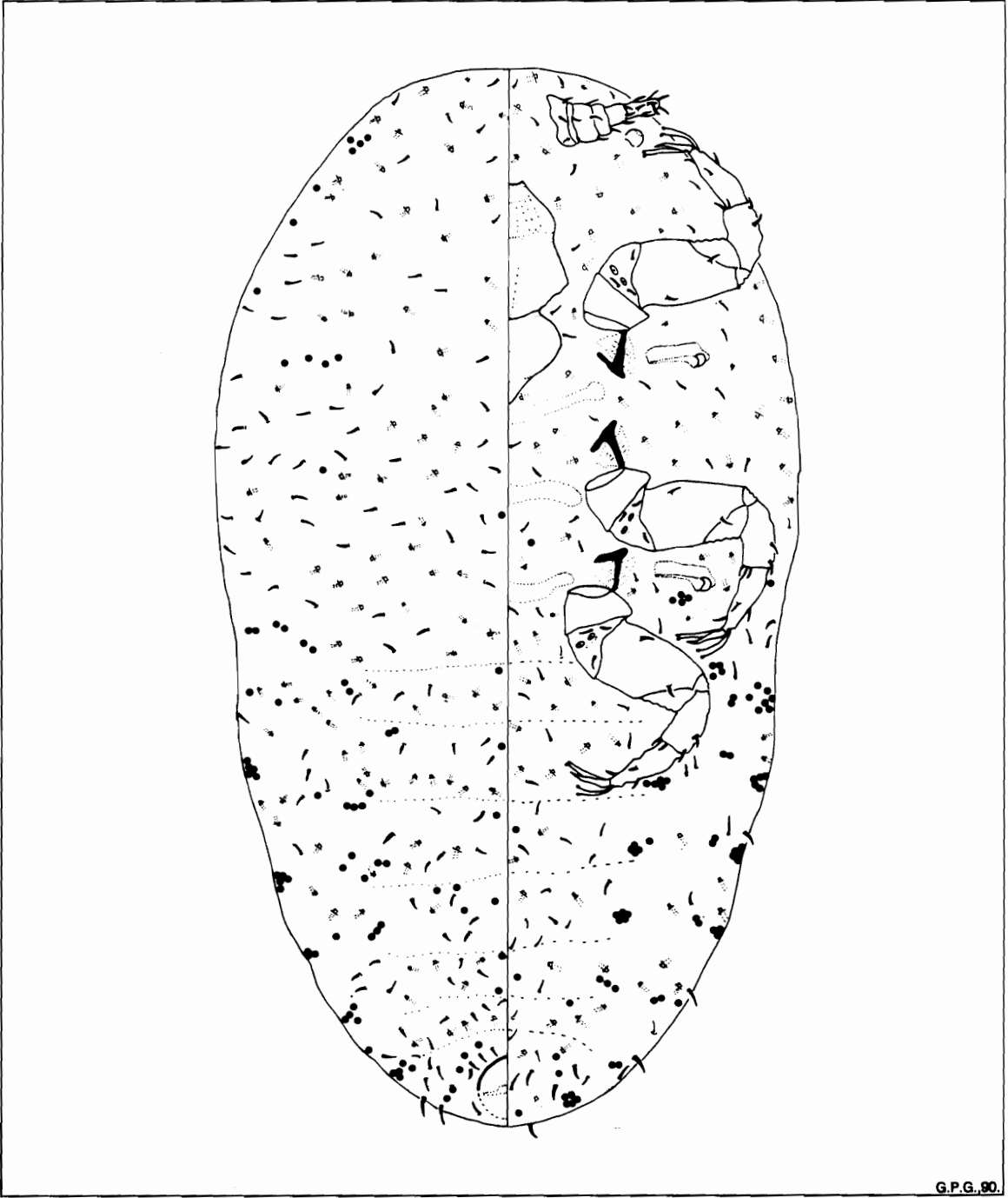


Plate 6. Second instar male of *Dactylopius coccus* Costa

Behavior. Approximately four days after the first molt, the second instar male starts to form a white cylindrical cocoon from wax filaments that arise from pores in the body. The cocoon, which is open at its posterior end, is approximately 2.5 mm long and 1.4 mm wide. The first wax filaments are attached to the substrate, and then the insect slowly starts to rotate on its longitudinal axis to form the cocoon. Approximately one day later, the cocoon is completed. The young male remains in the cocoon without feeding during the prepupal and pupal stages until the adult emerges.

Molting to the third, fourth and fifth (adult) instar takes place in the cocoon and the exuviae are extruded from the posterior end of the cocoon.

At 24^o C the nymphs started to form the cocoon 40 days after hatching from the egg. At 26^o C this happened 31 days after the egg stage.

PREPUPAL MALE OF DACTYLOPIUS COCCUS COSTA

Plate 7

The prepupal male is formed inside of the cocoon secreted by the second instar male. The derm of the prepupa is membranous. The head, thorax, and abdomen can be differentiated. On each margin of the mesothoracic region is a lateral projection where the wing develops. The segmentation of the legs and antennae can not be clearly distinguished. The appendages develop inside membranes. The prepupa has slender setae (Fig. C, D & E) and multilocular pores (Fig. A & B), especially on the abdominal segments. The insect is about 1.2 mm long, 0.6 mm wide, and reddish in color.

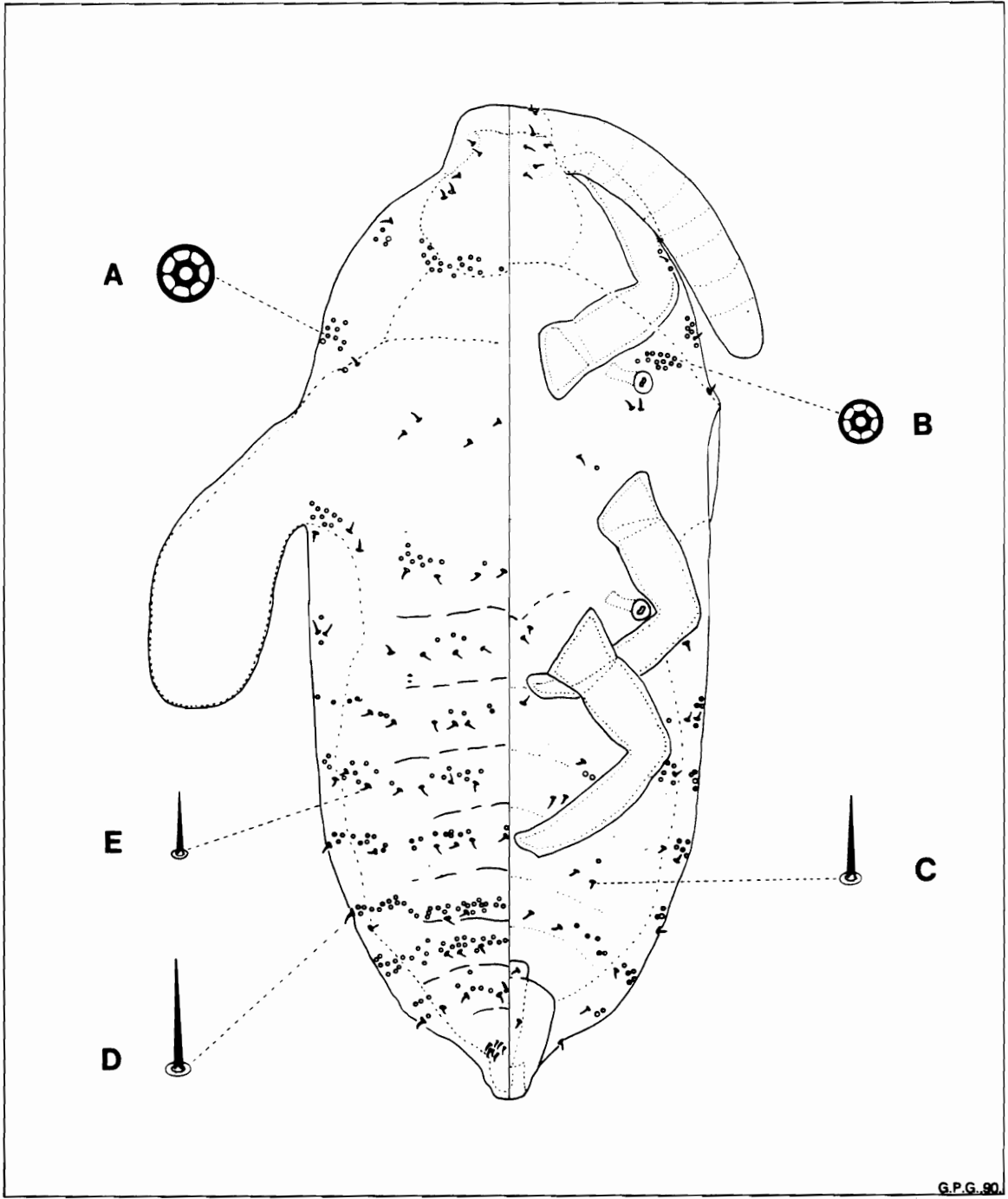


Plate 7. Prepupal male of *Dactylopius coccus* Costa

PUPAL MALE OF DACTYLOPIUS COCCUS COSTA

Plate 8

The prepupa molts into the pupa or fourth instar. In this instar the body segmentation is more distinct. Legs, antennae, wings, and genital structures have progressed to a more definable state. The antennae and legs are longer than 1/3 the body length, and segmentation is more distinct. The penial sheath is elongate and pyriform. Also numerous slender hairlike setae (Fig. C, D & E) and multilocular pores (Fig. A & B) are scattered over the entire body. The pupa is about 1.5 μ long and 0.7 μ wide, and red-brown in color.

ADULT MALE OF DACTYLOPIUS COCCUS COSTA

Plate 9

Description. The adult male has a moderately robust body although significantly smaller than the females. The body, from the anterior margin of the head to the apex of the penial sheath, is 3.0-3.5 mm long, and about 1.3-1.5 mm wide at the mesothorax. The dark-red color of the integument is covered with white wax powder. The body regions are well differentiated. The head is somewhat circular in dorsal and lateral view, with six eyes: two dorsal simple eyes about 61.5 μ in diameter and separated by 399 μ ; two ventral simple eyes which are slightly larger than dorsal, about 73.8 μ far apart; and two lateral large ocelli, about 590 μ far apart from each other. Postocular ridge strongly developed, demarcating the ocular sclerite posteriorly, producing an anterior branch connecting with the preocular ridge below the ocellus, and curving posteriorly to join

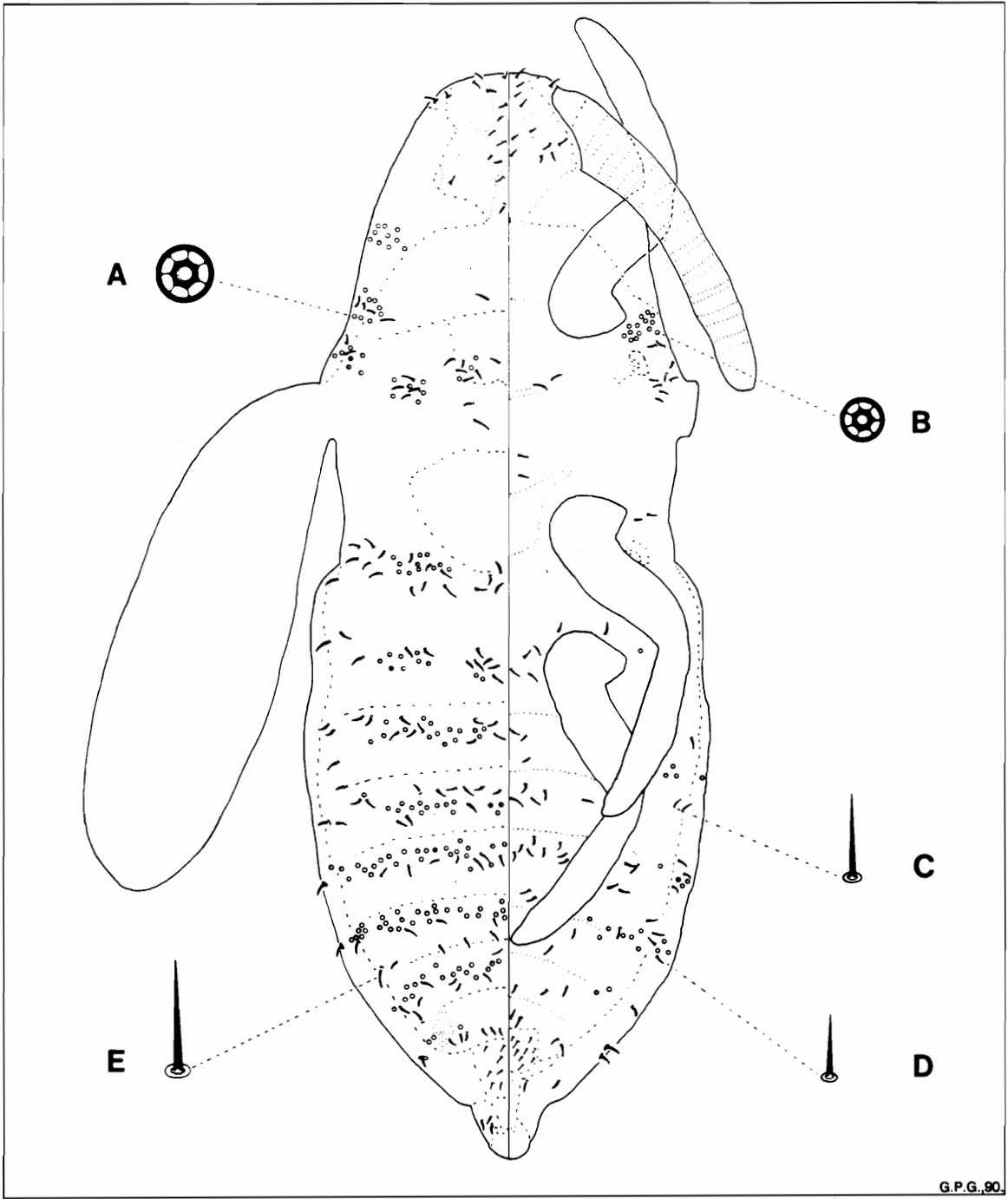
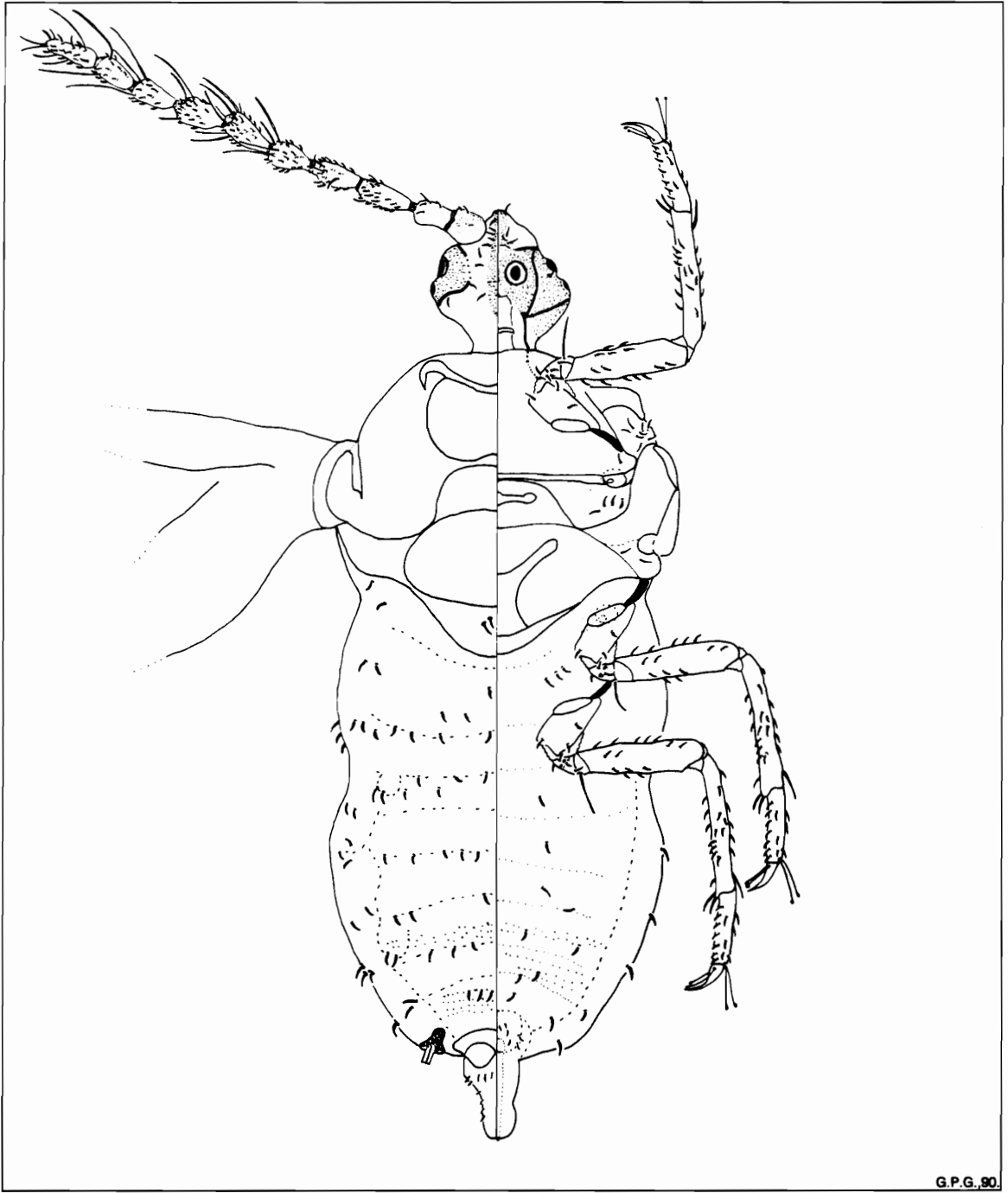


Plate 8. Pupal male of *Dactylopius coccus* Costa



G.P.G.,90

Plate 9. Adult male of *Dactylopius coccus* Costa

proepisternal and cervical sclerites by means of a small sclerite. The cranial apophysis is slightly trifurcated, with the apex not reaching the level of the posterior margin of the ventral eyes. Antennae are well-developed, 2.2 mm long with ten filiform segments and with both fleshy and hairlike setae. The scape is about as wide as long, 184 μ long and 172 μ wide, and is sclerotized basally with a dorsal and ventral process on the pedicel. The adult males lack mouth parts, and thus they do not feed, but they still have vestiges of a mouth opening. The head is clearly separated from the thorax by a short neck. The thorax is about 1.2 mm long and 1.4 mm wide at the mesothorax, where a pair of white wings is clearly visible. The wings are membranous and as long as the body with the radial and median veins distinct and not visibly connected. The total length from the tip of one wing to the tip of the other is about 5 mm. There are no hamulohalterae. The lateropleurite is large with 2 setae. The legs are slender with numerous setae, all similar and the same length, 2.5 mm with the claw included. Both tarsal and unguis digitules are developed; tarsal digitule is about 221 μ long and unguis digitule 141 μ long. The abdomen appears 8-segmented, 1.6 mm long, membranous, with fine setae arranged in transverse rows on each segment. Live specimens have two caudal, white, waxy filaments at each side of the genital segment. These filaments are about as long as the body. The genital segment is about 535-608 μ long, pyriform, broad, at the base 338-369 μ wide, and tapers distally to 79.9-92.2 μ in width with a broadly rounded apex.

Life cycle. The experiments conducted at different temperatures and humidities in the Canary Islands showed that the temperature has a high impact on the rate of development of the *D. coccus* Costa. At 24^o C, 65% R.H., the male became an

adult 67 days after hatching from the egg. At 26^o C, 60% R.H the adult males matured after 43 days. They were very much affected by the change of a couple degrees in temperature.

Behavior. After the last molt, the teneral adult remains inside the cocoon for about 24 hours. On emergence, the tips of the abdominal filaments appear first and then the insect emerges backwards. After eclosion, the wings are still folded and the insect finds protection in the wax of the female. After one hour or more, the insect becomes active and fully expands its wings.

The adult males do not feed, and live for two or three days during which time they fertilize the females. Isolated males without females were kept alive for four or five days.

The adult male rarely flies and usually walks when searching for female colonies. Sometimes, a male may fly to another female colony but in general the male appears to be a weak flier and does not travel long distances.

REPRODUCTION

Genetics. Danzig (1986) stated that the chromosome systems in Coccinea, like their external structures, are unusual and diverse. Geneticists point out three different chromosomal patterns found in Coccinea. They named these patterns after the taxonomic group in which they were first detected: Comstockiella, Diaspidoid, and Lecanoid. In each pattern, the number of chromosomes of paternal origin present during spermatogenesis in the heterochromatic phase is the most important characteristic. According to Nur (1980) the family Dactylopiidae has a Comstockiella system of chromosomes. In the Comstockiella system the sex ratio is likely to be under the control of the female. Nur (1982) described the Comstockiella sequence from *D. opuntiae* (Cockerell) with a karyotype of five pairs of chromosomes ($2n=10$) in which one chromosome pair is about three to four times longer than the others. This karyotype was observed in cells of second instar males and the young embryos. Nur (1982) noted that other workers have mentioned a similar karyotype in *D. ceylonicus* (Green).

Fertility of the male. The females of *D. coccus* only lay eggs after being fertilized by males. In order to learn how many females can be fertilized by a male, the following experiment was conducted in the laboratory of the Escuela Universitaria de Ingenieria Tecnica Agricola, Universidad Politecnica, La Laguna, Tenerife on the Canary Islands.

One cladode of *Opuntia-ficus indica* was placed in each of five small transparent boxes covered with a cloth of very fine mesh. Each host plant was infested with male and female second instar nymphs. One male was allowed to

emerge if the colony had ten or fewer females, and two males if the female colony had more than ten individuals.

RESULTS OF THE FERTILITY OF THE MALES

Box	Nº females	Nº males	Females fertilized
1	15	2	11.0
2	7	1	3.0
3	13	2	9.0
4	6	1	3.0
5	10	1	7.0

In none of the colonies were all the females fertilized. A male can fertilize up to seven (range 3-7) females depending on the number of females in the colony.

Sex ratio. This was determined in the laboratory. It was observed and the nymphs counted from the same mother in the trials above. The nymphs were separated by their sex. The sex ratio was nearly 2 females to 1 male.

Mating behavior. When the male found a suitable female in the colony, he stopped on her with its antennae held apart and backwards and the wings just slightly open toward the rear. After resting for a few minutes upon the female, the male would take a characteristic position with the first pair of legs toward the head of the female, surpassing his own head. The male uses the other two pairs of

legs to hold onto the dorsal abdominal segments of the female. The thorax and abdomen of the male follow the caudal curve of the female while the wax filaments of the male rest on the surface where the female is resting. The copulation took about 30 minutes, range 15-45 minutes. After copulation, the male returned into his normal position and started looking for another female. Sometimes the male went back to the same female with which it copulated earlier and copulated again.

FACTORS THAT AFFECT THE DEVELOPMENT OF DACTYLOPIUS COCCUS COSTA

There are factors that limit the satisfactory development of the cochineal insect colonies in the field. Some factors includes natural enemies and diseases, others are climatological, while some are host plant dependent.

Natural enemies and diseases. The most important limiting factors of cochineal populations are the predators which have a devastating effect on the colonies. The predators are cited at each *Dactylopius* species description under "Natural enemies". The cochineal insects can also be affected with diseases, apparently of bacterial origin. Piña-Luján (1977) listed the two most common diseases for *D. coccus* in Mexico: "chamusco" which kills the insect leaving it of black color, while "chorreo" produces a kind of diarrhea which dehydrates the insect.

Climatological factors. The climatological factors affecting the production of cochineal insects are listed below:

- **Hail.** Karny (1972) noted that hail was observed on one occasion to be extremely destructive to a heavy cochineal infestation.

- **Extreme temperature.** In general, temperature under 20^o C and above 30^o C has a retarding effect on the development of the cochineal colonies. In areas where the temperature is under 20^o C the cochineal production is poor.

- **Rain.** Heavy rain showers may damage field populations. The water not only washes unattached nymphal stages of the plant, but also washes the protective wax from the insects; increasing their vulnerability to weather conditions and natural enemies. If the rain is very heavy, it may even remove the adult females from the host plants.

- **Sunshine.** The insects prefer plants or areas on the plants where they can be protected from sunshine, especially during the first nymphal stage. During this period, the insects are negatively phototactic. Once the insect is attached to the plant, the development is normal regardless of the sunshine.

- **Wind.** Cochineals prefer wind-protected areas on their host plant. Air currents help with dispersal during the first nymphal stage, but may also carry molting individuals. During the molting period the insect is unprotected and not attached; therefore, a strong wind can carry it off the plant and then it is usually unable to attach to a new plant. Wind also removes the male cocoons, leaving more space for the production of females. Marin & Cisneros (1983) stated that strong winds

stick sand to the body of the females, affecting their normal development and the oviposition process.

Host plant factors. There are different factors that affect the development of the insects and which are related to the host plant:

- AGE OF THE HOST PLANT. Marin & Cisneros (1983) pointed out that the potential capacity for cochineal production on the host plant is determined by the number of new shoots and not by the total number of stems 2 year old or older. They also mentioned that the nymphs may attach to the surface of the cactus fruits, where colonies can develop.

- DEGREE OF INFESTATION ON THE HOST PLANT. The longevity of a plant infested with cochineals depends upon the degree of infestation and the health of the plant. Usually the stems of the plant infested with insects of the second generation, desiccate and die. Apparently necrosis in the tissues of an infested plant is caused by a foreign agent, virus or toxin, that is introduced by the insect when feeding. Because of this detrimental effect, in Australia for example, some species of *Dactylopius* have been used as biological control agents of weed cacti.

- HOST PLANT SPECIES. The cochineal insects do not live on all species of Cactaceae, and will develop suitable colonies only on certain species. The species of cacti that are very spiny are generally believed to be more favorable to the insects than are the spineless ones. Marin & Cisneros (1983) stated that such differences are important for the harvesting of cochineal scales, because the

cochineals are more difficult to harvest on spiny cacti than on spineless cacti. Greater numbers of insects also remain on the spiny cactus so that new infestations are more easily started.

METHODS USED FOR THE ARTIFICIAL DISPERSAL OF DACTYLOPIUS COCCUS COSTA.

An even distribution of *D. coccus*, the cultivated or domestic cochineal, on the host plants is desired to obtain more insects. Marin (1987) gave some artificial methods for dispersal of the insects on the plant that are cited below:

1. Simple method of infesting plants- A plant or part of it, infested with fully developed adult females is selected. This is best indicated by females in the first stage of oviposition. The source material is placed close to the plant that is to be infested. A new host plant should be 2 or 3 years old and sufficiently strong to maintain the infestation. When nymphs hatch, they will move up toward the fresh shoots on the new plant.

With this efficient method 8 to 10 new plants can be infested. However, a uniform ratio of infestation on the new plants should not be expected, because it is impossible to control the dispersal of the nymphs. Marin & Cisneros (1977) also pointed out that this method is expensive.

2. Cone method- Twenty to twenty five gravid females are chosen during their first day of oviposition. The insects are scraped from the plant with a big spoon with large handle. When the insects are removed from the plant, the feeding

stylets break and remain in the plant. The insects are no longer able to feed and die shortly. Therefore, it is important to select the oldest females as they are filled with fully developed eggs and can produce numerous nymphs for up to two weeks after their separation from the host plant (Marin & Cisneros, 1977).

The gravid females are placed into a "cone" made from a sheet of newspaper or other rough paper. The cone is fixed vertically to the plant with the open side up and will house the insects, protecting them from sunlight and wind. The nymphs which hatch will leave the cone shelter and infest the new host.

3. Tulle bag method- The tulle bag is a variation of the "cone method". Here the gravid females are placed in a small bag (7 X 7 cm) made from tulle material instead of paper. The nymphs are able to escape through the small openings of the tulle netting. These little bags must be protected from direct sunlight and rain, the two most important climatological factors that affect the survival of nymphs.

4. Hay nest method- As in the two previous methods, 20-25 gravid females are selected and placed in a small "nest" of about 6 cm. made of hay. The insects will be protected from the direct sunlight by the hay covering. The "nest" is attached to the plant and when the nymphs hatch will infest the host.

5. Liberation from the base of the plant- Twenty to sixty gravid females are selected and placed at the base of the new plant. This method is not very safe because the newly hatched nymphs can get lost before crawling to the new host. Also depending on the plant size, there is less control of the distribution of the

insects on the plant. With this method the gravid females cannot be recaptured for later utilization as with the methods mentioned above.

6. Cloth method- For this method only the nymphs are utilized. After harvesting the insects in the field, some of them are placed on a piece of sack-cloth (10 X 10 cm) in a shady place. Another piece of fabric is placed over these insects, then another thin layer of insects and so forth. After a period of 6-24 hours the cloths are full of nymphs. The pieces of cloths are carried to the field and placed over 2 or 3 year old plants that are to be infested. Infestation typically occurs in about 24 hours. Marin (1987) pointed out that some practice is necessary to calculate the number of new shoots that can be infested with a piece of cloth full of nymphs. With this method, the distribution of the insects on the plant and the uniformity in their development can be controlled.

ECONOMIC IMPORTANCE

Baranyovits (1978) mentioned that when the Spaniards conquered King Montezuma in the XVI Century, they were astonished to find a highly developed textile and dye industry. He also wrote: "Next to the treasures in gold, the beautiful red color of their garments impressed the Spaniards most". The red color came from the dry female bodies of the insect known as *D. coccus*.

Nowadays there are nine species in the genera *Dactylopius* which form the family Dactylopiidae. All the *Dactylopius* species have carmine dye in their body, but only *D. coccus* has been "cultivated", not only because it produces dye of the

highest quality, but also because it yields four times more pigment than the other wild species. The Aztec Indians in Mexico discovered this and they chose this species for cultivation.

The commercially cultivated insect is also known as "grana fina" and is different from the "grana silvestre" of wild insects. Donkin (1977) pointed out that the differences between the "fina" and "silvestre" forms appear to be largely the result of processes of domestication operating over a considerable period of time. The wild population must have always been kept severely in check by natural enemies, and it is difficult to visualize species which had improved through the time. *D. coccus* tends to disappear quickly when cultivation and protection cease.

Piña-Luján (1977) stated that sometimes the "grana fina" was adulterated with "grana silvestre", or with ash, flour or other substances creating "grana de harina" (grana of flour) which was of lower quality. To avoid this fraud during the XVI Century in Mexico, laws with severe punishments against adulteration were established and buyers were warned to examine each sample carefully.

Description of the carmine source. The titer of carmine dye in the insect body is higher when females are fully developed and before oviposition. Insects need about 100 days to reach this stage in which the female is full of eggs, when they are ready for harvest. The insects look like seeds because they are oval, convex, and wrinkled. Depending on the method used to kill the insects and clean the wax, they will show different colors after the treatment. Verhecken & Wouters (1989) stated that the grana was termed:

a) *Renegrída* or *denegrída*, for a red-brown color obtained by killing the insects in boiling water;

b) Negra, for a blackish color obtained by roasting the insects on hot plates;

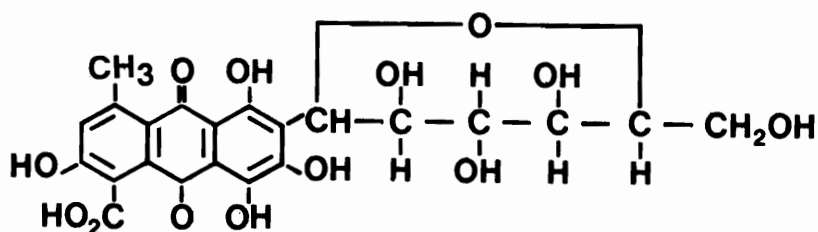
c) Jaspeada, for a grey speckled color when the insects were killed in an oven; and

d) Plateada or blanca, for a silvery ash-gray color, when the insects still had some white waxy powder after drying in the sun.

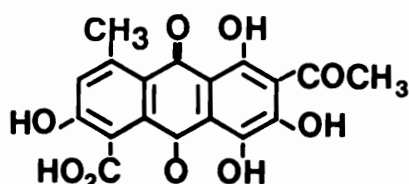
After drying, the insects were placed into sacks and marketed. About 150,000 dried insects are required to make one kilogram of cochineal.

Chemistry of the carmine dye. Verhecken & Wouters (1989) stated that the pigment of cochineal is carminic acid, one of the few natural C-glycosides known. Thomson (1960) stated that this anthraquinone is rare in the animal kingdom, but is produced by some scales such as: *D. coccus* (carminic acid), *Kermococcus ilicis* (kermesic acid), and *Laccifer lacca* (erythrolaccin). He also suggested that these anthraquinone pigments may be built up in the animals from acetate units by symbiotic micro-organisms. Their structures are:

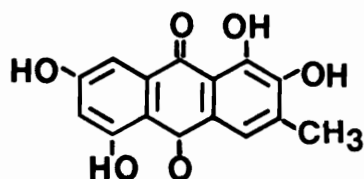
Carminic acid



Kermesic acid



Erythrolaccin



Eisner & Nowick (1980) found that carminic acid is a potent feeding deterrent to ants. This may reflect the natural function of the compound, which may have evolved in cochineals as a chemical weapon against predation. They also noticed that some predators utilize the ingested carminic acid for defensive purposes of their own.

Use of cochineal insects. In America the Indians used the cochineal as a dye for hundreds of years before the Spanish conquest so that when the Spaniards arrived in the New World they found a well established cochineal industry. The

Peruvians began to use the cochineal during the Nazca period apparently since the pre-Toltec era. The pigments were used as cosmetics by Indian women and also for decorating various kinds of craftwork.

Dahlgren de Jordán (1961) claimed that the medicinal properties of cochineal were well known to the Mexicans. Some old recipes show that a mix of ground cochineal and some other ingredients such as vinegar were used to relieve mild illness of the head, heart, and stomach. But the main use of cochineal was for dye in the textile industry. Verhecken & Wouters (1989) stated that cochineal was mainly used for producing two important colors: crimson (bluish red) and scarlet (yellowish red).

After 1793, the red dye from cochineal was considered very important. Usually rough materials were dyed with madder (*Rubia tinctorum*) while fine cloths were dyed with cochineal. Carminic acid, first isolated in 1818 produces beautiful crimsons, pinks, and scarlets on wool and silk when mordanted with tin or alum; however, it is not a satisfactory dye for cotton. A mordant is a substance that is used to fix colors in dyeing. Frequently to alkaly the dye-bath the human urine was used during the dyeing process. Some authors have stated that the red dye from cochineal can retain its quality for at least 130 years in contrast to the dyes of Lac insects, gall-like scales (*Kermes* spp.), and Polish cochineal scale (*Porphyrophora polonica*) which retain color for a shorter time.

There are many old recipes for use of cochineal as dye. For centuries different dyers had their own procedures. Some professionals tried to reduce the costs by mixing cochineals with other dyeing materials but the quality was not the same.

An antique recipe for carmine dye (personal communication with source) gives as ingredients the following:

- 68 liters of water
- 4 handfuls of dried and crafted taffeta (*Hoffmannia refulgens*, Rubiaceae) leaves
- fresh juice from 80 limes
- 35,000 dried and finely ground female cochénilles (about 220 g.).

The ingredients were boiled until the desired color was obtained.

Adrosko (1971) gave some of the colors than can be obtained by dyeing wool with cochineal:

- American Beauty Red Wool (Alum mordant = aluminum potassium sulfate)
- Flag-Red Wool (No mordant before dyeing)
- Purple Wool (Chrome mordant = potassium dichromate)
- Rose-Pink Wool (No mordant before dyeing)

The red coloring materials from cochineal have been almost completely replaced in the textile industry by synthetic dyes which are cheaper.

In the United States, as in other countries cochineal red coloring materials are still in use in the cosmetic and drug industries. However, the cochineal pigment is not used in the food industry because it was found to contain salmonella bacteria. The use of synthetic dyes in the food industry has also been questioned because some of these are unsafe.

The current awareness of the importance of healthy life styles has brought an explosion of interest in natural products including cochineal, which again occupies an important place. Only Peru and the Canary Islands (Spain) still produce cochineal on an industrial scale. In some areas of Mexico the government has attempted to resurrect the cochineal cultivation. Peru exports

cochineal to North America and to some European countries. The Canary Islands are the main suppliers to France and England.

CHAPTER 6
SPECIES OF DACTYLOPIIDAE

KEY TO THE ADULT FEMALES OF THE SPECIES DACTYLOPIUS

1. Clusters of wide-rimmed pores normally without ducts 2
- Clusters of wide-rimmed pores always associated with 1 or more ducts 3
2. Single ducts on ventral sublateral areas of head, thorax, and first abdominal segments; spiracular opening with minute teeth along lateral margins; narrow-rimmed pores present mostly in median area of last three or four abdominal segments; most setae with truncate or rounded apex; specimens small, 0.8-2.5 mm long, covered with brittle threads of cottony wax..... *salmianus*
- Few clusters of wide-rimmed pores on last abdominal segments with 1 slim duct; spiracular opening with smooth margin; narrow-rimmed pores absent; few setae hairlike; specimens large, 4-6 mm long, covered with waxy powder.....*coccus*
- 3(1). With clusters of wide-rimmed pores on venter across middle-thoracic area ; narrow-rimmed pores on ventral abdominal segments only, numerous on last 4 or 5 segments; setae not numerous but increasing in size toward last abdominal segments
confertus

- Without clusters of wide-rimmed pores across middle thoracic areas of the venter 4
- 4. Rows of clusters of wide-rimmed pores across ventral median area of first 3 or 4 abdominal segments; dorsal setae larger and crowded on abdominal segments but smaller and fewer and scattered toward head.....*austrinus*
- No rows of clusters of wide-rimmed pores across ventral median area of first 3 or 4 abdominal segments..... 5
- 5. Truncate and rounded setae of different sizes in groups of 2 or 3 on dorsal margin, large setae form 2 longitudinal rows in medial and submedial areas of thorax and abdomen; anal ring obsolete.....
.....*tomentosus*
- Truncate and rounded setae not arranged in such groups or in rows; anal ring well developed.....6
- 6. All dorsal truncate and rounded setae almost of same size except for a few slightly larger ones on last few abdominal segments..... 7
- Some dorsal truncate and rounded setae much larger than others on last 3 or 4 abdominal segments..... 8
- 7. Large truncate and rounded setae longer than wide at base, 21.5-24.0 μ long and 14.0-16.5 μ wide; ventral narrow-rimmed pores numerous on last 3 abdominal segments *opuntiae*

- Large truncate and rounded setae almost as long as wide at base, 37.5-42.5 μ long, 30.0-32.5 μ wide; ventral narrow-rimmed pores numerous on last 4 abdominal segments.....*ceylonicus*
- 8(6). Large dorsal truncate and rounded setae only on last 3 or 4 abdominal segments; spiracular opening with minute marginal teeth; adults about 2 mm long; present in many countries, on different host plants *confusus*
- Large dorsal truncate and rounded setae on entire surface; spiracular opening with smooth margins; adults about 3 mm long; so far known only from Argentina, only on *Tephrocactus* sp.....
..... *zimmermanni*

DESCRIPTION AND ILLUSTRATION OF EACH SPECIES

Dactylopius austrinus De Lotto

Plate 10

Selected literature. *Dactylopius austrinus* De Lotto, 1974:174

Adult female. Live adult females have not been seen by the author but De Lotto (1974) gave a description from "pictures presented by Dodd (1940), Pettey (1948) and Mann (1970) the insect looks fully covered by cottony matter, the pattern of which has never been described in detail". Karny (1972), described the body color of the "species J" (= *D. austrinus*) is a very bright pale brownish-red. Adult females on slides are oval, about 3.0-4.5 mm long and 2.0-3.2 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores always in cluster associated with one or more ducts . On head 14-20 clusters mainly formed with 3 or 4 pores. On thorax 150-220 clusters mostly with 3, 4 or 5 pores. On abdomen 110-220 clusters approximately with up to 20 pores.

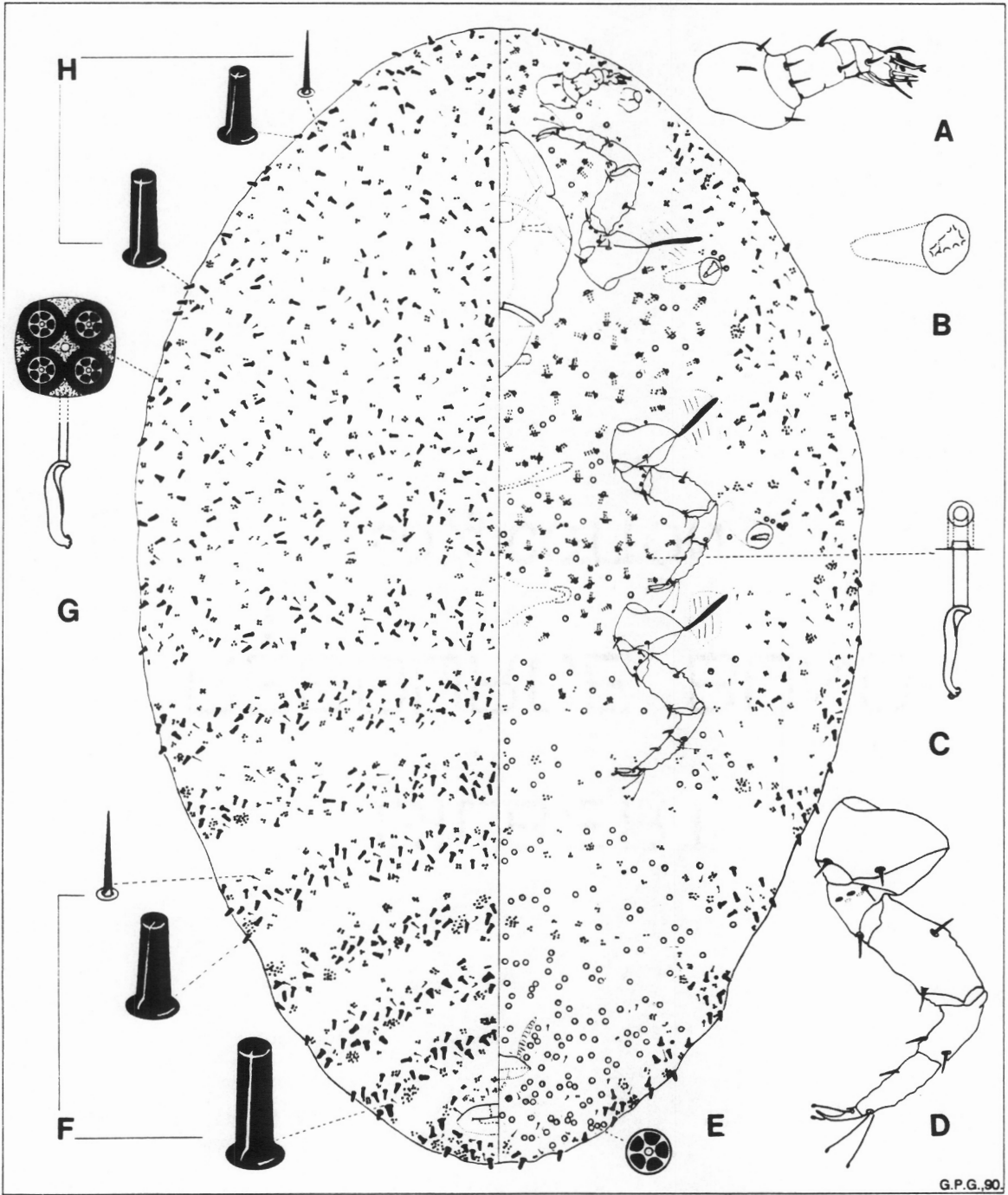


Plate 10. Adult female of *Dactylopius austrinus* De Lotto

Setae (Figs. F, H). Not very numerous on the entire body. The larger ones and most on last abdominal segments, becoming smaller and less dense toward the head.

SETAE (μ)	Large		Small		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	33.3	19.0	19.0	14.2	28.5	9.52
THORAX	40.4	19.0	31.0	12.0	35.0	9.52
ABDOMEN	45.2	21.4	35.7	14.2	59.5	16.6

Anal area. Anal ring ellipsoidal, 240-418 μ wide, 170-220 μ long. Anterior end sclerotized in a narrow band. About 25-30 clusters with up to 12 wide-rimmed pores. Setae of different size.

Ventral Surface

Eyes. Diameter at base 85.0-88.0 μ , distance between bases 492-960 μ .

Antennae (Fig. A). Six-segmented, rarely 7, 190-383 μ long. Distance between antennal bases 121-332 μ .

Segments	Lengths(μ)	Setae	Fleshy-setae
I	50.0-80.0	3	0
II	24.0-56.0	2	0
III	72.0- 102	2	0
IV	23.0-40.5	0	1

V	21.5-37.5	1	1
VI	47.5-67.0	4	3

In the material examined two specimens on slides 4548:1+2 with seven antennal segments with lengths average: I 55.5 μ , II 37.0 μ , III 37.0 μ , IV 31.0 μ , V 31.0 μ , VI 37.0 μ , VII 61.5 μ .

Clypeolabral shield. Large pentagonal shaped 523-572 μ long and 521-633 μ wide at base.

Labium. Three-segmented, 200-486 μ long, 300-467 μ wide at base.

Spiracles (Fig. B). Opening sclerotized with minute teeth-like along the margins. Anterior 295-331 μ long, atrium 98.5-135 μ wide, 0-3 associated narrow-rimmed pores. Posterior 227-390 μ long, atrium 116-217 μ wide, 0-6 associated narrow-rimmed pores.

Legs (Fig. D). Short and thin. Claws usually without teeth except in one specimen where the two first legs have a little tooth-like process. Tarsal digitules 85.0-105 μ long, claw digitules 62.0-90.0 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	67.5- 129	98.5- 125	104-155
Trochanter	55-129	74.0- 118	80-130
Femur	209-277	215-277	215-295
Tibia	123-160	129-180	120-160
Tarsus	125-185	165-209	170-185-
Claw	50.0-65.0	51.0-60.0	60-71
Entire leg	629-945	732-969	749-996

Setae. Same as on dorsal surface but located at lateral margins of the body. Numerous on abdominal segments and scarce toward the head.

Pores. Clusters of wide-rimmed pores in lateral and sublateral areas of the body and in rows in middle area across the first three abdominal segments. Narrow-rimmed pores (**Fig. E**) scattered on thorax and very numerous on last three or four abdominal segments.

Ducts (Fig. C). Crowded in the middle areas of head and thorax.

Vulvar area. Vulvar opening 260-301 μ wide, surrounded by a large number of narrow-rimmed pores.

Type material studied. Holotype 2290:4*, 1(1); two paratypes 2290:2+3, 2(2) from *Opuntia aurantiaca* South Africa, Cape Province, Bedford, Aug. 23, 1966, coll. W. A. Burger, PPRI. Two paratypes 2031:1+2, 2(2) from same host plant, country and province but at Uitenhage, Jan. 21, 1966, coll. W. A. Burger, PPRI. Two paratypes 2294:2+4, 2(2) from the same host plant, country and place same as above, Aug. 26, 1966, coll. W. A. Burger, USNM.

Material studied

ARGENTINA. *Opuntia aurantiaca*, La Rioja, Campanas, Mar. 15, 1971, coll. H. Zimmermann, 4689:1+2, 2(2) PPRI; D34:a-d, 4(4) VPI. Las Lomitas, Jan. 15, 1971, coll. H. Zimmermann, D12:a-c, 3(7) VPI. *O. canina*, Jujuy, Pampa blanca, May 15, 1979, coll. H. Zimmermann, 4693:1, 1(1) PPRI. *O. kiskaloro*, Catamarca, Merced, coll. H. Zimmermann, Oct. 15, 1970, 4681:1, 1(1) PPRI. *O. pampeana*, Catamarca, Feb. 15, 1972, coll. H. Zimmermann, 4548:1+2, 2(2) PPRI. *O. retrorsa*, Vipes, coll. H. Zimmermann, Jun. 6, 1972, D11:a+b, 2(2) VPI.

AUSTRALIA. *Opuntia aurantiaca*, New South Wales, Kinross, Ciulargambone, Sep. 14, 1978, coll. P. Deighton, 1(1) CDA. Tamworth, Aug. 13, 1973, coll. Zimmermann, 5268:1+2, 2(2) PPRI.

SOUTH AFRICA. *Opuntia aurantiaca*, Cape Province, Cookhouse, Feb. 26, 1965, coll. H. J. Loubser, 6(6) PPRI. Uitenhage, Jan. 21, 1965, coll. G. de Beer, 3(3) PPRI. Uitenhage, Jan. 21, 1966, coll. W. A. Burger, 2031:6, 6(6) PPRI.

Additional hosts. Mann (1969) established that for the near-confusus species of *Dactylopius* (= *D. austrinus*) the "usual host" is the low-growing, thick and rather large-jointed *O. sulphurea*.

Moran & Cobby (1979) wrote: "In South America, *D. austrinus* does not occur on *O. aurantiaca*; its original native host there is probably *O. utkilio* (H. G. Zimmermann, pers. comm.) and it has also been recorded from *O. canina*, *O. discolor*, *O. kiskaloro*, *O. palmadora*, *O. retrorsa*, *O. sulphurea* and *Austrocylindropuntia salmiana* (H. G. Zimmermann)".

Distribution. Discovered in central and western Argentina and introduced to South Africa in 1932, released in Australia in 1933.

Etymology. This species was named and briefly described by De Lotto (1974) who did not explain the etymology of the name. In my opinion, De Lotto named it as he did because it was found in the southern hemisphere (Argentina). He cited: 'This species was originally discovered in Argentina by Australian entomologists and subsequently referred to by Dodd (1940), Mann (1969; 1970) and Pettey (1948) as *Dactylopius* sp. near *confusus* (Cockerell), and by Karny (1972) as "species J" '.

Remarks. This species were named as "species J" by Karny (1972), and as *Dactylopius* sp. near *confusus* (Cockerell) by Dodd (1940), Pettey (1948), and Mann (1969).

Affinities and discussion. *Dactylopius austrinus* resembles *D. confusus* and *D. confertus*, the species can be separated because the former species has clusters of wide-rimmed pores across the mid-ventral area of the first three or four abdominal segments and in the other two species do not.

De Lotto (1974) reported that specimens from South Africa have rows of small clusters of wide-rimmed pores across the anterior of the first abdominal segments of the venter. The strain from Argentina and Australia does not have them or the pores are diminished. If these clusters are missing they are replaced by narrow-rimmed pores.

Natural enemies. No specific enemies are mentioned for this species in the literature consulted. Mann (1969) listed natural enemies for some *Dactylopius*. He mentioned that in Argentina there were two Diptera "where *D. indicus* and *Dactylopius* sp. near *confusus* (= *D. austrinus*) occur freely"; the syrphid *Eosalpingogaster conopida* (Philippi) and the agromyzid, *Leucopis bellula* Williston.

Biological control agent. This species has been very successful in Australia and South Africa where it was introduced for the control of *Opuntia aurantiaca* Lindley in the fields. This cactus has spread over large areas in these two countries and became a pest (Mann 1970, Hosking and Deighton 1979, Moran and Annecke 1979).

Dactylopius ceylonicus (Green)

Plate 11

Selected literature and synonymy.

Coccus cacti var. *ceylonicus* Green, 1896:7 [nomen nudum].

Coccus indicus Green, 1908:28; Green, 1912:80.

Dactylopius ceylonicus (Green) Sanders, 1909:38; Dodd 1940:97; Mann 1969:139; De Lotto, 1974:175.

Dactylopius argentinus Dominguez, 1915 (no descr. Autran, 1907:156); [nomen nudum Lizer, 1922:107].

Dactylopius indicus Green, 1922:358; Ferris 1955:90; Karny 1972:2.

Adult female. The author has not seen live adult females, but Green (1908) described them as: "deep purplish-brown, densely covered with white, mealy wax". Adult females on slides are almost circular, about 2.3-4.0 mm long and 1.5-3.5 mm wide. Segmentation of the abdomen is very conspicuous in this species.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores alone or in small clusters of one or more ducts; on head, about 10-15 clusters mostly with 2 or 3 pores. On thorax in median and submedian areas mostly singly, or in small clusters 70-100 usually with 2 or 3, sometimes 4, pores. On abdomen 120-150 clusters with up to 8 pores.

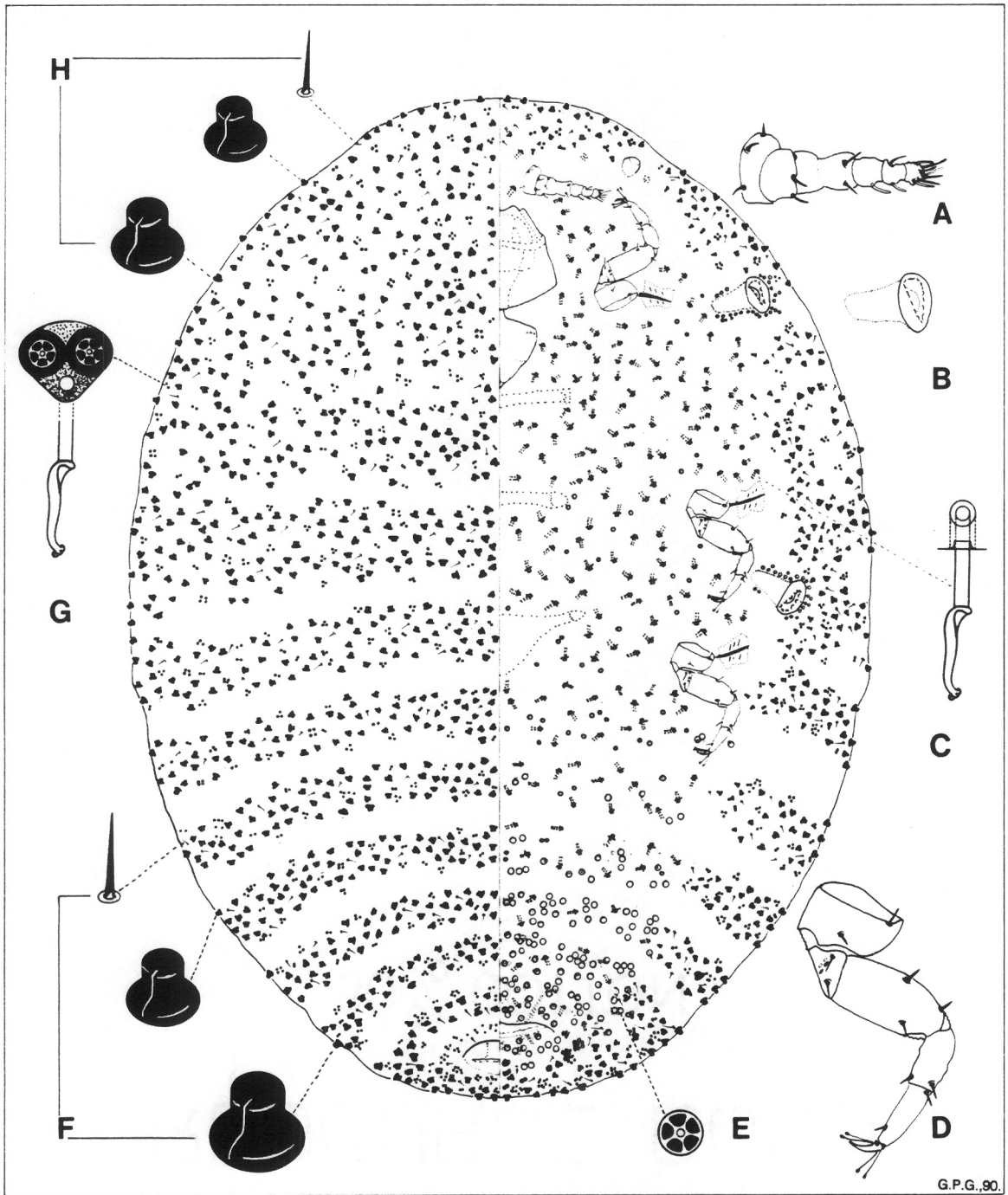


Plate 11. Adult female of *Dactylopius ceylonicus* (Green)

Setae (Figs. F, H). Setae numerous and evenly distributed on body. These are short, almost cylindrical with a truncate apex and a very expanded base. Although there is no marked difference in size, those on head slightly smaller than on abdominal segments.

SETAE (μ)	Large		Small		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	37.5	32.5	27.5	20.0	30.0	12.5
THORAX	37.5	32.5	27.5	16.0	30.0	12.0
ABDOMEN	42.5	30.0	30.0	12.5	35.0	12.0

Anal area. Anal ring is ellipsoidal 124-192 μ wide, 83.0-116 μ long. Anterior side with a sclerotized ring. Ring is surrounded by 10-20 pores and setae.

Ventral Surface

Eyes. Diameter at base 35.7-59.5 μ , distance between bases 380-533 μ .

Antennae (Fig. A). Short, six-segmented, 119-195 μ long. Distance between antennal bases 85.0-175 μ .

Segments	Lengths(μ)	Setae	Fleshy-setae
I	21.5-59.5	3	0
II	14.0-16.5	2	0
III	36.0-50.0	2	0
IV	12.0-21.0	0	1
V	12.0-17.0	1	1
VI	24.0-31.0	4	3

In the material examined three specimens with seven antennal segments, average lengths: I, 31.0 μ ; II, 20.0 μ ; III, 25.0 μ ; IV, 40 μ ; V, 16 μ ; VI, 12 μ ; VII, 21.0 μ .

Clypeolabral shield. Pentagonal, 110-317 μ long and 238-333 μ wide at base.

Labium. Triangular, 99-180 μ long, 119-170 μ wide at base.

Spiracles (Fig. B). Opening well developed and sclerotized with minute tooth-like processes along lateral margins. Anterior 123-191 μ long, atrium 52.3-95.0 μ wide, with 10-16 associated narrow-rimmed pores. Posterior 157-190 μ long, 64-83 μ wide, with 9-32 associated narrow-rimmed pores.

Legs (Fig. D). Short and stout. Claws without tooth. Tarsal digitules 51-60 μ long, unguis digitules 23-36 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	74.6-71.5	48.0-83.0	64.2-99.0
Trochanter	35.0-61.0	43.0-71.0	31.0-78.0
Femur	119-155	110-143	119-154
Tibia	61.8-99.0	66.0-81.0	71.0-97.0
Tarsus	67.0-83.0	71.0-88.0	71.5-88.0
Claw	25.0-38.0	27.0-37.0	25.0-37.0
Entire leg	449-507	365-503	381-553

Setae. Located on the lateral sides venter, of same shape as dorsal surface. Setae more numerous toward abdomen.

Pores. Small clusters of wide-rimmed pores in lateral and sublateral areas of the body. Narrow-rimmed pores (Fig. E) on thorax and abdomen, numerous around spiracles and on last four abdominal segments.

Ducts (Fig. C) On median area of head, thorax, and abdomen.

Vulvar area. Vulvar opening 108-202 μ wide, surrounded by large number of narrow-rimmed pores and some ducts.

Type material studied. One slide with one specimen* labeled as *Coccus indicus* Green from *Opuntia* sp., Kangra, India, coll. Burkill N^o 15467. Originally the specific name for the host plant was *O. dillenii* but it was crossed out. De Lotto (1974) wrote about this: "very likely following Burkill's remark (in: Green 1912) that in India the insect infested *O. monacantha* and neglected *dillenii*". The slide is located in USNM.

Material studied.

ARGENTINA. *Opuntia discolor*, Formosa, Ibarreto, Mar., 1978, coll. H. Zimmermann, 5434:1, 1(1) PPRI. *O. ficus-indica*, San Luis, 1918, coll. W. B. Alexander, 19 1(2) USNM. *O. quimilo*, Tucuman, Vipos, May 10, 1971, coll. H. Zimmermann, 4476:1, 1(1) PPRI. *O. retrorsa*, Santa Fe, Vera, Feb. 15, 1971, coll. H. Zimmermann, 4597:1, 1(1) PPRI. Camino la Fontana, Mar. 19, 1972, coll. H. Zimmermann, 322 (a-d), 1(1) VPI. *O. sulphurea*, San Carlos, Feb. 15, 1972, coll. H. Zimmermann, 293-1, 1(1) VPI.

AUSTRALIA. *O. monacantha*, Queensland, Sherwood, Feb. 26, 1967, coll. H. Zimmermann, 2861:a-d, 1(1) PPRI. One slide with 4 specimens (4920-2), only with host plant and country, MNHN. N.S.W. road to Camden, Oct. 18, 1927, coll. H. Compere, 2(5) UCD.

BANGLADESH. *Opuntia dillenii*, Gomostapur, Jun. 23, 1980, coll. Shahjahan, 12372, 1(1) BM.

BOLIVIA. *O. canina*, Santa Cruz, Camira, Jul. 7, 1972, coll. H. Zimmermann, 4700:1 PPRI. *O. cochabambensis* & *O. chuquisacana*, close to Cochabamba, Jul. 1, 1972, 4715:1 1(1), and Jul. 3, 1972, 4716:1 1(1), both coll. H. Zimmermann, PPRI.

BRAZIL. *Opuntia* sp, Belem Novo, April, 1964, coll. F. D. Bennett, 7947-19074 1(2); det. as *D. indicus* Green by D. J. Williams, BM.

MADAGASCAR. *Opuntia dillenii?*, Ambatomaroina, 1929, coll. C. Frappa, 4918-5 1(4) (iden. as *D. tomentosus* Lamk.), MNHN. Gimbazaza, Feb., 1949, coll. ?, 4919-6 1(5), MNHN. *Opuntia* sp, Nanisana, 1928, coll. C. Frappa, 4918:1 1(4), 4918:2 1(3), 4918:4 1(4); in the label also written *tomentosus* Lam. (probably by

another author because the writing is not the same). Ambohidratrimo, 1930, coll. C. Frappa, 4918:6 1(4) (labeled: *tomentosus* Lam.), 4918:11 1(4), MNHN.

MAURITIUS. No host plant, Dept. Agric., Mauritius, April 11, 1914, coll. de Charmoy ((April 22, 1949, R. Mamet remounted and identified: *D. indicus* Green), two slides without N^o, one with one specimen, the other with two, MNHN. "Prickly pear" Oct., 1914, coll. de Charmoy, written with ink on one side: *opuntiae*, 1(1) MNHN.

NEPAL. *Nopalea*, One slides with one specimen labeled: *D. ceylonicus* (Green), 87-3328 N^o 587.

PARAGUAY. *O.?* *canina*, Paraguay, Asuncion, June 15, 1970, coll. H. Zimmermann, 4157:1 PPRI.

SOUTH AFRICA. *O. monacantha*, Port Elizabeth, Aug. 30, 1938. Two slides, one specimen each without coll. N^o; one was originally labeled *Coccus indicus* Green, coll. F. W. Pettey, and the other *D. indicus*, neither have collectors name, PPRI. Cape Province, Gamtoos Ferry, May 30, 1977, coll. H. Zimmermann, 5278:1+2 PPRI.

SRI LANKA (CEYLON). *Opuntia dillenii*, Tangalla, E. E. Green, 80; MNHN. *O. monacantha*, labeled *Coccus indicus* Green, Ceylon material from Nalae (possibly refers to Nalanda), Jan. 4, 1914, 392521 N^o37. One slide with 1 specimen from Ceylon labeled as *Coccus cacti ceylonicus* Green (Maskell collection N^o452) without more data.

Additional hosts. Mann (1969), cites: *Opuntia anacantha*, *O. bonaerensis*, *O. salmiana*, and *O. utkilio*.

Distribution. Argentina, Australia, Bangladesh, Bolivia, Brazil, India, Madagascar, Mauritius, Nepal, Paraguay, South Africa, Sri Lanka (Ceylon).

Etymology. Green named this species after the Island Ceylon (Sri Lanka) from where he first received it.

Remarks. Green (1896) mentioned a variety of the "cochinilla del nopal" as *Coccus cacti* var. *ceylonicus*. The new species from Ceylon was collected on *Opuntia* sp. At that time Green did not give a good description of the new insect, just a few characteristics. Green (1908) named and gave a proper description for *Coccus indicus*, the same insect received in samples from India.

Autran (1907) listed *Dactylopius argentinus* in his catalog "Las cochinillas argentinas" but without a description. He did that because Dominguez in 1908 mentioned him about the new insect in a personal communication.

Ferris (1955) gave some evidence which prove that the species is native in South America. He wrote: "This being the case *Dactylopius argentinus* (Dominguez), described from Argentina in 1907, is possibly the same, and if it is, it has priority over *indicus* Green of 1912".

Lizer (1922) considered *D. argentinus* a nomen nudum when he realized that it is a synonym of *D. ceylonicus*, but did not provide a description.

Sanders (1909) listed *D. ceylonicus* in the "Catalogue of recently described Coccidae". He realized that *Coccus cacti* var. *ceylonicus* has priority over *C. indicus* and he also placed it in the genus *Dactylopius*.

Green (1922) accepted the new genus and named the species *Dactylopius indicus*, but because Signoret (1875) had a species with the same name (senior

homonymy) this has priority. To avoid a nomenclatural problem the insect was named *Dactylopius ceylonicus* (Green, 1896) by Sanders in 1909.

Affinities and discussion. *D. ceylonicus* can be separated from the rest of the species because it has the most characteristic setae, almost cylindrical, very short with a very wide base. However, De Lotto (1974) pointed out that some specimens show "variations in some structures, suggesting the presence of forms or strains: biological, ecological, etc."

Natural enemies. Lizer y Trelles (1939) mentioned a natural enemy of *D. ceylonicus* (Green 1896): *Eupelmus dactylopii* Blanchard (Hymenoptera: Eupelmidae).

Biological control agent. Karny (1972) refers to this species as *D. indicus* Green which was introduced to South Africa in 1913 against *Opuntia vulgaris* . He wrote: "This was the first attempt in biological control of prickly pear in South Africa and was so successful that within a few years this pear species was practically eradicated in most parts of the infested areas. Today it is only found in limited numbers in some isolated localities near the coast".

Dactylopius coccus Costa

Plate 12

Selected literature and synonymy.

Coccus cacti auct. Linnaeus, 1758:457; Goeze, 1778; Modeer, 1778; Fabricius, 1781, 1803; Gmelin 1789; Turton, 1802; Latreille, 1802; Guercio, 1823; Blanchard, 1840; Amyot, 1843,1848; Targioni Tozzetti, 1868:725; Cockerell, 1894,1899; Howard, 1897.

Coccus sativus Lancry, 1791:486 (nomen oblitum).

Coccus mexicanus Lamarck, 1801:299 (nomen oblitum).

Dactylopius cacti , Koteja, 1974:77.

Dactylopius coccus Costa, 1835:16; Lindinger, 1912:235; Bodenheimer, 1926:46; Balachowsky, 1927:188; Dodd, 1940:98; Fernald, 1903:82; Ferris, 1955:86; Mann, 1969:139; Williams, 1969:324; Karny, 1972:2; De Lotto, 1974:179; MacGregor-Loeza, 1974:81.

Pseudococcus cacti Westwood, 1840:448; Hempel, 1900.

Pseudococcus signoreti Cockerell, 1900:992.

Common names. Among the most widely used ones are: cochineal insect, true cochineal, cochineal carmine, grana fina, cochinilla del carmin.

Adult female. Live adult females are globose: 4.0-6.0 mm long, 3.0-4.5 mm wide, and 3.8-4.2 mm high. The average weight of an adult female could reach 40-47 mg, depending on the breeding conditions of the insect. The body is

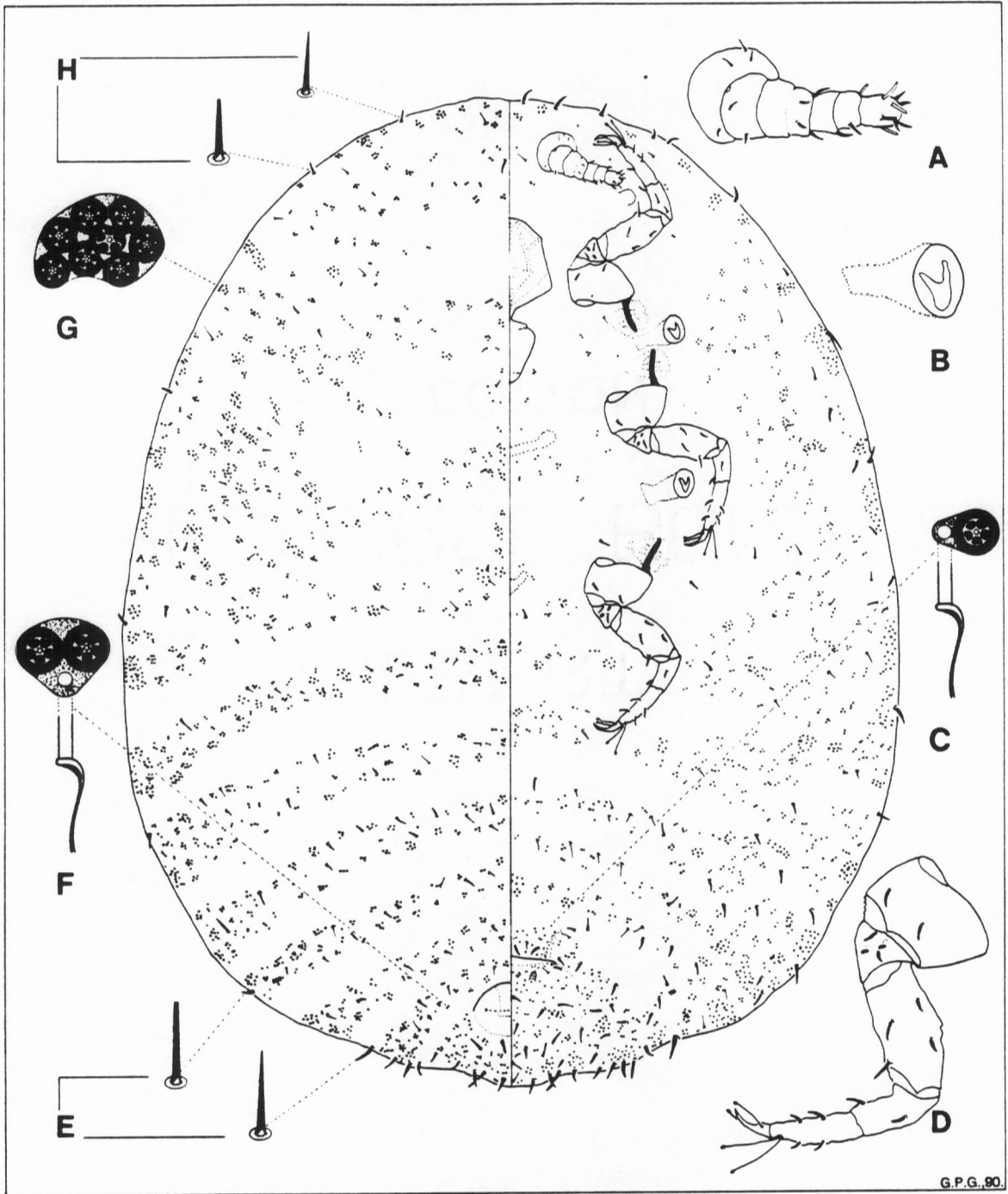


Plate 12. Adult female of *Dactylopius coccus* Costa

covered with waxy powder. If the wax is removed, the color of the insect is dark purple-red. Adult females on slides are almost circular in shape, about 4.2-6.0 mm long and 3.4-5.2 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. F, G). Wide-rimmed pores usually in clusters and devoid of ducts. On head 30-37 clusters formed with up to 15 pores. On thorax 90-130 clusters with up to 25 or 30 pores. On abdomen approximately 100 clusters, with up to 30 pores. On last abdominal segments a few single pores and small clusters of 2-5 pores may be associated with ducts.

Setae (Fig. E, H). In general very scarce on entire body, being more numerous toward last abdominal segments. In head and thorax these about 21.4 μ long and 9.52 μ wide at base with apex slender or just slightly truncate. On last abdominal segments, together with same kind of setae than on head and thorax, also larger setae, 26.1 μ long and 11.9 μ wide, with truncate apex. The longest setae 35.7 μ long, 7.14 μ wide and with slender apex.

Anal area. Anal ring broadly elliptical, 180-270 μ wide, 155-164 μ long. Anterior margin with a more or less thin sclerotized band. Ring surrounded by about 25-30 clusters of wide rimmed pores and some setae.

Ventral Surface

Eyes. Eyes halfway between clypeolabral shield and body margin. Diameter at base 39.5-46.5 μ , distance between bases 1.5-2.5 mm.

Antennae (Fig. A). Seven-segmented, 242-330 μ long. Some individuals without clear differentiation between 3rd and 4th antennal segment and appear six-segmented. Distance between antennal bases 283-290 μ .

Segments	Lengths (μ)	Setae	Fleshy-setae
I	35.7-41.0	4	0
II	25.5-34.4	2	0
III	35.5-40.3	0	0
IV	23.8-30.2	4	0
V	24.0-32.5	1	0
VI	30.9-37.3	1	1
VII	66.5-74.6	4	4

Clypeolabral shield. Typical of this family, 457-553 μ long and 430-450 μ wide at base.

Labium. Triangular, with three segments, 256-302 μ long, 147-189 μ wide at base.

Spiracles (Fig. B). Quite large and sclerotized. The opening small with smooth margins without any processes along borders. Anterior 181-271 long, atrium 105-150 μ wide, devoid of associated narrow-rimmed pores. Posterior 196-250 μ long, 105-150 μ wide, without associated narrow-rimmed pores.

Legs (Fig. D). Well developed but short. Claws devoid of tooth. Tarsal digitules 70-76 long, unguis digitules 49-57 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	90.6 -120	75.5 -105	90.6 -120
Trochanter	105 -135	105 -135	120 -151
Femur	226 -271	226 -256	226 -271
Tibia	151 -166	135 -166	151 -181
Tarsus	151 -160	135 -151	150 -178
Claw	45.3 -74.2	45 -68	75 -90
Entire Leg	769 -926	721 -881	812 -991

Setae. Setae spaced on entire ventral surface as on dorsal side. Not very numerous and with same characteristics as on dorsal surface.

Pores (Fig. C). Clusters of wide-rimmed pores, usually devoid of ducts, scattered on entire surface. Clusters more dense on lateral and sublateral areas of body. Around vulva may be a few single or small clusters associated with a duct. Narrow-rimmed pores totally absent.

Ducts. Entirely absent except for a few associated with small clusters of pores as explained above.

Vulvar area. Vulvar opening 400-450 μ wide, surrounded by setae of different sizes.

Type material studied. Designated one neotype* and three paratypes from cactus, from Juarez, Mexico, collected at El Paso, Sep. 6, 1934 by B. R. Anderson, N^o 41-420, NMNH. The specimens have been mounted from dry material and verified by the author.

Material studied.

AZORES ISLANDS. One slide labeled: *Coccus cacti* auct. (From *Opuntia* imported from Azores) Cape of Good Hope, 1940-180 1(4) BM.

CANARY ISLANDS. *Opuntia ficus-barbarica*, Valle Guerra, Tenerife, Feb. 21, 1986, coll. GPG, D1(a-e) 1(1) VPI. *Opuntia ficus-indica*, Iguete, Tenerife, Nov. 22, 1985, coll. GPG, D32 (c+h) 1(1), D32:5 1(3) VPI. *Opuntia tomentosa*, El Socorro, Tenerife, March 3, 1986, coll. GPG, D20(a-d) 1(1) VPI. *Opuntia* sp., Las Chumberas, Tenerife, Feb. 21, 1986, coll. GPG, D19(a-g), 1(1); D23:1 1(1) VPI, Gran Canaria, Nov. 4, 1927, coll. M, Kisiur, N^o1189, 1(3) BM. Loc. ?. 1912, coll. L. Diguët, N^o8659:1 1(2); N^o8659:3 1(2) MNHN, C.I.E. 9231-1523 1(2) BM. "Nopal", Las Palmas, Gran Canaria, coll.?, Jun. 1956, labeled as *Dactylopius cacti*, 6436 (1+5), 1(1) MNHN. "Cactus plant", April 18, 1974, N. Shapiro, JFKIA 16875 1(2) USNM.

ECUADOR. *Cactus* sp., Loja, M, A. C. Nov. 6, 1955, N^o56-619 1(3) USNM.

EGYPT. Cairo, C.I.E. 6826-18466 2(1) USNM.

FRANCE. Rouen, coll. P. Noel, Mar. 27, 1905, 2(3) MNHN.

GREECE. Eight slides each with one specimen labeled: *D. coccus*, Athens Market Greece, M. W. Ballard, USNM.

INDIA. Hyderabad, Sind. Material donated to BM, 3(6) labeled: *D. coccus* Costa. Dyestuff used by silkweavers, Coimbatore, Ramakriskna 208.

MADEIRA ISLANDS. *Opuntia* "tuna", Funchal, Madeira, July, 1921, coll. Cockerell, 1(3) USNM. *Opuntia* sp, Funchal, Madeira, coll. Cockerell, Dec. 31, 1920, 1(2) USNM. Funchal, Madeira, Nov., 1960, coll. Krauss, 61-0510 1(3) USNM. Madeira, Aug. 1936, coll. Balachowsky, 4914-1, 1(3) MNHN.

MOROCCO. *Opuntia* sp., Tiznit, coll. J. Mimeur, 2-19271 (1), 1(2) BCRIR.

MEXICO. *Opuntia* sp., Valle de Oaxaca, 1912, coll. L. Diguët, 8654-11, 1(2), 8655 (1+4), 1(2), 8656-6, 1(3) MNHN. "Nopal de San Gabriel", Amantego, Valle de Oaxaca, coll. L. Vazquez, N°13 RMG-d-173 U.N.A. 1(3) MNHN. ?, 10735-22 A. Leg. Verhecken, March 23, 1987, N°5 1(1) MNHN.

PERU. *Opuntia* sp., coll. K. Antunez in different places and deposited at USNM Izcuchaca, Huancavalica, elev. 2500 m, May 26, 1977, 77-13178:1, 1(1). Mayocc near Rio Mantaro, Huancavalica, elev. 2090 m, May 29, 1977 77-13178:3, 2(1). Km 18 toward Ayacucho, elev. 2100 m, May 29, 1977, 77-13138:4, 1(1). Between Churcampa and Mayocc, Huancavalica, elev. 2500 m, May 29, 1977. 77-13178:2, 1(1). 68 km Albancay toward Cuzco near Curahuasi, Albancay, elev. 2750 m, June 2, 1977, 77-13178:8, 2(1). Near Urubamba, Cuzco elev. 2910 m, June 15, 1977, 77-13178:9, 2(1). Limatambo, Cuzco elev. 2450 m, June 24, 1977, 77-13178:10, 2(1). 127 km, from Pisco toward Castrovirreyna elev. 1300 m, July 13, 1977, 77-13178:12, 2(1). 1 km from Cajamarca, elev. 2680 m, Sep. 4, 1977, 77-13178:15, 3(1). 10 km from Huanuco toward La Union, Huanuco elev. 2120 m, 77-13178:13, 2(1). *Opuntia* "tuna roja" Namora,

Cajamarca, elev. 2630 m, Sep. 8, 1977, 77-13178:16, 3(1). *Opuntia* "tuna roja".
Namora, Cajamarca, elev. 2630 m, Sep. 8, 1977, 77-13178:16, 3(1). Cactus, 25
km Ayacucho toward Quinoa near Huari ruins, Ayacucho, elev. 2680 m, May 31
1977, 77-13178:5, 2(1). 124 km. Chumbes from Ayacucho, Ayacucho, elev. 2630
m, June 1, 1977, 77-13178:6, 2(1). Ancash-Huarez near Anta airport, elev. 2620
m, Aug. 21, 1977, 77-13178:14, 1(1). Cajamarca, km 186 near Cochabamba,
elev. 1620 m, Sep. 11, 1977, 77-13178:17, 1(1). *Opuntia* sp. Apurimac, Cuzco,
Abancay Rd., coll. B. R. Ridout, 1972-55 3(1) USNM. Ayacucho, I. Ceballos, 1(2)
VPI. Ayacucho, Prov. Huamanga Huanta, San Miguel + Cangallo coll. J. D.
Flores, June 1965, 1(2) VPI. Urubamba, Cuzco, April 18, 1976, coll. R. Marin, 1
+ 2 VPI.

SOUTH AFRICA. *Opuntia* sp., Cape Town, Labeled: *Coccus cacti* auct. C.K.B.
Nov. 15, 1910, 39-252, 1(1) VPI. Cape Town, Bot. Gardens, Dec. 11, 1935, 2(1)
PPRI.

TURKEY. Istanbul, 9689-2 + 9689-3, 1(1) MNHN.

USA. Corvallis, OREGON, Sep. 6, 1940, from R. L. Post 41-817, 1(1) USNM.
From Ferris collection, specimens purchased from drugstore 1920, 5(1) UCD.

VENEZUELA. *Opuntia* sp, El Valle, Oct. 21, 1940, D. F. F. Fernandez, 44/1550
1(3) USNM.

Additional hosts. Mainly found on *Nopalea cochenillifera* and different species of
Opuntia. Mann (1969) also mentioned *O. streptacantha* and *O. tomentosa*.

Distribution. Originally from Central and South America. Due to its value to humans, it has been introduced into several countries, but was successfully established only in some of these (See countries in Material Studied).

Etymology. Originally the species was known as *Coccus cacti* L. Linnaeus (1758) included the species in the genus *Coccus*, and gave the specific name *cacti* because the plants (cactus) on which the insects breed. Later, Costa (1835) placed the species in the genus *Dactylopius*, and introduced the specific name *coccus*.

Remarks. *Dactylopius coccus* has been extensively cited in the literature. It was known in Europe during the 16th Century after the discovery of America. Due to its importance for the dye industry, it was introduced to other parts of the world for propagation. After being mentioned by several authors in different writings, Linnaeus (1758) referred to this species as : *Coccus cacti*. Many authors accepted this name, but others used different specific names. Costa (1835) called the Mexican cochineal *Dactylopius coccus* which is well known and now extensively used in literature.

Affinities and discussion. *Dactylopius coccus* lacks ducts on the ventral surface of the body as does *D. confertus* De Lotto. *D. coccus* is entirely different from other species because of scarcity and small size of the setae and the total absence of narrow-rimmed pores. The clusters of wide-rimmed pores usually are without ducts.

Natural enemies. Among the prickly pear plantations in the Canary Islands (Spain). The author has identified as predators the following: Coleoptera: Coccinellidae *Chilocorus renipustulatus* Scriba, *Coccinella septempunctata* (L.), *Cryptolaemus montrouzieri* Mulsant, *Exochomus flavipes* Thunb., and *Scymnus* sp. Piña-Luján (1977) listed from Mexico: Lepidoptera: Phycitidae *Laetilia coccidivora* (Comstock) and *Salambona analamprella* (Dyar); Coleoptera: Coccinellidae *Hyperaspis trifurcata* Schaeffer, *H. fimbriolata* Melsheimer, *Cybocephalus gibbulus* Erichson, *Nephus intrusus* (Horn), *S. horni* Gorham; Diptera: Syrphidae *Baccha* sp.; Diptera: Agromyzidae *Leucopis bellula* Williston; Neuroptera: Hemerobiidae *Hemerobius amicus* Fitch. He also mentioned that several birds, rodents and reptiles consume large amounts of cochineals. Marin & Cisneros (1983) reported the predator *Allograpta* sp. (Diptera: Syrphidae) from Peru.

Biological control agent. *D. coccus* in cases of heavy infestation can kill their host plants.

Dactylopius confertus De Lotto

Plate 13

Selected literature. *Dactylopius confertus* De Lotto, 1974:180

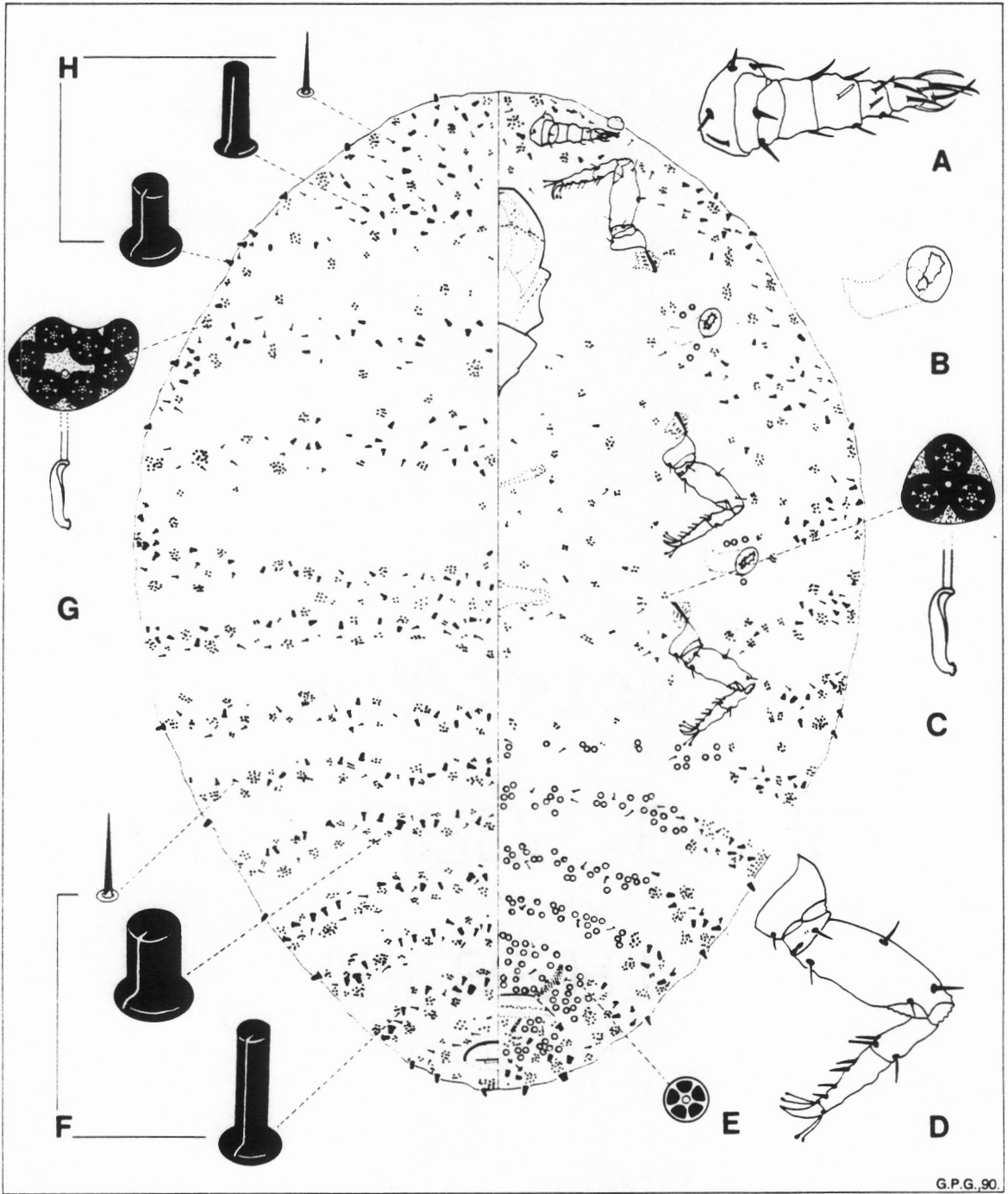
Adult female. Live adult females have not been seen by the author, and no information is available on the external appearance. Adult females on slides are oval; about 1.5-2.5 mm long and 1.1-1.8 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores singly or in clusters. On the head 7-15 clusters formed mainly with 2-11 pores. On the thorax 85-170 clusters mostly with 2-19 pores. On the abdomen approximately 200 clusters, with up to 20 pores.

Setae (Figs. F, H). In general not very numerous on entire body. Setae range from cylindrical with rounded apex to hairlike. The larger ones are mostly found on the last abdominal segments, becoming smaller and more scarce toward the head.



G.P.G., 90

Plate 13. Adult female of *Dactylopius confertus* De Lotto

SETAE (μ)	Large		Small		Hairlike	
	Length	Wide	Length	Wide	Length	Wide
HEAD	25.5	12.5	20.5	10.0	17.5	7.5
THORAX	30.0	12.5	22.0	12.5	18.0	7.5
ABDOMEN	32.5	17.5	27.5	15.10	37.5	12.5

Anal area. Anal ring elliptic 104-123 μ wide, 43.0-92.2 μ long. Anterior margin with a narrow sclerotized band. About 8-20 clusters with 2-15 wide-rimmed pores, some pores occur singly. Very few setae of different sizes present.

Ventral Surface

Eyes. Diameter at base 42.8-49.9 μ , distance between bases 154-565 μ .

Antennae (Fig. A). Seven-segmented, 92.8-159 μ long. Distance between antennal bases 73.8-246 μ . Frequently, segmentation not clear between 5th and 6th articles.

Segments	Lengths (μ)	Setae	Fleshy setae
I	14.2-30.9	4	0
II	7.14-16.6	2	0
III	14.2-10.0	0	0
IV	11.9-21.4	2	0
V	9.52-21.4	2	1

VI	11.9-21.4	2	1
VII	23.8-28.5	4	3

Clypeolabral shield. Normal for this family, 246-276 μ long and 215-276 μ wide at base.

Labium. Three-segmented, 135-159 μ long, 104-209 μ wide at base.

Spiracles (Fig. B). Opening sclerotized with minute teeth along the margins. Anterior 116-123 μ long, atrium 49.2-61.5 μ wide, 0-3 associated narrow-rimmed pores. Posterior, quite similar in shape and length to anterior, 104-123 μ long, 49.2-67.6 μ wide; with 0-3 narrow-rimmed pores.

Legs (Fig. D). Short and thick. In some specimens the claws have a very tiny tooth, sometimes the tooth is only on the metathoracic claws, in others no tooth was observed. Tarsal digitules, 45.0-60.0 μ long; claw digitules 28.0-31.0 μ long.

Leg Segments and Claw(μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	45.0-75.0	42.5-67.5	55.0-82.5
Trochanter	50.0-62.5	37.5-62.5	50.0-67.5
Femur	107-125	107- 130	100-145
Tibia	50.0-70.0	62.5-75.0	67.5-80.0
Tarsus	62.5-87.5	62.5-82.5	57.5- 100
Claw	26.0-35.0	25.0-37.5	27.5-40.0
Entire leg	413-553	415-543	435-612

Setae. Same as on dorsal surface but only on body margins.

Pores (Fig. C). Wide-rimmed, singly or in clusters on lateral and sublateral areas of head and thorax where they also extend to the middle area, on first two or three segments of abdomen. Narrow-rimmed pores (**Fig. E**) many, but only in median area of the last four or five abdominal segments.

Ducts. Ducts totally absent, but associated with clusters of wide-rimmed pores.

Vulvar area. Vulvar opening 184-369 μ wide, surrounded by a large number of narrow-rimmed pores and some setae.

Type material studied. Holotype 4619:2, 1(1)* and three paratypes 4619: 1+3 from *Cleistocactus* sp., Argentina, Salta, Morillo, Mar. 15, 1972, coll. H. Zimmermann, PPRI; one paratype 4619:11, 1(1) with the same information as above but located at USNM.

Material studied.

ARGENTINA: *Cleistocactus baumannii*, Formosa, Laguna Yema, Mar. 16, 1972, coll. H. Zimmermann, 4610:1-4, 4(4) PPRI. *Echinopsis leucantha*, San Luis, San Luis, Sep. 15, 1970, coll. H. Zimmermann, 4143:1-4, 4(4) PPRI.

USA: *Opuntia* sp., Claremont (Probably California because of the time in the year that was collected), Feb.16, 1935, coll. J. D. Maple, 3(3) UCD.

Additional hosts. Unknown.

Distribution. See above.

Etymology. None given by De Lotto (1974), but it is assumed that the name was derived from the Latin adjective "confertus", meaning closely compressed or dense arrangement of the wide-rimmed pore clusters on the thorax and abdomen. This character will distinguish it from *D. austrinus* and *confusus* (see Affinities and discussion).

Remarks. This species was named and briefly described by De Lotto in 1974.

Affinities and discussion. According to De Lotto (1974), this species could be confused with *D. austrinus* and *D. confusus*. *D. austrinus* does not have clusters of wide-rimmed pores on the venter in the median area of thorax as *D. confertus* does, but only on the first abdominal segments. *D. confusus* does not have clusters of wide-rimmed pores on venter in median area of thorax or on the abdominal segments.

Natural enemies. None known.

Dactylopius confusus Cockerell

Plate 14

Selected literature and synonymy.

Acanthococcus confusus Cockerell, 1893a.

Coccus confusus (Cockerell); Cockerell, 1893b, 1895:728; 1897:750; Green, 1912:89; MacGillivray, 1921:104.

Coccus cacti confusus (Cockerell); Cockerell, 1896:34.

Coccus confusus newsteadi, Cockerell, Fernald, 1903:82; Green, 1912:90; (*Coccus newsteadii*) MacGillivray, 1921:104.

Coccus tomentosus newsteadi Cockerell, 1898.

Coccus tomentosus confusus (Cockerell); Cockerell 1898.

Pseudococcus tomentosus newsteadi (Cockerell); Cockerell, 1899a.

Pseudococcus confusus (Cockerell); Cockerell, 1899a.

Pseudococcus confusus newsteadi (Cockerell); Cockerell, 1899b.

Dactylopius confusus (Cockerell); Cockerell, 1902 ; Lizer y Trelles, 1939:182; Dodd, 1940:98; Ferris, 1955:88; Mann, 1969:140; De Lotto, 1974:180; Koteja, 1974a:77; Gilreath & Smith, 1987:768, 1988:730.

Dactylopius confusus newsteadi (Cockerell); Cockerell, 1902.

Coccus confusus capensis Green, 1912:91; MacGillivray, 1921:104.

Dactylopius greenii Cockerell, 1929; Dodd, 1940:98; Mann, 1969:140.

Dactylopius newsteadi (Cockerell); Cockerell, 1929; Dodd, 1940:104; Mann, 1969:140.

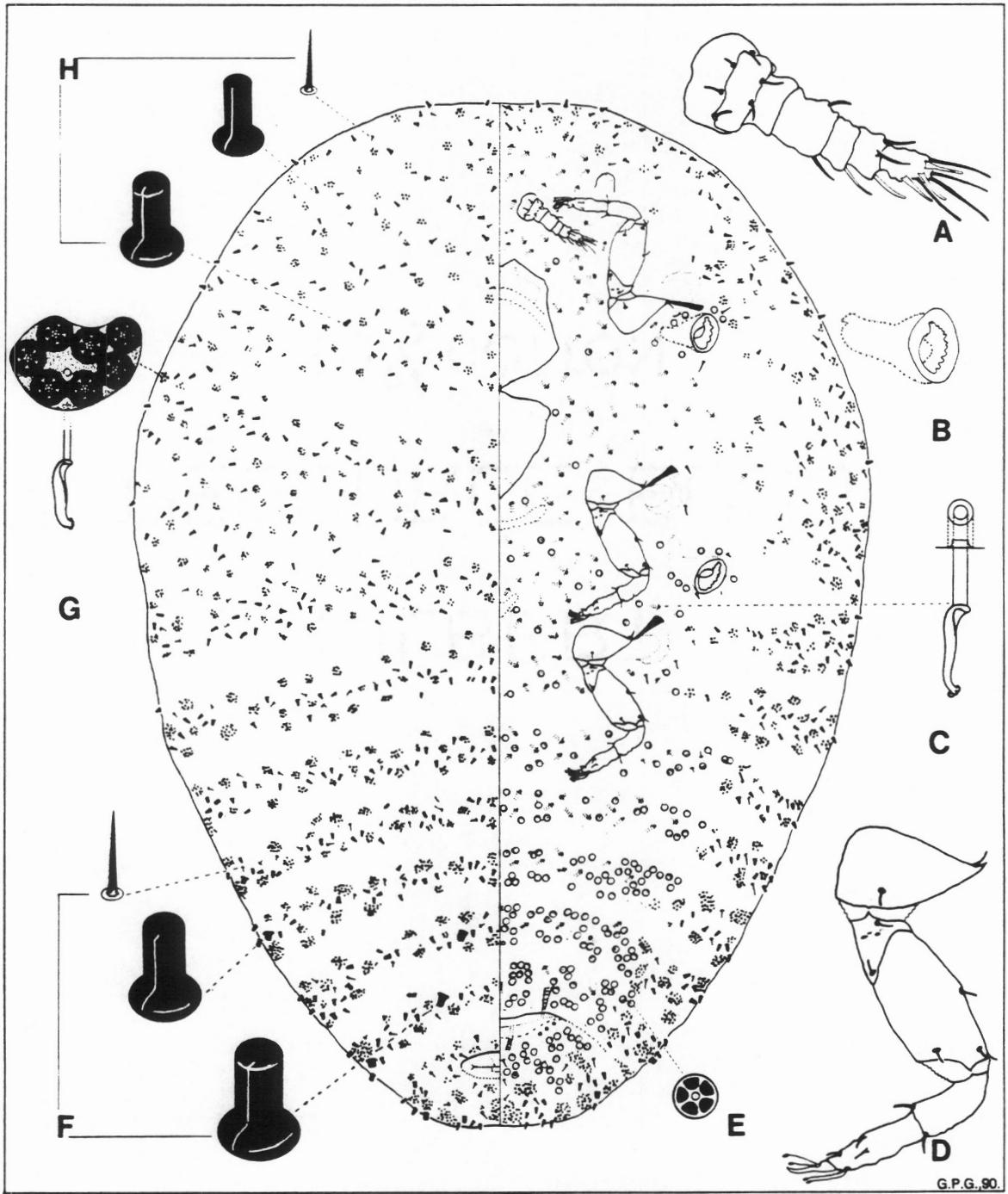


Plate 14. Adult female of *Dactylopius confusus* (Cockerell)

Adult female. Live adult females oval, 2.5-3.0 mm long, 1.5-2.0 mm wide, and 1.0-1.4 mm high. Body covered with profuse white cottony wax that conceals individuals; wax from several individuals can fuse together forming small cottony-balls on the host. If the wax is removed, insect appears purple-red, a typical color for members of this family. Adult females on slides sub-globular, 3.3-4.5 mm long and 2.5-4.0 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores in clusters with one or more associated ducts. On head 25-30 clusters, each normally with 4-6 pores. On thorax about 125 clusters, most of them with 4-6 pores. On abdomen approximately 200 clusters; clusters on lateral abdominal areas may have up to 30 or more pores each.

Setae (Figs. F, H). Numerous and large on abdomen, less numerous and shorter toward head. Some on last abdominal segments short, cylindrical, with truncate apex, others with more conspicuous apex.

SETAE (μ)	Large		Medium		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	20.8	12.0	14.2	9.50	19.0	7.10
THORAX	23.8	12.0	16.6	9.50	22.1	4.78
ABDOMEN	26.1	19.0	21.5	9.50	38.0	4.79

Anal area. Anal ring elliptical, 104-178 μ wide, 85-116 μ long. Anterior border well defined by a sclerotized rim. Surrounded by 5-9 clusters of wide-rimmed pores and some setae.

Ventral Surface

Eyes. Somewhat prominent and slightly sclerotized. Diameter at base 49-51 μ , distance between bases 430-450 μ .

Antennae (Fig. A). Seven-segmented, 119-175 μ long. Distance between antennal bases 123-264 μ . Some specimens without a clear segmentation between 3rd and 4th articles, so they appear six-segmented.

Segments	Lengths (μ)	Setae	Fleshy-setae
I	24.0-35.5	4	0
II	9.50-12.0	2	0
III	12.0-23.0	0	0
IV	19.0-26.0	2	0
V	9.50-21.5	0	1
VI	12.0-19.0	2	1
VII	33.3-38.0	4	3

Clypeolabral shield. Pentagonal, 307-338 μ long and 245-308 μ wide at base.

Labium. Triangular, 147-160 μ long, 166-209 μ wide at base.

Spiracles (Fig. B). Rather large with minute teeth along margins of sclerotized opening. Anterior 153-178 μ long, atrium 50.0-73.8 μ wide, with 3-6 associated narrow-rimmed pores. Posterior, slightly larger than anterior, 166-196 μ long, 55-61 μ wide; with 2-8 associated narrow-rimmed pores.

Legs (Fig. D). Moderately stout without tooth on claw. Tarsal digitules 50.0-59.5 μ long; unguis digitules 30.0-37.0 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	59.0-78.0	64.0-83.0	59.5-81.0
Trochanter	59.5-85.0	69.0-85.0	83.0-85.0
Femur	131-143	155-143	142-159
Tibia	71.5-90.5	73.0-90.5	71.0- 104
Tarsus	88.0- 102	95.0- 100	95.0- 109
Claw	33.0-38.0	19.0-40.0	19.0-38.0
Entire leg	442-536	475-541	469-576

Setae. Limited mainly to lateral and sublateral areas of body. Similar in shape to those on dorsal surface.

Pores. Clusters of wide-rimmed pores in lateral and sublateral areas on head, thorax, and abdomen. On abdomen, clusters with more pores. Narrow-rimmed pores (Fig. E) scattered on head, thorax and first abdominal segments; numerous on the last three or four abdominal segments.

Ducts (Fig. C). Very numerous, on median area of head, thorax and abdomen.

Vulvar area. Vulvar opening 123-246 μ wide. Surrounded by large number of narrow-rimmed pores and some setae.

Type material studied. One lectotype and eight syntypes on three slides, all labeled *Coccus tomentosus* var. *newsteadi* Cockerell, Walnut Creek Canyon near Flagstaff, Arizona, June, 1898, coll. E. M. Ehrhorn, 3(9) USNM. This material was remounted and designated as lectotype by De Lotto in absence of other type material.

Material studied.

ALGERIA. *Opuntia ficus-barbarica*, Alger, Aug. 1, 1950, coll. H. Lucas, N°8660:2+3, 2(4) MNHN.

AUSTRALIA. *Opuntia aurantiaca*, Lowood, Aug. 7, 1973, coll. H. Zimmermann, N°5292:1+2, 2(2) PPRI. *Opuntia streptacantha*, Feb. 17, 1963, Coll. Haseler, N° c-428, 1(3) BM. *Opuntia stricta*, Queensland, Rockhampton, May 5, 1967, coll. B. W. Willson, N°2909:1-6, 6(6) PPRI. *Opuntia tomentosa*, Feb. 12, 1963, coll. Haseler, N°C-427, 1(2) BM. "Prickly pear", Victoria, Broad Meadow, Sep. 9, 1970, coll. H. J. Banks, N°A4214, 1(3) BM. Canberra, 1972, coll. H. J. Banks, N°A5913, 1(2) BM.

BAHAMAS. *Opuntia* sp., Long Island, June 1972, coll. F. D. Bennett, N° A5720, 1(2) BM.

CANADA. *Opuntia polyacantha*, Saskatchewan, Big Muddy Lake, April 26, 1974, coll. P. Harris, N°5048:1+2, 2(2), PPRI.

HAITI. "Seleniocereus", at Quarantine in D. C., June 9, 1817, coll. H. L. Sangord, 1(2) USNM. *Opuntia sp.*, at Hoboken (New Jersey), Oct. 1, 1948, coll. Albright, N°12220, 1(4) USNM.

MAURITIUS. ?, April 22, 1949, coll. Dept. Agric., 1(2) NMHN.

MEXICO. *Cereus versicolor*, San Francisco, Aug. 26, 1938, coll. M. Galbraith, N° 15693, 1(1) USNM. *Opuntia pumila*, Mitla, June 16, 1973, coll. H. Zimmermann, N°5290:1, 1(1) PPRI. "Cactus sp.", 20 mi. W. of Linares, Nov. 8, 1946, coll. ?, 1(1) UCD. Cuantla, July 25, 1897, coll. Koebele, N°5817, 2(14) USNM. Laredo, Feb. 29, 1948, coll. Walton, N°48-1022, 1(1) USNM. 15 mi. N. Rodeo, Hidalgo Co., Aug. 3, 1966, coll. D. R. Miller, N°695, 1(1) UCD. *Opuntia sp.*, Cuernavaca, Aug. 26, 1944, coll. N. L. Krauss, N°C-8, 1(3) USNM. Taxco, Sep. 7, 1944, coll. N. L. Krauss, N°C-16, 1(2) USNM. Barranca de Oblatos, Guadalajara, June 1945, coll. N. L. Krauss, N°46-1767, 1(2) USNM. Nogales, March 21, 1949, N°68768, 1(1) UCD. El Salto, April 1964, coll. D. J. Williams, N°8291, 1(3) BM. 3 mi. N. W. Petlalcingo, Puebla, March 4, 1972, coll. F. D. Parker, N°38 2(3) USNM. From Juarez, quarantined at El Paso, Feb. 4, 1978, coll. Bejarano, 1(1) USNM.

PERU. *Opuntia exaltata*, Quispicanchi Hacienda, Capana, Nov. 17, 1922, coll. F. L. Herrera, 1(3) USNM. *Opuntia sp.*, Lima, May 5, 1986, coll. R. Marin, 1(2) VPI.

USA. ARIZONA. *Opuntia engelmannii*, Hacienda del Sol, Tucson, Oct. 10, 1932, coll. E. Anole, 10(44) UCD. El Encanto Estates, Oct. 1, 1934, coll. Minor, 1(4) UCD. Tucson, Oct. 31, 1941, coll. M. Stegmeier, 2(8) UCD. Page Ranch, Nov. 1, 1941, coll. L. P. Wehrle, N°1216, 5(5) UCD. Pima Co., June 4, 1956, coll. L. P. Wehrle, N°1226, 1(1) UCD. Green Valley, Nov. 9, 1970, coll. E. J. Hambleton, N°4, 4(6) USNM. *Opuntia sp.*, Tucson, Feb. 6, 1928, coll. A. A. Nichol, 1(5) UCD. John Harlow Nursery, Alameda St., Tucson, Pima Co., Dec. 30, 1948, coll. G.

Nickel, N^o1438, 3(6) UCD. Chiricahua Mts., Cochise Co., June 15, 1964, coll. M. Kosztarab, Ariz.:a-d, 5(10) VPI. Bright Angel Creek, Grand Canyon, July 23, 1964, coll. R. P. Allen, N^o6463-33, 1(1) CDA. Prescott, Aug. 31, 1969, coll. M. Kosztarab, N^o D5:a-c, 3(5) VPI. Silver Peak, Cochise Co., July 4, 1971, coll. G. W. Robison, N^o 14:a-d, 4(5) VPI. Tucson area, April 16, 1974, coll. T. Eisner, 2(4) USNM. Plants in greenhouse of VPI from Portal, April 5, 1990, coll. G.P.G., D13:a, 1(3) VPI. "Prickly pear", Cave Creek, Sep. 16, 1959, coll. F. F. Bibby, N^o1613, 1(2) USNM. "Flat *Opuntia*", Clemenceau, 1924, G. F. Ferris, 2(4) UCD. CALIFORNIA. *Opuntia* sp. Deep Springs, March 23, 1937, coll. G. F. Ferris, 2(4) UCD. San Diego Co., March 25, 1959, coll. J. K. Holloway, N^o59-0922, 2(11) USNM. Devore, San Bernardino Co., May 15, 1961, coll. D. W. Ricker, 5(5) UCD. Surprise Canyon, Inyo Co., May 6, 1961, Coll. Cavagnaro, 4(4) UCD. Irwindale, San Gabriel Rt., Los Angeles Co., April 4, 1963, coll. R. R. Snelling 2(2) UCD. 5 mi. E. San Bernardino, April 2, 1963, coll. D. R. Miller, N^o66, 5(5) UCD. 4 mi. E. El Toro, Orange Co., April 4, 1964, coll. D. R. Miller, N^o238, 3(5) UCD. Etiwanda, San Bernardino Co., May 11, 1963, coll. R. R. Snelling, 7(7) UCD. Fresno, Jan. 15, 1968, coll. H. V. Dunnegon, N^o 62A16-15, 1(1) CDA. Riverside, Riverside Co., Oct. 20, 1972, coll. E. Reeves, N^o 72J24, 1(1) CDA. Westgaard Pass, Inyo Co., June 25, 1980, coll. Gilbert, 1(3) CDA. "Cactus sp.", San Fernando Valley, Feb. 2, 1927, coll. L. E. Myers, 2(4) UCD. Plant Institute Station, Chico, Feb. 18, 1915, coll. Bougles, 1(2) UCD. Harvard, San Bernardino Co., Sep. 28, 1965, coll. Stickney, N^o 65J44, 1(1) CDA. "Platyopuntia", Outer Hwy. 60, Devore, San Bernardino Co., Feb. 10, 64, coll. D. W. Ricker, 24(24) UCD. Hwy.. 99 San Dimas Ave., Pomona, Los Angeles Co., Jan. 16, 1962, 16(16) & March 18, 1964, coll. D. W. Ricker, 24(24) UCD. Kagel Canyon, San Fernando, Los Angeles Co., March

18, 1964, coll. D. W. Ricker, 13 (13) UCD. Pigeon Pass Rd. Highgrove, Riverside Co., April 16, 1964, coll. D. W. Ricker, 6(6) UCD. Mt. Rubidoux, Riverside, Riverside Co., April 22, 1964, coll. D. W. Ricker, 15(15) UCD. Padua Ave. Claremont, Los Angeles Co., April 22, 1964, coll. D. W. Ricker, 13(13) UCD. Three mi. E San Juan Capistrano, Orange Co., April 16, 1964, Coll. T. W. Fisher, 16(16) UCD. COLORADO. *Opuntia* sp., Gregory Canyon, April 1906, coll. W. P. Cockerell, N^o5817, 1(3) USNM. Geneva Park, April 6, 1929, coll. E. D. Bucker, N^o393359, 2(8) UCD. FLORIDA. *Opuntia* sp., Silver Springs, Oct. 1955, coll. N. L. Krauss, N^o 55-12395, 1(5) USNM. Archbold Bio. Sta., Lake Placid, Dec. 25, 1960, coll. F. C. Craighead, N^o 61-1467, 1(3) USNM; Oct. 13, 1979, coll. S. Nowicki, N^o 79-10903, 1(2) USNM. Delano, June, 1973, coll. H. Zimmermann, N^o5286:1, 1(1) PPRI. Cedar Key, Levy Co., April 25, 1975, coll. J. A. Davidson, N^o 2760, 1(1) USNM. Eureka, Marion Co., May 26, 1975, coll. R. F. Denno, N^o 2766, 1(1) USNM. "Cactus sp.", Fort Pierce, June 20, 1940, coll. W. Mathis, N^oQ.32383, 1(4) USNM. Palm Beach, May 3, 1945, coll. Anderson, N^o 25422, 1(3) USNM. Cortez, Nov. 19, 1971, coll. J. R. McFarlin, N^o125447, 1(1) USNM. IDAHO. "Cactus sp.", Challis, June 26, 1960, coll. G. F. Knowlton, N^o41, 1(2) USNM. MONTANA. *Opuntia* sp., *polyacantha?*, Helena, May 1917, coll. R. W. Doane, 7(9) UCD. NEBRASKA. *Opuntia* sp., Fairsbury, Jefferson Co., Oct. 20, 1977, coll. S. V. Johnson, N^o71-13306, 2(2) USNM. NEVADA. *Opuntia* sp., 5 mi. W. of Ely, Aug. 1, 1960, coll. T. R. Haig, 3(8) VPI. Las Vegas, Clark Co., Oct. 21, 1977, coll. W. F. Hoff, 1(2) CDA. NEW MEXICO. *Opuntia* sp., Mesilla, Oct. 8, 1896, coll. Townsend, N^o5817, 2(5) USNM. NEW YORK. *Opuntia* sp., Botanical Garden on plants from Florida, May 1936, coll. Kau, 1(1) UCD. OKLAHOMA. *Opuntia* sp., 10 mi. W. Medford, Grant Co., June 28, 1979, coll. D. R. Miller, N^o1525, 1(1) USNM.

SOUTH CAROLINA. *Opuntia* sp., Kiawah Islands, July 9, 1990, coll. H. Hendricks, D33:1, 1(3) VPI. TEXAS. *O. discata*, Brazos Co., Nov. 24, 1984, coll. M. E. Gilreath, N^o85-2125, 2(4) USNM. *O. lindheimeri*, Kingsville, Nov. 3, 1920, coll. J. C. Hamlin, 2(5) USNM. *Opuntia* sp., Brownsville, Cameron Co., Aug. 1965, coll. N. L. Krauss, N^o8218, 3(8) USNM. 10 mi. N. Amarillo, Potter Co., coll. D. R. Miller, El Paso, Aug. 17, 1972, coll. G. R. Dunn, N^o3929, 1(2) USNM. 7 mi. from Main Rd. on old Santa Elena Canyon, Brewster Co., May 7, 1976, coll. R. D. Gordon, N^o3088, 2(4) USNM. July 1, 1970, N^o1590, 1(1) USNM. Hwy. 107, 1.8 mi W. of jct. Hwy. 2671, Coryell Co., Aug. 2, 1984, coll. M. E. Gilreath, N^o 85-2125, 2(5) USNM. "Cactus sp.", Baird, May 20, 1918, coll. Porlaks, T-639, 3(6) UCD. Weslaco, Dec. 18, 1930, coll. S. W. Clark, N^o 16, 1(2) USNM. Donges, Montell, Jan. 20, 1932, 2(4) CDA. San Saba, Nov. 1945, coll. P. M. Scheffer, N^o 461, 1(3), USNM. Big Bend Nat. Park, May 15, 1976, coll. M. Kosztarab, 14(18) VPI. "Prickly pear", Sterling City, Oct. 7, 1933, coll. G. H. Entira, N^o34220, 1(4) USNM. Horne Ranch, Coleman Co., June 23, 1982, coll. G. Hackler, N^o 82-663, 19(19) USNM. SOUTH DAKOTA. *Opuntia* sp., Claremont, Feb. 16, 1935, coll. J. D. Maple, 5(5) CDA. Badlands Nat. Monument, Ponnington Co., Aug. 12, 1970, coll. D. R. Miller, N^o1846 USNM. UTAH. *O. polyacantha*, 1.5 mi. N. crescent, Jensen, Grand Co., May 28, 1987, coll. C. R. Nelson, 4(9) CDA. "Cactus sp.", Zion Nat. Park, Nov. 1933, coll. D. E. Beck, N^o36 1608, 1(2) USNM. *Opuntia* sp., near Park City, July 29, 1936, coll. C. L. Haywood, 1(1), UCD. WASHINGTON. *Opuntia* sp., Richland, Benton Co., June 16, 1981, coll. L. Rogers, N^o81-6523, 2(3) USNM.

SOUTH AFRICA. *Opuntia monacantha*, Cape Province, Gantoos Ferry, Aug. 13, 1938, coll. F. W. Pettey, 2(2) PPRI. *Opuntia* sp., Cape of Good Hope, coll. E. Green, N°78, 1(2) MNHN.

Additional hosts and distribution. Cockerell (1929) listed this species from the Rocky Mountain districts including Colorado and Texas. Mann (1969) mentioned it from *O. polyacantha*, *O. tortispina*, and related species, for some northern states in USA. He also cited *D. confusus* on *O. tortispina* in Colorado, Kansas, Nebraska, and Oklahoma. On *O. polyacantha* in Colorado, Utah, and Wyoming; in Arizona on *O. basilaris*. Mann also wrote that in Florida this species occurs everywhere on host plants such as *O. austrina*, *O. dillenii*, *O. polyacantha*, *O. stricta*, and *O. tracyi*. In Australia the insect was reared on *O. inermis*.

Etymology. The name derivation is not discussed in any of the literature consulted, but probably comes from the Latin "confusus" meaning confusing, disorderly; probably because some authors were confused with this species.

Remarks. Cockerell (1893) described this species twice, first as *Acanthococcus confusus* and then as *Coccus confusus*. Five years later, the same author designated a new name for the wild cochineal: *Coccus tomentosus* var. *newsteadi* from Arizona. De Lotto (1974) pointed out that the references that Cockerell gave in the original description for *newsteadi* (= *confusus*, Ferris' suggestion) should be regarded as a misidentification. De Lotto also mentioned that *Coccus confusus capensis* Green, 1912 (later *D. greenii* Cockerell, 1929) has the same morphological characteristic as *confusus*, and it is considered a synonym.

Affinities and discussion. Apparently *D. confusus* could be mistaken as *D. zimmermanni* because both species have some large truncate setae on dorsal surface. However, *zimmermanni* has these setae on the head, thorax and abdomen, and *confusus* only on middle area of last abdominal segments. Also the spiracles can be used in the separation of both species. The spiracles in *confusus* have minute teeth along the margin of the sclerotized opening, but in *zimmermanni* these are smooth.

Natural enemies. Girault (1916) cited *Formicencyrtus thoreauini* Girault (Hymenoptera: Encyrtidae) as a parasite of *D. confusus*. Goeden et al. (1967) reported that may be a mistake. Gilreath & Smith (1988) listed as common predators of *D. confusus*: *Laetilia coccidivora* Comstock (Lepidoptera: Pyralidae), *Hyperaspis trifurcata* Schaeffer (Coleoptera: Coccinellidae), and *Leuccopis bellula* Williston (Diptera: Chamaemyiidae).

Biological control agent. Julien (1982) reported that *D. confusus* has never been employed successfully as a biological control agent. Its capacity to control prickly pear in the absence of indigenous natural enemies is unknown (Gilreath & Smith, 1988).

Dactylopius opuntiae (Cockerell)

Plate 15

Selected literature and synonymy.

Coccus tomentosus: Cockerell, 1896.

Coccus cacti opuntiae Cockerell, 1896.

Dactylopius opuntiae (Cockerell); Cockerell, 1929:328; Dodd, 1940:100; Pettey, 1948:105; Mann, 1969:139; Karny, 1972:1; De Lotto, 1974:184; Annecke & Moran, 1978:171; Nur, 1982:520; Hartley, Walter & Morrison, 1983:97.

Adult female. Live adult females are oval: 2.1-2.3 mm long, 1.4-1.7 mm wide, and 1.3-1.5 mm high. The body is covered with profuse white cottony wax. If the wax is removed, the color of the insect is purple-red. Adult females on slides are sub-globular in shape; 2.0-3.1 mm long and 1.8-2.7 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores in clusters with an associated duct. On head 15-20 clusters, each with 2-4 pores. On thorax around 110 clusters most of them with 2-4 pores. On abdomen approximately 200 clusters with up to 20 pores each.

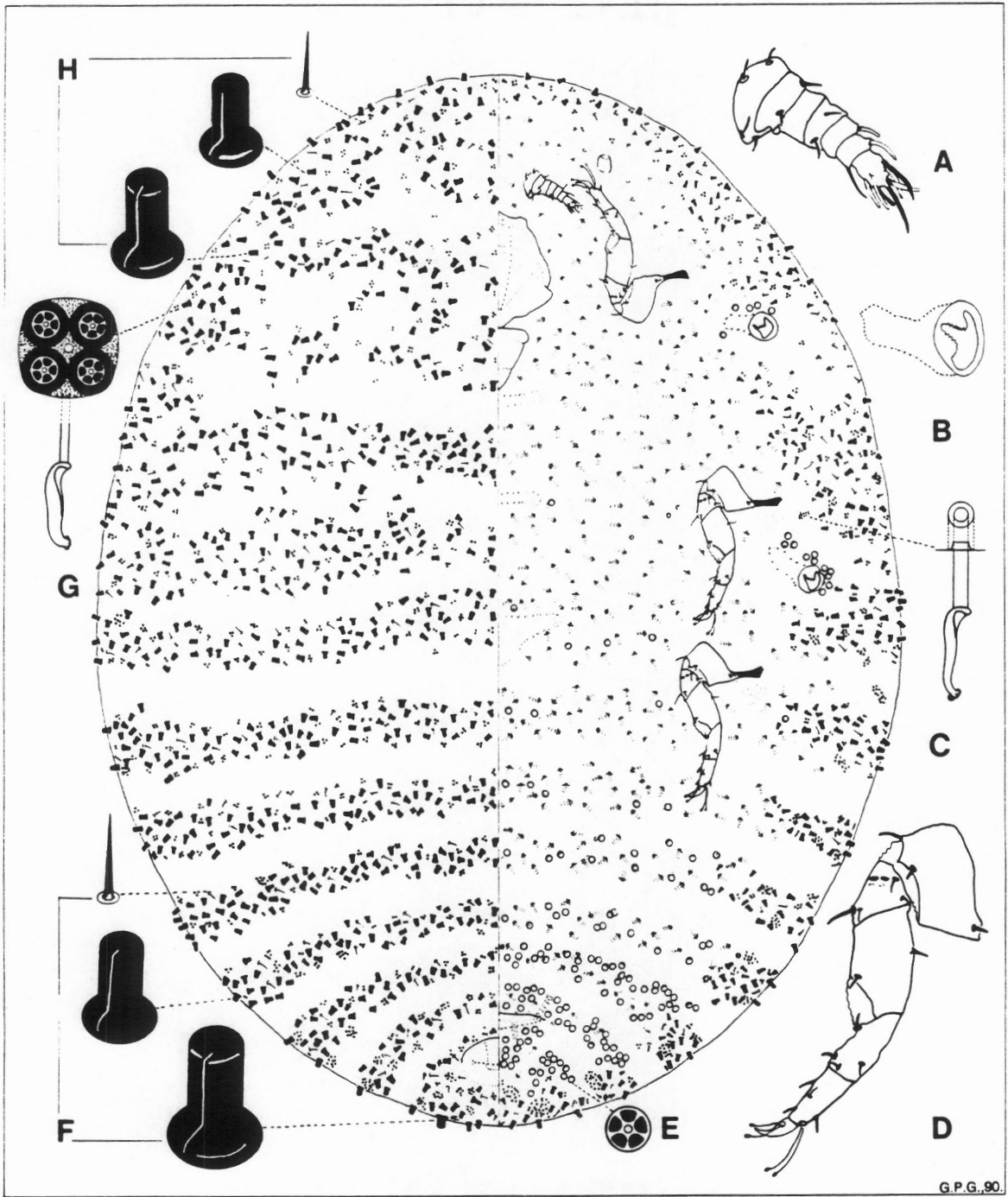


Plate 15. Adult female of *Dactylopius opuntiae* (Cockerell)

Setae (Figs. F, H). Quite numerous on entire body. Setae range from short cylindrical with truncate apex to hairlike setae. Setae similar in size and shape on entire body, except for a few larger ones on last abdominal segments.

SETAE (μ)	Large		Medium		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	21.4	14.2	19.0	11.9	26.1	9.50
THORAX	21.4	14.2	19.2	11.7	26.0	9.50
ABDOMEN	23.8	16.6	19.0	14.2	40.0	9.50

Anal area. Anal ring elliptical, well developed 135-165 μ wide, 89-100 μ long. Anterior border with a sclerotized rim. Surrounded by 7-15 clusters of wide-rimmed pores and some setae.

Ventral Surface

Eyes. Moderately conspicuous and slightly sclerotized. Diameter at base 36.0-41.0 μ , distance between bases 457-650 μ .

Antennae (Fig. A). Seven-segmented, 102-126 μ long. Distance between antennal bases 119-180 μ . Some specimens without a clear segmentation between 3rd and 4th segment, so they appear six-segmented.

Segments	Lengths (μ)	Setae	Fleshy-setae
I	19 -22	4	0
II	9.5-13	2	0
III	14 -17	0	0
IV	14-20	2	0
V	12-15	0	1
VI	11-13	1	1
VII	23-26	3	4

Clypeolabral shield. Typical in shape for this family, 247-276 μ long and 287-305 μ wide at base.

Labium. Triangular, 52-56 μ long, 46-52 μ wide at base.

Spiracles (Fig. B). Rather large with minute teeth along margins of sclerotized opening. Anterior 129-141 μ long, atrium 49-55 μ wide, 8-15 narrow-rimmed pores associated. Posterior, quite similar in length to anterior, 131-166 μ long, 47-61 μ wide; with 12-20 narrow-rimmed pores.

Legs (Fig. D). Short and robust without a tooth on claw. Tarsal digitules 46-58.5 μ long; unguis digitules 29-38 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	47.5- 59.0	59.5- 64.2	54.0- 71.4
Trochanter	46.0- 59.5	59.5- 64.2	45.0- 60.0
Femur	107- 115	95 0- 123	95.0- 110
Tibia	61.9- 71.5	57.1- 73.7	59.5- 69.0
Tarsus	69.0- 72.0	69.0- 76.0	69.0- 83.0
Claw	23.8- 35.7	23.0- 33.0	28.0- 33.0
Entire leg	355- 412	372- 424	350- 426

Setae. Similar in shape and size to those on dorsal surface but less numerous, mainly restricted to lateral and sublateral areas.

Pores. Clusters of wide-rimmed pores in lateral and sublateral areas on head, thorax, and abdomen. On abdomen clusters with more numerous pores. Narrow-rimmed pores (**Fig. E**) scattered in median area of thorax and first abdominal segments, and quite numerous on last three abdominal segments.

Ducts (Fig. C). Very numerous on median area of head, thorax, and abdomen.

Vulvar area. Vulvar opening 175-205 μ wide. Surrounded by many narrow-rimmed pores, some ducts and setae.

Type material studied. One syntype and one lectotype designated by De Lotto (1974) from Cockerell's collection. These were labeled as *Coccus tomentosus* Lmk. on Cactus. Guanajuato (Mexico), July 24, 1893 (Cockerell). N^o5852 89/1 (1+2) USNM. From the same type material eight slides were prepared and marked as topotypes D26 (a-c), D25 (a-b), D31 (a-c) VPI, from USDA dry material

that were kept with two notes: one marked as *Acanthococcus tomentosus* Lmk., the other: *Coccus tomentosus* Lmk.

Material studied.

AUSTRALIA. *Opuntia inermis*, New South Wales, Kortingal, Oct. 5, 1978, coll. P. Deighton, 1(2) BM.

BRAZIL. *Opuntia palmadora*, Peruambuco, Arco Verde, April 28, 1973, coll. Zimmermann, N^o4868, 2(2) PPRI.

FRANCE. *Opuntia* sp., New Caledonia, N^o11148-3+4, 2(4) NMHN.

INDIA. *Opuntia dillenii*, Orissa, Bhubaneswar, Oct. 15, 1982, coll. D. D. Ghosh, N^o14875, 1(2) BM. *Opuntia* sp., 25 mi. S. W. Madras, Nov. 14, 1964, coll. S. W. Brown, N^o551, 2(2) CDA. 33 mi, N. E. of Ambala, 1.5 mi. S. of village Sandhora on Nahn-Ambala Rd., Feb. 14, 1973, coll. L. R. Batra, N^o73-3846, 1(3) USNM.

JAMAICA. *Opuntia* sp., Kingston, 1919, coll. Cockerell, 1(2) UCD. F. N. da carta, Kingston, coll. Cockerell, D22: 1+2, (2) VPI. Campus U.C.W.I. Kingston, June 22, 1962, coll. S. W. Brown, N^o112, 6(1) CDA. "Platyopuntia", Kingston, Dec. 3, 1964, coll. J. R. Parnell, 45(45) UCD.

KENYA. *Opuntia* sp., Naivasha, Jan. 21, 1979, coll. Bennett & Woodford, N^o10918, 1(2) BM.

MAURITIUS. Four slides each with three specimens labeled: *D. tomentosus* (Lam.) on "*Opuntia tuna*" coll. & det. R. Mamet, March, 1949, N^o81:6,7,8 MNHN.

MEXICO. *Opuntia coccinelifera*, Mexico City, April, 1922, coll. Riveles, 1(2) UCD. *Opuntia vulgaris*, Feb. 21, 1950, coll. I. Moreno, N^o50-940, 1(2) USNM. *Opuntia* sp, Valle de Oaxaca, 1912, coll. L. Diguët, N^o8657:1,2, 2(3) MNHN. Michoacan, 1912, coll. L. Diguët, N^o8658 (1+2+7) MNHN. Ensenada, Baja California, April,

1941, coll. T. D. Cockerell, N° 411372, 1(1) USNM. Mexico City, Feb. 2, 1947, coll. Krauss, N°1052, 4(4) USNM. Chapingo, March 3, 1954, coll. D. Barnes, N°1969-674, 1(4) BM. Chapingo, June 3, 1954, coll. D. Barnes, N°3845, 1(4) MNHN. Cuautla Morelos, Aug. 8, 1961, coll. R. MacGregor, N°3846, 1(7) MNHN. Tamaulipas, Nov. 2, 1965, coll. Krauss, N°65-27426, 1(4) USNM. Contreras, May 1965, coll. Krauss, N°65-27426, 2(1) USNM. Texcoco, Aug. 12, 1967, coll. Miller & Villanueva, N°891, 3(1) USNM. ?, Aug. 1, 1969, coll. D. H. Bixby, N° 28, 1(1) USNM. 15 mi. S. Sabinas, Hidalgo, Nuevo Laredo, coll. F. D. Parker, Feb. 23, 72, N°1967 1(1) USNM. 5 min. S. W. Durango, Durango Province, March 13, 1972, coll. F. D. Parker, 2315, 1(3) USNM. Baja California, coll. J. Gross, Jan. 2, 1975, N°5798 1(1) USNM. Durango, July 25, 1975, coll. E. Elliott, N° 6084, 1(1) USNM. Cactus sp., Laredo, Sep. 21, 1945, coll. Trotter, N°37612, 1(1) USNM. Laredo, June 2, 1949, coll. T. P. Chapman, N°48830, 1(1) USNM. Laredo, April 22, 1973, coll. C. R. Guettler, N°5664, 1(1) USNM. *Nopalea* sp., 5 min. W. Morelia Michoacan, March 6, 1972, coll. F. D. Parker, N°2215, 1(3). Mitla, Oaxaca, Jan. 10, 1981, coll. H. R. Herren, 1(4) BM. "Tuna fruit", El Paso, Aug. 28, 1939, coll. C. F. Haller, N°11103, 1(2) USNM.

PAKISTAN. *Mammillaria tenuis*, Jan. 6, 1967, coll. ?, N° 9255-1506, 1(3) BM.

REUNION ISLANDS. *Opuntia tuna*, La Bretagne, Aug. 8, 1951. coll. J. R. Williams, N° 76, 1(5) MNHN.

RHODESIA. *Opuntia* sp., Bulawayo, Aug. 22, 1964, coll. ?, N°8400-19780, 1(2) BM.

SOUTH AFRICA. *Opuntia fuscicaulis*, Cape Province, Middleburg, Jan. 4, 1965, Da3, 3(1). PPRI. *Opuntia megacantha*, Patensie, April 21, 1961, coll. W. A. Burger, N°6177-1702, 2(4) BM. Parys, Nov. 7, 1966, coll. De Lotto, N°2315/3, 1(1) PPRI.

Opuntia sp., Pretoria, Nov., 1964, coll. G. De Lotto, Da2, 1(1), PPRI. Hermon CP, Dec. 12, 1964, coll. J. Loubser, Da1, 2(1) PPRI. Orange Free State, Bloemfontein, Jan., 1965, 3(1) PPRI. Uitenhage, Cape Province, Jan. 1, 1965, Da4, 2(1) PPRI. Queenstown, Feb. 10, 1965, coll. Burger, 5(1) PPRI. Pietermaritzburg, June 8, 1965, coll. Loubser, 1(1) PPRI. Blyderivier, N.R.Transvaal, Feb. 25, 1990, coll. Giliomee, D17 (a-e), 3(1) VPI.

SRI LANKA. *Opuntia* sp., Batticola, April 25, 1972, coll. R. Dharmadhikari, N^oA5566, 2(4) BM.

U.S.A.: ARIZONA. *Cactus* sp., Tucson, Oct. 23, 1922, coll. E. Mortensen, 2(4) USNM. *Opuntia* sp., Redington, Pima Co., Oct. 9, 1943, coll. M. Griffiths, N^o 1223, 3(3) UCD. Tucson, Pima Co., Feb. 11, 1925, coll. A. A. Nichol, N^o1227, 6(1) UCD. June 4, 1956, coll. L. P. Wehrle, N^o1226, 2(2) UCD. *Platyopuntia*, Supai, Hauasu Canyon, April 9, 1965, coll. D. W. Ricker, N^o1-66, 1(1) UCD.

CALIFORNIA. *Opuntia littoralis*, 2 mi. W. Cascada, Santa Cruz Is., Santa Barbara Co., May 5, 1968, coll. D. R. Miller, N^o1156, 1(2) USNM. Coches Prietos, Santa Cruz Is., Santa Barbara Co., May 10, 1968, coll. D. R. Miller, N^o1179, 1(2) USNM. *Opuntia occidentalis*, San Diego Co., May 21, 1959, coll. B. Puttler, N^o59 1019, 2(9) USNM. *Cactus* sp., La Jolla, Jan. 30, 1924, coll. C. R. Orcutt, 1(4) USNM. Lemon Grove San Diego Co., March 14, 1956, coll. G. S. Hill, 1(1) UCD. *Opuntia* sp, Santa Cruz Is., Santa Barbara Co., Feb. 26, 1959, coll. R. W. Harper et al., 2 (4), CDA. Santa Cruz Is., Santa Barbara Co., April 18, 1961, coll. Ricker, 3(1) UCD. Santa Cruz Is., Santa Barbara Co., Nov. 16, 1961, coll. Ricker, N^o9, 5(1) + N^o18, 4(1) UCD. Dulzura, San Diego Co., Dec. 3, 1963, 19(1) UCD. 5 minutes S.E. Fallbrook, San Diego, May 9, 1964, coll. D. R. Miller, N^o 232, 2(2) UCD. Winterhaven, Imperial Co., Aug. 16, 1968, coll. L. Ogle, 1(1) CDA. Cañada del

Medio, Santa Cruz Is., May 20, 1979, coll. R. J. Gill, N^o5-79, 5(1) CDA. Santa Barbara, S. B. Co. March 20, 1985, coll. J. Davidson, N^o85C28-3, 1(3) CDA. Soledad, Monterey Co., Sep. 4, 1987, coll. B. Oliver, N^o831064, 1(5), 1(4) CDA. "Happlopappus", Venetus, Fraser Point, Santa Cruz Is., Santa Barbara Co., May 11, 1968, coll. D. R. Miller, N^o 1189, 1(2) USNM. "Platyopuntia", Vail Company 5 miles east of Temecula, Riverside Co., Feb. 26, 1964, 9(9) & March 25, 1964, coll. D. W. Ricker, 8(8) UCD. San Diego Co., 2 mi. S.W. Bonsall, Jan. 15, 1965, coll. D. W. Ricker, N^o1-65, 6(1) UCD. Pala Mesa, Hwy 395 at 76, Jan. 4, 1966, N^o1-66, 7(1) USNM. Barrett Junction, Jan. 4, 1966, N^o4-66 10,(1) USNM. San Vicente Res., below Dam, Lakeside, Jan., 6, 1966, N^o1-66, 4(1) USNM. Hwy 78, 5 min. east Escondido, Jan. 4, 1966, N^o4-66, 9(1) USNM. 3 miles east Chula Vista, Telegraph Canyon Rd., Jan. 4, 1966, N^o1-66, 7(1) USNM. "Prickly pear", San Diego Co., Jan. 3, 1972, coll. Demmer, N^o72A4-5, 4(3) CDA. Vista, San Diego Co., Feb. 5, 1979, coll. R. Desserich, N^o79B7-10, 1(2) CDA. Salinas, Monterey Co., Oct., 1979, coll. N. F. McCalley, N^o79529-35, 2(1) CDA. ?. Oxnard, Ventura Co., Aug. 27, 1984, coll. Hagy, N^o84H29-91, 1(3) CDA. "Haplopappus", Venetus, Fraser Point, Santa Cruz Is., Santa Barbara Co., May 11, 1968, coll. D. R. Miller, N^o1189 1(1) USNM. "Cactus", Solano Co., Velato-Benicia Rd., Sep. 18, 1940, coll. H. W. Marshall, N^o40I102, 2(3) CDA. Pauma Valley, San Diego Co., Nov. 12, 1958, coll. M. K. Hess, 1(1) UCD; Oratilla, Imp. Co., Nov. 20, 1961, coll. J. V. Taylor, N^o61I22-61 1(3), 1(1) CDA. Santa Maria, Santa Barbara Co., April 4, 1980, coll. J. Keefe, N^o80D7-1: 2(3),CDA. Carlsbad, San Diego Co., May 10, 1974, coll. W. Parker, N^o74E2087, 2(2) CDA. HAWAII: *Opuntia megacantha*, Near Naalehu, Aug. 21 1958, coll. J. W. Beardsley, N^o58-2266, 1(2) USNM. Waimera, 2500 foot elev., coll. E. Yoshioks, 1(3) USNM. *Opuntia* sp., Honolulu, Sep. 2,

1955, coll. P. W. Weber, N°56-530, 1(6) USNM. Hwy 26, 1 mile so Jct Hwy 25, April 4, 1965, coll. Fisher, N°XI-65, 7(1) UCD. TEXAS: Two slides, one with 4 specimens the other with seven, labeled: *Opuntia*, Arroyo, Texas, *C. tomentosus*, Dec. 10, 94, (Townsend) N°5859,116/10 USNM. Uvalde, Uvalde Co., coll. D. W. Ricker, June 13, 1961, 12(1) UCD. Hwy 83, Hidalgo Co., June 30, 1984, coll. H. W. Browning, 101 85-2125, 1(3), 1(1) USNM. Kingsville, at King Ranch, Dec. 26, 1979, coll. U. Nur, USNM. "*Opuntia platy*", Langtry, Valverde, May 13, 1976, coll. R. D. Gordon, N°3201, 1(1) USNM. *Opuntia* sp., Mission, March 17, 1927, coll. F. F. Bibby, 1(1) USNM. La Feria, Aug. 23, 1937, coll. H. K. Plank, N° 3711383, 1(2) USNM. Edimburg, Nov. 17, 1948, N° 49-11, 3(7) USNM. "Prickly pear", Mercedes, Oct. 3, 1952, coll. 52-1452, 1(6) USNM.

Additional hosts and distribution. In Fernald's (1903) catalogue, this species is also recorded from *Opuntia fulgida* in USA (Arizona & New Mexico), Mexico and England. Mann (1969) listed it from AUSTRALIA on *O. dillenii*, *O. elatior*, *O. inermis*, *O. microdasys*, *O. monacantha*, *O. nigricans*, and on *Nopalea dejecta*; from MEXICO on *O. cantabrigiensis*, *O. ficus-indica*, *O. fuliginosa*, *O. hyptiacantha*, *O. leucotricha*, *O. macdougaliana*, *O. megacantha*, *O. robusta*, *O. streptacantha* and on *O. tomentosa*. From USA: ARIZONA, on *O. engelmannii*, *O. phaeacantha* and their various relatives; and *O. tortispina* types (dwarf pears); CALIFORNIA, *O. littoralis*; NEW MEXICO, *O. engelmannii*, and *O. phaeacantha*; TEXAS, *O. aciculata*, *O. atripina*, *O. cacanapa*, *O. engelmannii*, *O. lindheimeri*, *O. macrocentra*, and *O. phaeacantha*. Mann (1969) also mentioned that *D. opuntiae* is established in MADAGASCAR, INDIA, and CEYLON.

Etymology. In the literature consulted the name derivation is not discussed, but it may have come from its most frequent host plant genus: *Opuntia*.

Remarks. A. Dugès in 1893 took some samples of "grana silvestre" from Guanajuato, Mexico. They were identified as *Coccus tomentosus* Lamarck. Cockerell (1896) proposed that these insects could be referred to the species as suggested by Lichtenstein (1884); Cockerell called them as *Coccus cacti opuntiae*. Other authors, like Fernald (1903) and Green (1912) treat the species in the same way. In two publications Cockerell (1898, 1899) indicated that *opuntiae* is a synonym of *tomentosus*, but in 1929 Cockerell stated that *opuntiae* is the correct name for what was called *tomentosus* earlier. According to De Lotto (1974), it became a practice to call *opuntiae* the wild cochineal that is morphologically distinct from *tomentosus*. He proposed to reestablish the validity of the name *opuntiae* (Cockerell) basing it on studies of two mounted specimens given him by Cockerell.

Affinities and discussion. This species has all of the setae on the body practically of the same size, except for a few on the last abdominal segments. Because of its characteristic setae, this species can not be confused with other species in this family. *D. ceylonicus* is a species with similar characteristics, but it can be easily separated because setae in *ceylonicus* are shorter and with a wider base than in *opuntiae*.

Natural enemies. Pettey (1948) mentioned several factors that affect the population size of *D. opuntiae*. The most important are the coccinellid insect

predators, either *Exochomus flavipes* Thunberg, or *Cryptolaemus montrouzieri* Mulsant, or both. But also the fungus *Empusa*, as well as climatological factors, affect the colonies of this cochineal insect.

Biological control agent. According to Dodd (1940) *D. opuntiae* was very successful in controlling certain prickly pears in Australia. The first introduction was made in 1920 from the Cactus Experiment Station at Chico, California, and it became well established in different Australian localities. Later, in 1921 and 1922, more insects were imported from Arizona and Texas. All new cochineals were able to develop on certain prickly pears. Their capacity to increase their population on the host plants and cause their destruction varied considerably. Dodd pointed out that in Dulacca District the insects were released in July 1921. By July 1924, some of the large plants had been killed and it was possible to use that area.

The strains of *D. opuntiae* imported from the USA to Australia were also imported to Sri Lanka and India where some species of prickly pears as *Opuntia dillenii* and *elatiior*(=*nigricans*), were very common. Once more the insects performed a good biological control on the host plants in those countries.

Some specimens were imported to South Africa from Australia in 1937 to be used against the pest prickly pear, *Opuntia megacantha*. Several authors (Petty 1948, Anneck, et al. 1969) noted a great success in controlling some species of *Opuntia*. Karny (1972) referred to this species as "species P", the most important for biological control of *Opuntia* sp. and also it has the widest distribution in South Africa. He stated that besides *O. megacantha* it also attacks

O. tardospina and occasionally *O. vulgaris* and a number of spineless cactus varieties.

Dactylopius salmianus De Lotto

Plate 16

Selected literature. *Dactylopius salmianus* De Lotto, 1974:186.

Adult female. Live adult females have not been seen by the author. De Lotto described: "living adult females are sparsely covered with very thin and very brittle threads of cottony matter, which may attain a length of 30 mm". Adult females on slides are almost circular, about 0.8-2.5 mm long and 0.6-1.7 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Generally very few and scarce. Wide-rimmed pores without tubular duct in small cluster on head, thorax and abdomen. Clusters formed with 2 and in some with 3 or more pores, also devoid of tubular ducts. On head 4-8 clusters mainly formed by 2, seldom 3 or more pores. On thorax 15-30 clusters mainly with 2, sometimes 3 pores. On abdomen approximately 50-75 clusters with up to 6 pores on last segments.

Setae (Fig. F, H). Generally not very numerous. On last abdominal segments more numerous than on head and almost same size. All setae with truncate or rounded apex, except for the hairlike setae with a very slender apex. Hairlike setae very few on entire body, most on last abdominal segments.

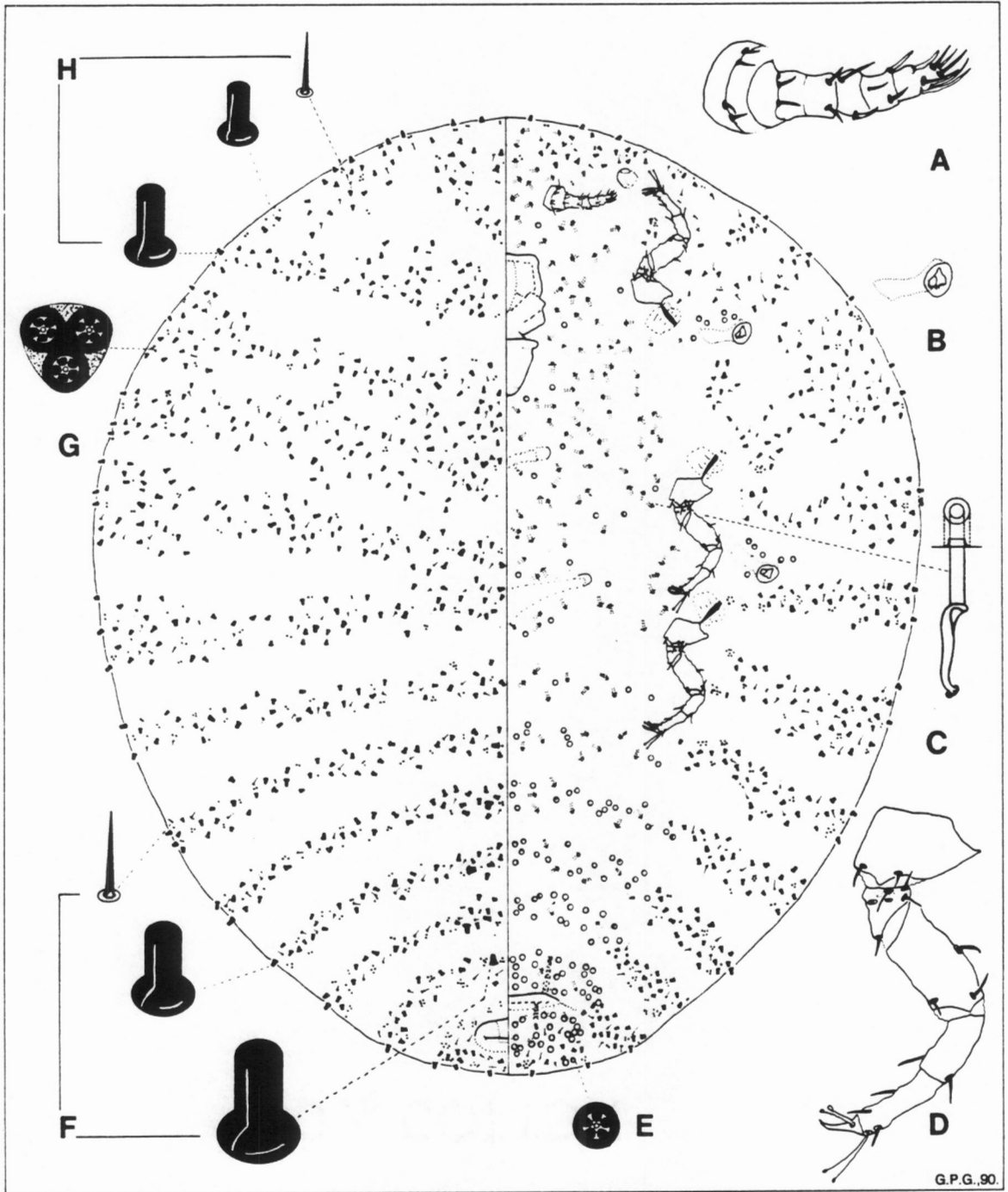


Plate 16. Adult female of *Dactylopius salmianus* De Lotto

SETAE (μ)	Large		Medium		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	26.0	19.0	16.5	14.2	16.0	4.76
THORAX	28.0	19.0	19.0	14.2	19.0	4.76
ABDOMEN	31.0	23.0	21.4	15.0	23.8	7.14

Anal area. Anal ring ellipsoidal, 117-185 μ wide, 50.0-119 μ long. Anterior margin with a very thin sclerotized band. About 8-15 clusters, each with 2-10 wide-rimmed pores. Approximately 10-20 setae of different sizes.

Ventral Surface

Eyes. Diameter at base 27.5-55.3 μ , distance between bases 162-644 μ .

Antennae (Fig. A). Seven-segmented 132-190 μ long. In one specimen one antenna with six segments and the other with four. Sometimes because segmentation between 3rd and 4th articles not clear, individuals appear to have antennae six-segmented.

Segments	Lengths(μ)	Setae	Fleshy-setae
I	15.0-31.2	4	0
II	7.50-25.0	2	0
III	16.7-81.2	0	0
IV	11.9-26.2	2	0
V	11.9-20.0	1	1

VI	14.2-32.5	2	1
VII	28.0-33.0	3	4

Clypeolabral shield. With the characteristic shape for the family, 187-369 μ long and 197-231 μ wide at base.

Labium. With three segments, 107-130 μ long and 100-172 μ wide at base.

Spiracles (Fig. B). Opening sclerotized with minute teeth along lateral margins. Anterior 100-129 μ long and 36.9-50.0 μ wide, with 3-13 associated narrow-rimmed pores. Posterior quite similar in shape and length to anterior one, 100-137 μ long and 36.9-57.5 μ wide, with 1-14 associated narrow-rimmed pores.

Legs (Fig. D). Short and strong. Claws without tooth. Tarsal digitules 40-52 μ long; claw digitules 21-32 μ long. The first coxae without microspines.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	35.7-55.0	52.0-62.5	47.6-75.0
Trochanter	19.0-62.5	45.0-62.5	45.0-62.5
Femur	95.2-115.0	90.4-115.0	71.4--115
Tibia	50.0-65.0	62.5-71.4	63.0-75.0
Tarsus	64.2-83.3	70.0-82.5	74.0-85.0
Claw	28.5-38.0	25.0-30.9	30.0-38.0
Entire leg	293-419	345-425	331-451

Setae. Same as on dorsal surface but only on body margins.

Pores. Wide-rimmed pores occurring singly or in small clusters in lateral and sublateral areas, some with associated tubular ducts. Narrow-rimmed pores (**Fig. E**) concentrated in middle area of last three or four abdominal segments, some dispersed on rest of abdominal segments and on head and thorax.

Ducts (Fig. C). On middle area of head, thorax and first abdominal segments.

Vulvar area. Vulvar opening 175-268 μ wide, surrounded by many narrow-rimmed pores and a few hairlike setae.

Type material studied. Holotype and one paratype from *Opuntia salmiana*, Chaco, Santa Sylvina, ARGENTINA, Feb. 15, 1971, coll. H. Zimmermann, 4628:3+4, 2(2) PPRI. One paratype with same records 4628 (8)*, 1(1) USNM.

Other material studied.

ARGENTINA: *Opuntia salmiana*, Catamarca, La Puerta, May 15, 1970, coll. H. Zimmermann, 4145:1-4, 2(2) PPRI.

Additional hosts. None known.

Distribution. This species only has been listed from Argentina.

Etymology. De Lotto did not specify the etymology of this species but it was probably named after the host plant, *Opuntia salmiana*.

Affinities and discussion. In this species small clusters of wide-rimmed pores are devoid of ducts as in *Dactylopius coccus* and *D. confertus*. Among other characteristics, it can be separated from the other two species because *D. salmianus* has ducts on the ventral middle area of the head, thorax, and abdomen.

Natural enemies. No known.

Biological control agent. None reported.

Dactylopius tomentosus (Lamarck)

Plate 17

Selected literature and synonymy.

Coccus silvestris Lancry, 1791:486 (nomen oblitum).

Coccus tomentosus Lamarck, 1801; Targioni Tozzetti, 1868:725; Green, 1897:75; 1912:87.

Acanthococcus tomentosus (Lamarck); Cockerell, 1893:366.

Coccus tomentosus newsteadi Cockerell, 1898.

Pseudococcus tomentosus (Lamarck); Cockerell, 1899.

Dactylopius tomentosus (Lamarck); Cockerell, 1902; Lizer y Trelles, 1939:183; Ferris, 1955:92; De Lotto, 1974:188.

Adult female. Live adult females have not been seen by the author but Newstead (in Green 1912) described them as "slightly elongate ovate, dark crimson, completely covered with white cottony material". Adult females on slides are subglobular, 2.3-3.8 mm long and 1.5-2.5 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores in clusters with an associated duct. On head 15-20 clusters with 2-4 pores. On thorax about 130 clusters most of them with 2-5 pores. On abdomen approximately 180 clusters with up to 14 pores.

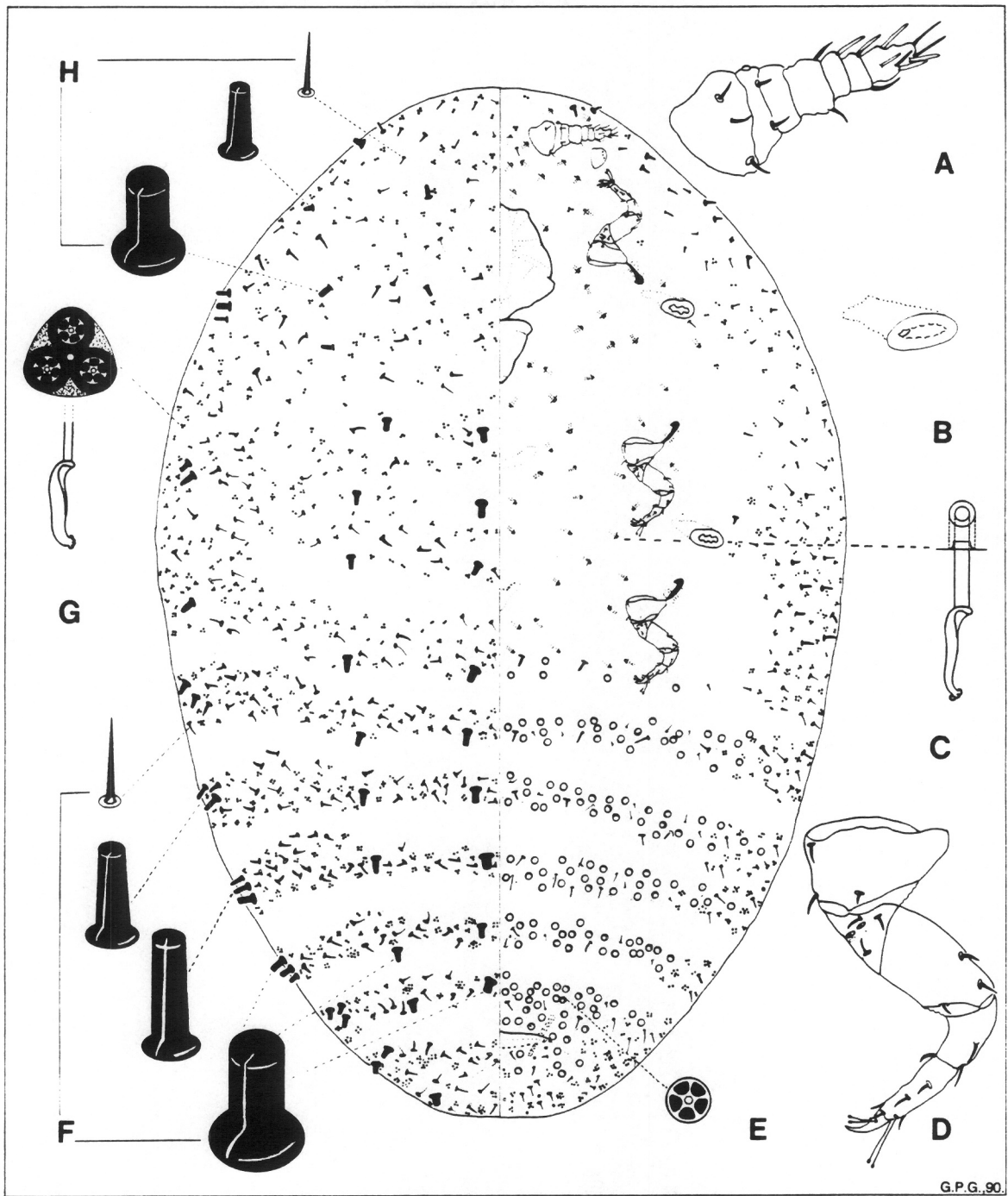


Plate 17. Adult female of *Dactylopius tomentosus* (Lamarck)

Setae (Figs. F, H). Scattered over entire body, more numerous toward last abdominal segments. Setae range from cylindrical with truncate apex to hairlike. On thorax and on most abdominal segments, large cylindrical setae with truncate apex, in two longitudinal medial and submedial rows, and in groups of 2-3 on body margin.

SETAE (μ)	Large		Medium		Small		Hairlike		
	Length	Width	Length	Width	Length	Width	Length	Width	
HEAD	23.8	16.6	---	-	---	16.5	9.50	21.5	7.14
THORAX	35.7	31.0	30.9	19.1	23.8	9.30	23.5	9.50	
ABDOMEN	45.2	31.0	33.2	16.5	31.1	12.2	38.5	9.50	

Anal area. Anal ring obsolete. A vague anterior margin sometimes visible. Surrounded by 4-9 clusters of wide-rimmed pores and some hairlike setae.

Ventral Surface

Eyes. Moderately prominent and slightly sclerotized. Diameter at base 47-51 μ , distance between bases 676-840 μ .

Antennae (Fig. A). Seven-segmented, 121-158 μ long. Distance between antennal bases 120-135 μ .

Segments	Length(μ)	Setae	Fleshy-setae
I	30-47	3	0
II	9-11	2	0
III	14-16	0	0
IV	24-31	2	0
V	9-11	0	1
VI	9-11	1	1
VII	36-31	3	4

Clypeolabral shield. Pentagonal in shape, 190-250 μ long and 215-252 μ wide at base.

Labium. Triangular, 123-153 μ long, 93-125 μ wide at base.

Spiracles (Fig. B). Not very large, with some small processes along margins of sclerotized opening. Anterior 90-93 μ long, atrium 59-61 μ wide, with 0-3 narrow-rimmed associated pores. Posterior, slightly larger than anterior, 89-116 μ long, 37-61 μ wide, with 0-5 narrow-rimmed pores.

Legs (Fig. D). Small, moderately stout, claw without tooth. Tarsal digitules 59-61 μ long; unguis digitules 35-38 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	45-62	54-64	62-66
Trochanter	50-60	52-58	49-59
Femur	107-119	109-120	110-121
Tibia	59-71	59-64	59-65
Tarsus	73-83	73-85	73-95
Claw	27-31	26-31	28-30
Entire leg	361-426	373-422	381-436

Setae. Not very numerous, restricted to marginal and submarginal areas. No rows of large setae or marginal groups of these.

Pores. Clusters of wide-rimmed pores in lateral and sublateral areas on head, thorax, and abdomen. Clusters on abdomen with more pores than on rest of body. Sometimes a few scattered narrow-rimmed pores (Fig. E) in median areas of head and thorax; crowded on terminal abdominal segments.

Ducts (Fig. C). Not numerous, scattered in median area of head and thorax.

Vulvar area. Vulvar opening 138-155 μ wide, surrounded by numerous narrow-rimmed pores and some setae.

Type material studied. In the absence of type material, De Lotto (1974) established the identity of these insects as defined and illustrated by Ferris (1955). Ferris (1955) stated "Apparently the type locality is Guanajuato, State of Guanajuato, Mexico". However, the specimens that he had for his description and illustration came from Baja California (Mexico) and the USA (Arizona,

California, Texas, and Utah). The author had the opportunity to examine dry material from Guanajuato, Mexico which had two labels, one as: "*Acanthococcus tomentosus* Lamk., on cactus, coll. A. Dugés"; and the other as: "*Coccus tomentosus* Lamk.". Eight specimens were mounted and identified as *Dactylopius opuntiae* (Cockerell). Because of this discrepancy a neotype for *D. tomentosus* was established. One slide with two specimens was chosen and marked as neotype from the Ferris collection (UCD). The neotype slide is labeled as: "*Dactylopius tomentosus* (Lam.), on cylindrical opuntia, Cabo San Lucas, Baja California (Mexico), Aug., 1919, G. F. Ferris^{*}"

Material studied.

AUSTRALIA. *Opuntia imbricata*, New South Wales, Bingara, Feb. 15, 1967, coll. V. H. Gray, N^o 2817:1-6, 6(6) PPRI.

MEXICO. *Opuntia acanthocarpa*, Rumarosa, Baja California, Nov. 27, 1965, coll. D. K. Wiggins, N^oXII-65, 3(1) UCD. Cactus, Juarez, El Paso, Sep. 6, 1934, coll. B. R. Anderson, N^o 1795 (a-c), 3(1) VPI. *Opuntia* sp., Baja California, San Jose del Cabo, July 1919, coll. G. F. Ferris, 3(5) UCD. Baja California, San Jose del Cabo, N^o42324, 1(1) USNM. Salina Cruz, N^o1013, 6(7) UCD.

USA: ARIZONA. Cactus sp., Tucson, Feb. 9, 1938, coll. L. Wehrle, 1(6) UCD. Yermo, March 3, 1977, coll. W. C. Thompson, N^o II-77, 1(1) CDA. "Cholla", Tempe, July, 1918, 2(4) UCD. Tucson, May 2, 1933, coll. S. R. Roca, 2(10) UCD. Tucson, Pima Co., Feb. 9, 1938, coll. L. P. Wehrle, N^o1206, 4(1) UCD. Douglas, July, 1936, coll. L. P. Wehrle, 3(17) UCD. **CALIFORNIA.** *Opuntia bigelovi*, Niland, Imperial Co., April 12, 1968, coll. R. A. Flock, N^o 68D19-21, 1(1) CDA. Cactus sp., Colorado Desert, Jan. 18, 1892, 2(7) USNM. Wasco, Kern Co. Aug. 12, 1911,

coll. T. Gallion, N^o 41N126, 1(2) CDA. Redwood City, San Mateo Co., May 15, 1934, coll. M. Leonard, N^o 34E67, 1(2) CDA. Sacramento, Sep. 7, 1933, coll. Marshall, N^o 34I8, 1(5) CDA. Bakersfield, Kern Co., Feb. 13, 1936, coll. C. S. Morley, N^o 36B56, 1(5) CDA. Kern Co., Aug. 13, 1941, coll. L. A. Burtch, N^o41H161, 1(2) CDA. Near Glamis, Imperial Co., Nov. 21, 1960, coll. G. L. Osborn, 1(1) CDA. Turlock, Stanislaus Co., Nov. 27, 1961, coll. G. E. Wilhite, N^o 61K30-7, 1(2) CDA. Nevada at Yermo, April, 22, 1962, coll. C. A. Mitchell, 1(1) CDA. 29 Palms, S. Bernardo Co., Aug. 23, 1964, coll. J. F. Miller, N^o 391, 1(1) UCD. 1 minute N. White Water, Riv. Co., Jan. 25, 1965, coll. D. R. Miller, N^o 424, 2(2) UCD. 5 minutes S. W. Palo Verde, Imperial Co., Jan. 28, 1965, coll. D. R. Miller N^o460, 1(1) UCD. Chico, Butte Co., Nov. 5, 1978, coll. A. Sutton, N^o 78I6-29, 1(4) CDA. Oroville, Butte Co., Dec. 24, 1979, coll. Pooler, N^o 79L28-7, 2(4) CDA. Owens Valley, Inyo Co., 1(3) UCD. San Diego, 1(2) CDA. *Cereus* sp., S. Bernardino Co., July 12, 1893, Coquillett, N^o1893, 1(5) USNM. *Opuntia* sp., Colo. Desert, Jan. 18, 1892, 1(4) USNM. "Cholla cactus", Cabazon, Riverside Co., Aug. 27, 1942, coll. Tower, N^o 42H164, 1(3) CDA. Trona, San Berdo Co., Aug. 6, 1962, coll. Crank, N^o 62H6-36, 2(4) CDA. Browns Valley, Yuba Co., 1976, coll. Wilson, N^o 76A15-2, 2(4) CDA. "Cylindropuntia", Vail Lake, Riverside Co., Jan. 31, 1964, coll. D. W. Ricker, 18 (18) UCD. Vail Ranch 5 miles east of Temecula, Riverside Co., April 30, 1964, coll. D. W. Ricker, 8(8) UCD. NEW MEXICO. *Opuntia imbricata*, Carlsbad, Oct. 1924, coll. A. P. Dodd, N^o3, 1(4) USNM. Las Cruces, Dona Ana Co., coll. R. Tafanelli, N^o85-8905, 2(4) USNM. NEVADA. *Opuntia* sp., S. Alamo 34 miles, Lincoln Co., June 28, 1960, coll. T. R. Haig, 2(5) UCD. TEXAS. *Opuntia leptocaulis*, El Paso, 1921, coll. G. F. Ferris, T-221 + T-224, 2(3) UCD. San Angelo, Tom Green Co., Dec. 13, 1983, G. Hackler, N^o103, 2(6) USNM.

Opuntia sp. San Antonio, Dec. 2, 1895, coll. Townsend, N^o 6990, 1(3) USNM.
Cactus sp. Yuma, July 24, 1943, coll. Thompson, N^o43G18, 1(5) CDA. UTAH.
Cactus sp., Saint George, Sep. 1933, coll. Tanner, N^o28, 1(2) UCD.

Additional hosts and distribution. In addition to the hosts, states, and countries above, Green (1897) identified this species from the Kew Gardens in London (England) on *Opuntia fulgida* where they were imported from Arizona. Lizer y Trelles (1939) cited *D. tomentosus* in Argentina on *Opuntia sulphurea* and *Cereus aethiops*; he also added that this species was not very abundant. De Lotto (1974) mentioned it from South Africa on *O. imbricata* and *O. tunicata*.

Etymology. The name derivation is not discussed in the literature consulted, but probably came from Latin "tomentum" meaning dense hair or pubescence; due to the amount of wax threads produced by the insect.

Remarks. *D. tomentosus* has been confused with another *Dactylopius* historically. Some workers, like Targioni Tozzetti (1868), Signoret (1875), Lichtenstein (1884), etc., cited as *tomentosus* any cochineal insect that was not used for the production of dyestuff. Earlier, Lancry (1791) listed *Coccus silvestri* or wild cochineal under *Coccus cacti* or domestic cochineal. According to the opinion of De Lotto (1974), the most practical solution to this situation is to consider the identity of *D. tomentosus* as described by Ferris (1955). In Ferris work there is an illustration and description of this insect.

Affinities and discussion. *Dactylopius tomentosus* has some large dorsal setae among other smaller ones, as does *D. confusus* and *D. zimmermanni*. Two characteristics can easily differentiate *tomentosus*: first, the anal ring is obsolete, but it is not well developed in *D. confusus* and *zimmermanni*; second, the largest truncate setae in *D. tomentosus* are dorsally located in two medial and submedial longitudinal rows and on the body margin, forming groups with one or two more setae of different sizes.

Natural enemies. Apparently, natural enemies are unknown for this species.

Biological control agents. *D. tomentosus* and *D. opuntiae* have been confused for quite some time. Not only are both common in the south-west USA, and Mexico, but they can also infest the same host plants. Dodd (1940) cited the introduction in Australia of *D. opuntiae* from California, Arizona and Texas for the control of prickly pear. He wrote: "There was a difference in the manner of attack, especially in the case of the Texas and Arizona strains on *stricta*; the former tended to infest the lower segments; the latter preferred to attack the upper growth". Probably Australians introduced both *D. opuntiae* and *tomentosus* and *D. tomentosus* became established in Australia.

De Lotto (1974) pointed out that in South Africa *D. tomentosus* was established in the field following release of specimens in April 1970 that were imported from Queensland, Australia.

Dactylopius zimmermanni De Lotto

Plate 18

Selected literature. *Dactylopius zimmermanni* De Lotto, 1974:189.

Adult female. Live adult females have not been seen by the author and no information is available on external appearance. Adult females on slides are oval, about 2.2-3.4 mm long and 1.3-2.6 mm wide.

MORPHOLOGICAL DESCRIPTION

Dorsal Surface

Pores (Fig. G). Wide-rimmed pores in clusters associated with one or more ducts. On the head 10-20 clusters each predominantly with 2-6 pores. On the thorax 180-200 clusters mostly with 4-6 pores. On the abdomen approximately 250 clusters, these larger and with 21 or more pores. Those close to body margin with more pores.

Setae (Figs. F, H). Not very numerous on the head, but variable in size. On thorax usually in groups of 2 or 3. The largest setae on terminal abdominal segments, especially on marginal and in median areas.

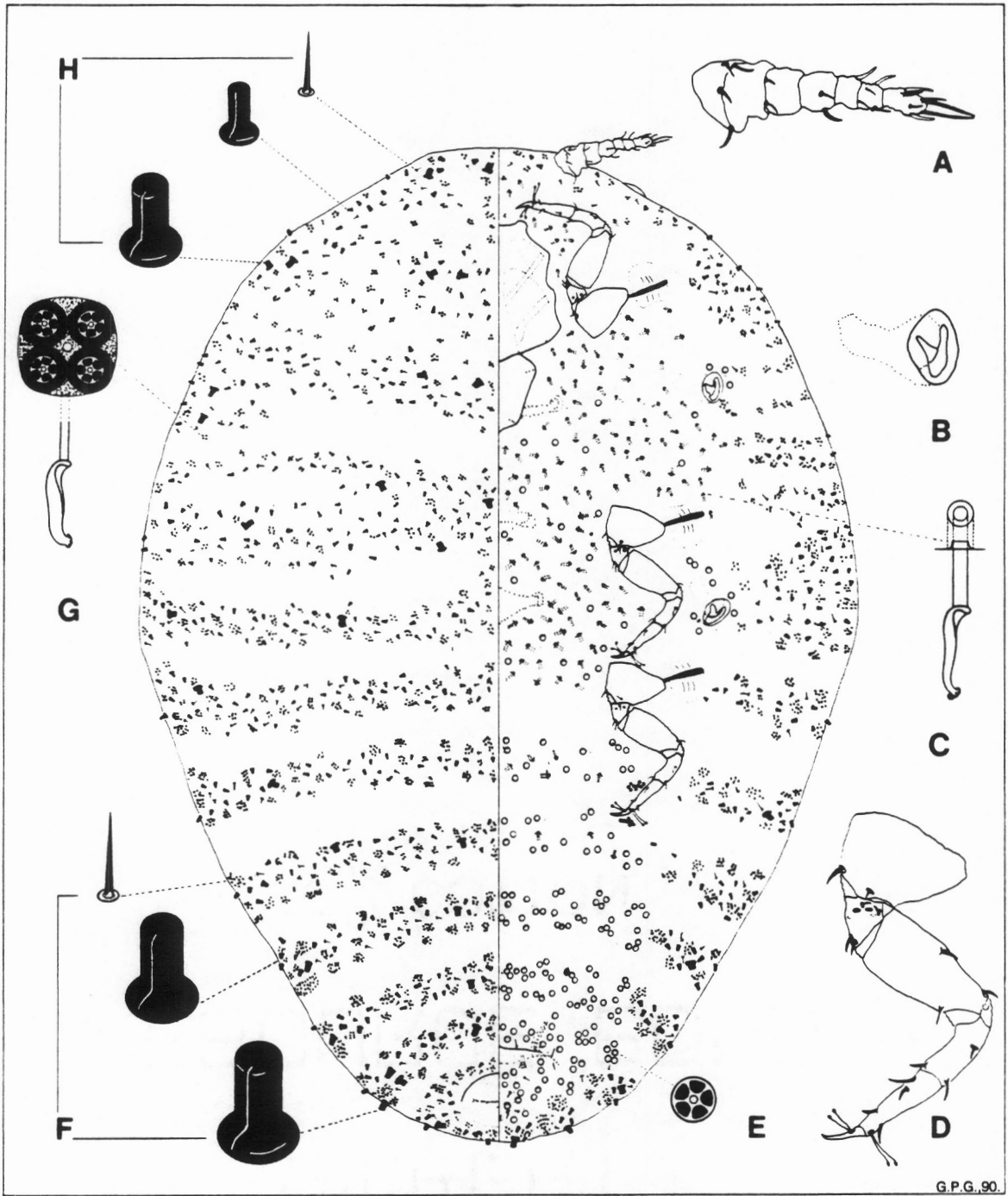


Plate 18. Adult female of *Dactylopius zimmermanni* De Lotto

SETAE (μ)	Large		Small		Hairlike	
	Length	Width	Length	Width	Length	Width
HEAD	25.0	15.0	12.5	7.00	17.5	7.5
THORAX	27.5	20.0	17.5	10.0	30.0	7.5
ABDOMEN	30.0	22.5	15.0	12.0	40.0	7.5

Anal area. Anal ring oval 181-227 μ wide, 129-166 μ long. A narrow sclerotized band on anterior margin. About 22-27 clusters with a large number of wide-rimmed pores, and setae of different sizes.

Ventral Surface

Eyes. Diameter at base 26.1-47.6 μ , distance between bases 400-787 μ .

Antennae (Fig. A). Seven-segmented, 155-294 μ long. Distance between antennal bases 129-307 μ .

Segments	Lengths(μ)	Setae	Fleshy-setae
I	26.0-73.0	4	0
II	2.50-23.8	2	0
III	23.8-38.0	0	0
IV	28.5-52.3	2	0
V	16.6-33.3	0	1
VI	16.6-27.5	3	1
VII	30.9-45.2	5	2

Clypeolabral shield. 250-369 μ long and 187-190 μ wide at base.

Labium. 187-190 μ long, 153-187 μ wide at base.

Spiracles (Fig. B). Opening sclerotized with smooth margins. Anterior 123-153 μ long, atrium 61.5-104 μ wide, 0-7 associated narrow-rimmed pores. Posterior, similar shape to anterior one but slightly larger, 153-190 μ long, 55.3-129 μ wide; with 1-10 associated narrow-rimmed pores.

Legs (Fig. D). Well developed, stout. Claws without tooth. Tarsal digitules, 57.5-75.0 μ long, claw digitules 37.5-42.5 μ long.

Leg Segments and Claw (μ)	Lengths Prothoracic	Lengths Mesothoracic	Lengths Metathoracic
Coxa	62.5-92.2	62.5- 100	62.5-92.2
Trochanter	62.5-75.0	62.5-75.0	62.5-75.0
Femur	143-168	131-162	150-168
Tibia	62.5-87.5	68.7-87.5	68.7-87.5
Tarsus	87.5- 100	93.7- 112	87.5- 125
Claw	35.0-42.5	37.5-42.5	37.5-45.0
Entire leg	453-565	456-579	468-592

Setae. Same as on dorsal surface but only on body margins.

Pores. Wide-rimmed pores occurring in small clusters in lateral and sublateral areas, with one or more associated tubular ducts. Narrow-rimmed pores (**Fig. E**) concentrated in middle area of last four abdominal segments, some dispersed on the first abdominal segments and on thorax.

Ducts (Fig. C). Numerous on middle area of head and thorax, a few scattered on first abdominal segments.

Vulva. Vulvar opening 306-430 μ wide, surrounded by a large number of narrow-rimmed pores and a few hairlike setae.

Material examined. Holotype slide number 4146:11, 1(1) and eight paratypes, slide number 4146: 2+3+7+10+12+13^{*}+15+16, 8(8) from *Tephrocactus ovatus*, Vargas, Mendoza, ARGENTINA, Aug.15, 1970, coll. H. Zimmermann, PPRI except 7+13 at USNM.

Host and distribution. So far this species has only been found on *Tephrocactus ovatus* in the Province of Mendoza, ARGENTINA.

Etymology. De Lotto named this species in honor of H. Zimmermann.

Remarks. This species was named and briefly described by De Lotto in 1974.

Affinities and discussion. *D. zimmermanni* may resemble *D. confusus* since both have some large setae distributed on abdominal segments. *D. zimmermanni* can be separated from others because some large truncate setae can be also found on thorax and head; in *confusus*, large setae are limited to last three or four abdominal segments. Another characteristic that separates these two species is the margins of the spiracular opening; they are smooth in *zimmermanni*, while in

confusus tooth-like processes are present. Overall *zimmermanni* is larger than *confusus*.

Natural enemies. None known.

Biological control agent. Nothing specifically is mentioned about this species in the literature consulted .

CHAPTER 7

PROPOSED PHYLOGENY OF DACTYLOPIIDAE

REVIEW OF THE PROPOSED PHYLOGENY OF THE FAMILY

Danzig (1986) stated: "the establishment of phylogenetic relations among taxa and the construction of a natural system of classification for coccids are rendered difficult by their reduction in the course of evolution". She, with a number of earlier authors, made suggestions on the phylogenetic placement of Dactylopiidae. Balachowsky (1942, 1948) suggested that the Dactylopiidae are closely related to the Pseudococcidae, Eriococcidae and Kermesidae and he included all these groups together with families such as the Coccidae and Lacciferidae (Kerriidae) in his Lecanoid subdivision of the Coccinea. Ferris (1955) associated the Dactylopiidae with the Eriococcidae (in which he also included the Kermesidae) and these families together with the Pseudococcidae and Acleridae are included in his Eriococci branch.

Ferris (1957) and Borchsenius (1958) agreed to adapt their view on the Coccinea evolution in which the insects have become highly specialized through loss or reduction of morphological structures. It is very difficult to establish a good geological time scale because of a lack of fossil evidence. Beardsley (1969) stated that the first evidence of Coccinea in amber dates from the Oligocene and Miocene Epoch origin (ca. 26 to 53 million years ago). Borchsenius (1958) gave a schematic representation of the interrelations of the families of Coccinea through geological periods. He placed the family Dactylopiidae between Stictococcidae and Apiomorphidae, with all of them developing during the Jurassic Period of the Mesozoic era (ca. 136-195 million years ago). These three

families of Coccinea are also related to Kerriidae which evolved later. Borchsenius also suggested the Early Carboniferous (ca 320-345 million years ago) as the period of origin for the Coccinea, but offered no scientific evidence for this assumption. Other authors think that his suggestion is not reliable. Koteja (1974a) based his classification on a comparative study of the labium in the females. In this scheme of classification, the labium of the *Dactylopius* is close to that of Acanthococcidae (Eriococcidae in part). This author, as all of the others based his conclusions only on studies of the females.

Loubser (1966) studied the males of two *Dactylopius* species and noted that the Dactylopiidae appear more closely related to the Pseudococcidae than to the Coccidae, indicating that Dactylopiidae are more highly specialized than the Pseudococcidae. Also Kermesidae were found to be only remotely related to Dactylopiidae and Pseudococcidae. It appears that the males of Eriococcidae resemble males of Dactylopiidae to a considerable degree.

Boratynski and Davies (1971) also based their phylogenetic studies on male characteristics only. They concluded that Dactylopiidae and Eriococcidae were derived from Pseudococcidae.

The phylogenetic arrangement of the different scale insect families has been based on characteristics of adult females by some authors and on characteristics of adult males by others. However, most investigators classify the Coccinea into two main groups:

- 1.-Orthezioidea (Archaeococcoidea), which includes the most primitive families: Margarodidae, Ortheziidae, and Phenacoleachiidae;
- 2.-Coccoidea (Neococcoidea), which includes the rest of the families.

Although the family Dactylopiidae is highly specialized morphologically and biologically, it retains some primitive characteristics. That they only feed on Cactaceae plants shows a higher degree of evolution and adaptation because of the specialization in food plants.

The phylogenetic scheme of classification for the scale insect families proposed by Danzig (1986) is based on comparative morphology of a few structures in females that are progressively evolving. These are discussed below.

1.- Segmentation. Females with a large oval body, soft integument and distinct segmentation are regarded as the most primitive types. *Dactylopius* species have such characteristics, while the phylogenetically advanced groups such as Diaspididae, have a reduction in body size and retain segmentation only on the ventral surface of the abdomen.

2.- Antennae. In the most primitive Coccinea, the antenna is large and many segmented (i.e. 11-segmented in Margarodidae), with many setae. Further specialized Coccinea, have the antennae reduced in the number of segments as well as in size and in chaetotaxy (i.e. in Diaspididae it is reduced to an unsegmented tubercle with a seta at the apex). All the species in the family Dactylopiidae have 6 or 7 antennal segments, so it is clear that they have proceeded only about halfway toward reduction in the number of segments.

3.- Eyes. The primitives ones have large, projecting eyes. In Dactylopiidae as some others families, the eyes are slightly bulging . In the most advanced families the eyes are completely absent in the adult stage.

4.- Mouthparts. Koteja (1974b) cited that the most primitive families have a four-segmented labium; Dactylopiidae as well as many other families have a three-segmented labium, and among the more specialized ones as Coccidae, the

segments are reduced to two or one. He also pointed out that the enlargement of the labium in Dactylopiidae is a type of specialization.

5.- Legs. In the most specialized scale insects, there is a trend toward the reduction of the legs; in families such as Aclerdidae, Asterolecaniidae, Diaspididae, etc, the legs are absent. Although the adult females of Dactylopiidae are sessile, they have legs which are relatively long, as in some of the other more primitive families, and all of the leg segments are free. In Conchaspidae, Kermesidae, and Kerriidae some leg segments are fused.

6.- Spiracles. All of the Coccinea have two pairs of thoracic spiracles similar in structure. Only members of the superfamily Orthezioidea retain abdominal spiracles. Depending on the degree of evolution of the family, the spiracles could be more or less developed, have different forms or be associated with plates or pores. In some species of Dactylopiidae, from zero to many narrow-rimmed pores are found around of the spiracular opening. In the most highly specialized species, the spiracles became more embedded in the body and developed into a tubelike structure.

7.- Anal ring. The anal ring, together with some associated structures can play an important role in the Coccinea. The insects excrete drops of an excess sugary liquid, known as honeydew. The drops need to be ejected as far as possible from the colony to avoid the formation of black fungus or sooty mold on the contaminated substrate. Also the insects need to protect themselves against the rapid evaporation of water in the honeydew drop because it might adhere to the intestinal wall. Hence, the development of structures near the anal opening, such as anal ring setae and pores, have been significant in the evolution of these insects.

In the most primitive families, (e.g. Margarodidae) the anal ring does not have associated setae, withdraws inside the body and is located at the inner end of a sclerotized anal tube. In most pseudococcid genera the anal ring consists of one or two bands of multilocular pores. In all life stages of *Dactylopius* species there is a total absence of a setiferous anal ring with pores. In Dactylopiidae the anal lobes are absent, the anal opening is located in the middle of the dorsum of the abdominal surface and the anal lobes are evidently fused, while only part of the anal setae are retained.

8.- Formation of wax. The wax is formed in disk pores, cylindrical tubes, and at the base of the setae. Sulc (1932) stated that the disk shaped pores discharge powdery wax. They consist of a cluster of quinquelocular pores with one or more tubular ducts opening at different places inside the cluster. They are found in the less specialized groups and are typical in the species of *Dactylopius*. The length and width of the cylindrical ducts are taxonomically important because they show modifications in several families. The ducts have a tubular form in Pseudococcidae but are bottle-shaped in Eriococcidae, Kermesidae and Dactylopiidae. They are highly specialized in the rest of the families. The setae also discharge wax; this is very important in the family Ortheziidae, but is also found in Eriococcidae, Dactylopiidae and Kermesidae, although they are not the only structures that discharge wax.

9.- Protective tests. The most highly developed and specialized Coccinea (Diaspididae) have a thick protective test made from a very dense wax secretion, excretion, and from nymphal exuviae. In this aspect, Margarodidae as well as Dactylopiidae are among the most primitive forms because their protective tests

are made from powdery wax or by loose wax filaments without shape. This type of test offers protection for the females as well as the eggs and first instar nymphs.

Shcherbakov (1990) discussed the relationship of Nabiidae (an extinct winged precoccin) that may serve as the missing link between the Aphidomorpha and Coccoomorpha.

PROPOSED PHYLOGENETIC TREE FOR THE SPECIES OF DACTYLOPIUS.

The phylogeny and evolutionary relationships of the species of *Dactylopius* have not been studied previously. A comprehensive study of the evolution of *Dactylopius* species requires consideration and analysis of the similarities and differences for all stages in each species, as well as for both sexes. This type of analysis must consider all of the taxonomically useful characters, including morphological, ecological, behavioral, and biological characters. Unfortunately, only limited information was available for this study; therefore, a general discussion based on what can be considered important morphological characteristics is provided here.

Studies on the phylogeny of scale insects have shown evolutionary changes with regard to specific characters; these often include a loss or reduction of morphological features, a thicker test for protection, and increased food specialization. Together these factors may be used to establish an evolutionary hypothesis with regard to probable phylogeny. The proposed phylogenetic tree for the Dactylopiidae species is based on such characteristics as the distribution, number and shape of body setae, the number of wide-rimmed pores in clusters, and the natural geographical distribution for each species. Both the setae and the

wide-rimmed pores are associated to wax glands and are related to the secretion of wax. The different patterns of wax is thus a function of the size and shape of the setae. A proposed phylogenetic tree for the *Dactylopius* species is shown in Fig. 1.

Dactylopius coccus is considered the most primitive of the species in Dactylopiidae. The insect produces powdery wax, a characteristic which places them closely to members of the Pseudococcidae and some of the Eriococcidae. The setae in *D. coccus* are few in number and hairlike in appearance. Clusters of wide-rimmed pores are present on dorsum and venter. They are large with 20 or more pores in each cluster, and are not associated with tubular ducts. This species is mainly found in Central America.

D. salmianus has few setae, but some of them are thick and located on the last abdominal segments. Because of this, this species has been further evolved than *coccus*. However, although the clusters of wide-rimmed pores are smaller, they usually are devoid of tubular ducts as in *D. coccus*. This species is known only from Argentina.

D. confertus also has few setae and some of those located on the last few abdominal segments are stout. This species has large clusters of wide-rimmed pores on the dorsum and small clusters of wide rimmed pores on the ventral thoracic area. In contrast to the two species above, the clusters in this species are associated with tubular ducts and therefore are considered more highly evolved. This species is known from Argentina .

D. austrinus has many setae and these become numerous towards the last abdominal segments where these also become thicker in size. The clusters of wide-rimmed pores are small toward the head and are associated with tubular

ducts. Similar clusters of wide-rimmed pores can be found across the first few ventral abdominal segments. This species is known from Argentina and has been placed near *D. confertus* in the tree because it has also larger setae on abdominal segments but in larger number. The same characteristic is shared with *D. confusus*.

D. zimmermanni has thick setae located from the head to the abdominal segments, and towards the last abdominal segments, where they became thicker in size. The clusters of wide-rimmed pores have few pores towards the head and are associated with tubular ducts. This species is only known from Argentina. It represents a more evolved species because of the location of the thick setae on the entire body. Because of this characteristic, this species is also placed near to *D. tomentosus* which has thick setae in longitudinal rows from the head to the abdominal segments.

The last species in the left side of the tree is *D. ceylonicus* has numerous thick setae all over the body. The clusters of wide-rimmed pores near the head do not have many pores and are associated with tubular ducts. This species is also found in Argentina and it is considered the most highly evolved because almost all the setae are thick, similar in size and shape.

On the right side of the tree, *D. confusus* has thick setae on the last three or four abdominal segments. This feature places this species near *D. austrinus* and *D. confertus*. The clusters of wide-rimmed pores are large, have many pores and are associated with tubular ducts. This species is primarily found in Central America, but it is also abundant in Florida.

D. tomentosus has different type of thick setae which are found to extend from the head to the abdominal segments. These become thicker towards the last

abdominal segments. The clusters of wide-rimmed pores do not have many pores towards the head and are associated with tubular ducts. This species is found in Central America, and it has been placed close to *D. zimmermanni* in the tree because the presence of thick setae in longitudinal rows from the head to end of the abdominal segments. It is the only species in the family where the anal ring is obsolete, a characteristics considered here to indicate further evolution.

The last species in the right side of the tree is *D. opuntiae* which has numerous thick setae all over the body, as is also in *D. ceylonicus*. The species which has thicker and more abundant setae produce more cottony wax for protection against adverse enviromental conditions and natural enemies. The clusters of wide-rimmed pores in *D. opuntiae* have few pores towards the head and are associated with tubular ducts. This species is found in Central America.

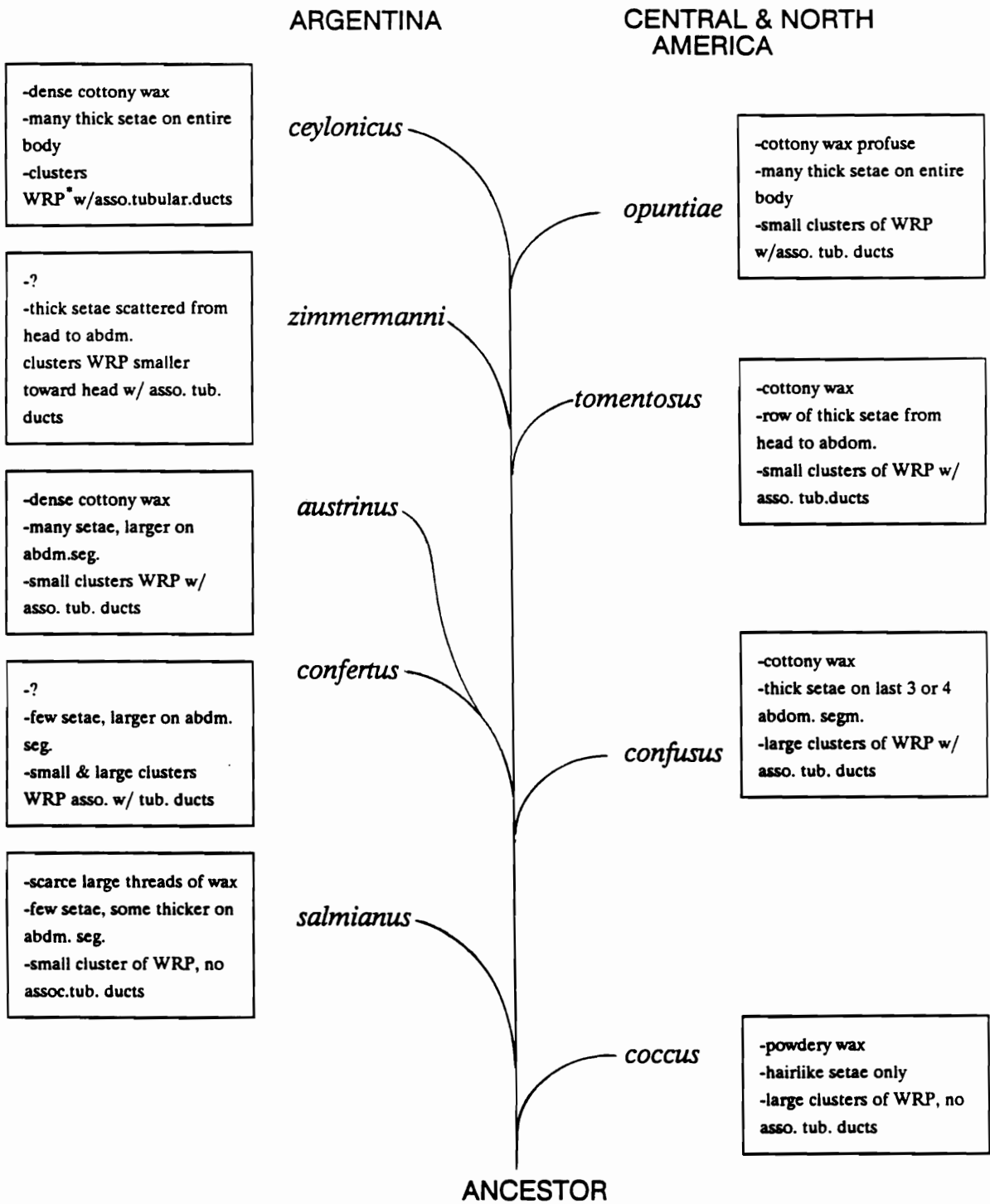


Fig.1. Proposed phylogenetic tree for the species of *Dactylopius*.

* WRP: Wide-rimmed pores.

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A handwritten signature in black ink, appearing to read 'Gema', enclosed within a large, loopy oval shape.

Gema Pérez Guerra.