"Purchased by United States
Department of Agriculture
for official use"

BIOSYSTEMATICS OF *CHIONASPIS NYSSAE* COMSTOCK (HOMOPTERA: DIASPIDIDAE), WITH EVIDENCE SUPPORTING LEAF AND BARK DIMORPHISM OF THE SCALE[1]

By

Richard C. Knipscher, Douglass R. Miller, and John A. Davidson[2]

[1]Scientific Article No. A2234, Contribution No. 5222 of the Maryland Agricultural Experiment Station, Department of Entomology.

[2]Microbiological Associates, 4733 Beth Ave., Bethesda, MD 21811; Systematic Entomology Laboratory IIBIII, Agric. Res. Serv., USDA, Beltsville, MD 20705, Adjunct Associate Professor, Dept. of Entomology, Univ. MD; Dept. of Entomology, Univ. of MD., College Park, MD 20742.

TABLE OF CONTENTS

Abstract 1

Introduction 1

Literature Review 1

Materials and Methods 2

Results 3

Conclusions and Summary 12

Acknowledgments 12

Literature Cited 13

Tables 1 and 2 15

Figures 1-19 16

ABSTRACT

For many years, some scientists believed that the genus *Phenacaspis* was the leaf form of the bark infesting genus *Chionaspis*. Evidence is given to establish that *Phenacaspis nyssae* is the leaf form of *Chionaspis sylvatica*. A detailed life history of both forms of the species is presented with illustrations and descriptions of each instar. Evidence is given to suggest that factors effecting morphological differences in the leaf and bark forms are derived from the host.

INTRODUCTION

For many years the armored scale-insect genera *Chionaspis* Signoret and *Phenacaspis* Cooley and Cockerell have been maintained as distinct, commonly used taxonomic entities. However, Takahashi (1952, 1953) noticed that hosts infested with a species of *Phenacaspis* frequently contained a species of *Chionaspis*. He further observed that on the same host the *Phenacaspis* species was remarkably similar morphologically to the *Chionaspis* species except for the shape of the median lobes. He noted that *Phenacaspis* species were predominantly on the leaves, and *Chionaspis* species were principally on the bark or stems. Based on these observations, Takahashi concluded that *Phenacaspis* was the leaf form of *Chionaspis*, and that *Phenacaspis* was a junior synonym of *Chionaspis*.

After Takahashi's work, Ferris was the primary proponent for the retention of *Phenacaspis* as a valid name. Although in 1953 Ferris expressed "...considerable doubt... [about]...recognizing *Phenacaspis* as distinct from *Chionaspis*...", he separated them for the following reasons: 1. Intergradations of the morphological characters used to separate the genera are rare. 2. Geographically, *Chionaspis* is primarily European and North American, and *Phenacaspis* is principally Oriental with the "exception [of] a few species [from Australia], two or three species [from Africa, and] four species" from North America. 3. If the genera were united, a large unwieldy group of species would be formed which would not reflect zoogeographic boundaries and which, pragmatically, would be difficult to handle because of its large size. Based on these weak arguments, and on the fact that Takahashi studied only Japanese species, Ferris (1955, 1956) was able to persuade the coccidology community, including Takahashi, to retain *Phenacaspis* as a separate genus.

No further "progress" was made until the work of Takagi and Kawai (1967) in which they restated the synonymy of *Phenacaspis* and *Chionaspis* suggested by Takahashi. Takagi and Kawai based their conclusions on observations made before 1967 (Takagi, 1961 and Takagi and Kawai, 1966) when they found specimens of *Phenacaspis* on the leaves that were remarkably similar to specimens of *Chionaspis* on the bark of the same host. They pointed out the North American species of *Phenacaspis* and *Chionaspis* that occur on the same genus of host plant and suggested that the leaf and bark forms from each host genus be treated as one species. One of the species placed in synonymy in this manner was *Phenacaspis nyssae* (Comstock) which is the type-species of *Phenacaspis*; *P. nyssae* was treated as the leaf form of *C. sylvatica* Sanders. Based on 2nd-instar males and 1st-instar crawlers, Takagi and Kawai also discovered 2 distinct groups of species in *Phenacaspis*. They placed one group, which apparently is principally Oriental, in *Pseudaulacaspis* MacGillivray and the other group, which is Holarctic, in *Chionaspis*. The adult females, upon which the classification was based, do not reflect the differences demonstrated by the crawlers and 2nd-instar males and are apparently convergent forms of distantly related lineages. Takagi and Kawai also noted that although some species of both *Chionaspis* and *Pseudaulacaspis* have leaf and bark forms, many species are found exclusively on the leaves or stems of their hosts. Some species that occur on both the leaf and bark do not have 2 forms.

Since 1967, the synonymy of *Phenacaspis* and *Chionaspis* has gained general acceptance. Although the evidence provided by Takahashi, Takagi and Kawai, and others is very strong, it is circumstantial. The purpose of the present paper is to provide conclusive evidence that the synonymy of the above genera is valid. In so doing, we provide detailed information on the life history of *C. nyssae* with descriptions of all life stages and give some general insight into the possible causes of the leaf and stem induced changes in the morphology of this species.

LITERATURE REVIEW

Examples of variable morphologies apparently attributable to environmental factors have been reported in other scale insects. Perhaps the most detailed studies of this kind were carried out independently and almost simultaneously by Lupo (1943) in Italy and Stafford and Barnes (1948) in California on the fig scale *Lepidosaphes conchiformis* (Gmelin) (=*L. ficus* (Signoret)). These workers found that the species has 2 generations/yr–i.e., an overwintering generation that occurs on the bark and a summer generation on the leaves. Before these studies, the bark and leaf forms were treated as separate species or even separate genera (Borchsenius, 1966); the bark or winter form was named *L. conchiformis*, and the leaf or summer form was *L. ficifoliae* (Berlese). Morphological differences used to separate the "species" were the structure of the lobes, the basal sclerotization of the median lobes, and the size and shape of the scale cover. Eggs of each form were placed on isolated, uninfested hosts where they hatched, settled, and developed into adults. Crawlers from bark-form (winter) females settled

on the leaves and produced leaf-form (summer) females; crawlers from leaf-form (summer) females settled primarily on the stems and developed into bark-form females. These experiments established that *L. ficifoliae* was a leaf derivative of the overwintering *L. conchiformis* bark form. In both studies the authors were careful to call the dimorphic morphologies the summer and winter forms rather than leaf and bark forms. This was apparently because late in the year bark forms were occasionally found on the leaves, and leaf forms rarely inhabited the green growth of the stems. It is interesting to note that on *Tilia* in Poland *L. conchiformis* has only a single generation/yr and is limited to the bark of its host; no *ficifoliae* forms were reported (Komosinska, 1975).

Tinker (1957) conducted detailed biological field studies on "*Aspidiotus*" *ancylus* (Putnam) on elm. In following the life history of the species, he was surprised to find that *A. ancylus* apparently had an overwintering bark form and a summer leaf form. Specimens of each form were sent to Dr. Lewis J. Stannard, Illinois Natural History Survey, who identified the bark form as *A. ancylus* and the leaf form as *A. howardi* Comstock. Differences between the "species" centered primarily on the structure of the pygidial plates and lobes. Stannard (1965) pursued the matter further. Realizing that *A. ancylus* was common on the bark of sugar maples, he examined infested trees to see if a leaf form was also present on this host. He found a form which was virtually identical with another species, *A. comstocki* Johnson. Differences between *A. ancylus* and *A. comstocki* again related to the structure of pygidial lobes. Stannard found a single specimen on a leaf petiole which had lobes characteristic of *A. ancylus* on one side of the body and of *A. comstocki* on the other.

Danzig (1970) briefly discussed the typological concepts of most coccidologists as a significant hindrance to understanding variation caused by clinal or seasonal environmental factors. She noted that seasonal forms occur in species with 2 generations/yr. The winter generation inhabits the stems and branches and the summer generation inhabits the leaves. She further stated that pygidial structures are apparently affected by differences in the nutritional content of the ingested sap at different feeding sites. Artificial transfers of scales from one part of the plant to another are cited as evidence for leaf and stem form dimorphism, but she presented no further information relative to this evidence.

Similar results have been found for soft scales. Several workers (Ebling, 1938; Marchal, 1908; Sanders, 1909; Voukassovitch, 1930) have examined the numerous body shapes and colors of the coccid *Lecanium corni* Bouche. Based on host transfer work, it appears that many of these forms are directly related to host plant differences. In the study by Ebeling, *L. corni* was examined on apricot and Christmas-berry. Specimens collected on apricot had short legs and antennae and large body size compared to material collected on Christmas-berry. When eggs were transferred from one host to the other, the resultant adult females assumed the characteristics of specimens typical of the new host.

MATERIALS AND METHODS

Dimorphism Experiments

An experiment was undertaken to determine whether the leaf and stem forms were members of the same species. One to 3' tall *Nyssa sylvatica* plants were collected from Greenbelt and Scotland, Maryland. The plants were placed in 10" clay pots and were allowed to become established in a greenhouse at the University of Maryland. On April 16, 1972 the leafless plants were removed from the greenhouse and were fumigated with methyl bromide by the procedures described in the Plant Protection and Quarantine Treatment Manual, Anon. (1976) for treatment of "surface feeders" on dormant woody plants. Following fumigation, the plants were immediately returned to the greenhouse, and each plant was placed in an isolation apparatus similar to the one described by Bartlett and Kats (1969). This system utilized inflated polyethylene bags which covered the potted plant. After 5 days each bag-isolated plant was examined, and all specimens of *C. nyssae* were removed for microscopic examination. No live scales were found.

From May 1–15 infested twigs collected in College Park were cut into 2-3" sections and were attached with plastic tie-ons to the isolated trees in the greenhouse. At least 10 sections with 5 or more live females were attached to each uninfested tree. The isolated trees were infested only one time. Ten trees were infested, and 3 bag-isolated trees were left uninfested as controls. After 2 weeks the infested sections were removed, and all specimens on the sections were mounted in Hoyer's mounting medium on microscope slides and were determined as leaf or bark forms.

On June 15 one of the artificially infested trees was sampled. Specimens from the bark and leaves were mounted in Hoyer's mounting medium and examined under a compound microscope. In November, 8 artificially infested plants were sacrificed. The scales on these plants were mounted and records were kept relative to their position on the host. Control plants were examined periodically for scales.

In early July infested leaves were placed on 5 unifested, isolated plants in the greenhouse. After 2 weeks the leaves were removed, but because the isolated plants remained uninfested, specimens on the leaves were not mounted.

Determination of Life History in the Field

Specimens were taken from March 1971 to February 1973 at 3 collecting sites; the primary site was located in Hyattsville, Maryland and the secondary sites were on the College Park Campus about one mile apart. At the primary

site weekly bark collections were made from March to December, weekly leaf collections were made from April to November, and monthly bark samples were made at the secondary localities at irregular intervals. Life-history charts are based solely on samples collected in Hyattsville; samples taken on campus were used to determine whether there was any geographic deviation in the development of the species. Collections were taken from a single mature tree about 80' tall at the Hyattsville locality; several small trees about 25' tall were sampled at the other localities.

Methods for determining the life cycle and for constructing the life-history charts are as described by Stoetzel and Davidson (1971) except that specimens were collected from the bark and the leaves. Field-collected samples were returned to the laboratory, and when available, a minimum of 100 individuals from the bark and 100 from the leaves were mounted on slides in Hoyer's mounting medium. The life stage of each mounted specimen was determined using a Wild, M20 compound microscope at magnifications of 20-1,000X. Because the number of individuals sampled could vary from week to week, life history charts were constructed on a percentage basis rather than on actual numbers. It is emphasized that only 1 or 2 crawlers might be found on the leaves early in the year. Based on these 2 specimens, 100% would be recorded for that date in the crawler category on the life-history chart.

Descriptions of Life Stages

Numerical values given in the descriptions pertain to one-half of the body only. Numbers are given as follows: Range (mean, mode) and are based on counts from 15 specimens, when available, collected in the study areas. Ranges are normally given as whole numbers, but when a structure is located in the center of the body, it is recorded as 0.5 or a multiple thereof. The mode may consist of 1, 2, or 3 values.

Scanning Electron Microscope

A Cambridge Mark II Stereoscan was used for this study. Specimen preparation techniques included gluteraldehyde and/or osmium tetroxide fixation followed by freeze-drying, or gluteraldehyde fixation followed by air drying. Specimens were coated with a platinum-palladium alloy.

RESULTS

Dimorphism Experiments

Small sections of branches infested with gravid females and eggs of *C. nyssae* were attached to uninfested, isolated *Nyssa sylvatica* plants. Crawlers from the infested sections dispersed and settled on both the bark and the leaves of the uninfested hosts. After removal of the infestation-source sections, all specimens from the sections were mounted and found to be bark form females.

For the next several weeks, the isolated plants were examined for scale infestations. Leaves containing 1st instars were obvious because each settled crawler produced a chlorotic spot that was visible from the top of the leaf. The control plants showed no evidence of scales.

In June scale samples were taken from the leaves and stems of one of the isolated plants. At that time, crawlers and 2nd instars were the only stages present. From these samples, 10 leaf form 2nd-instar females were found on the leaves, and 5 bark form 2nd-instar females were found on the stems.

In September, October, and November, 8 of the 10 isolated plants were systematically depleted of their scale populations. More than 300 leaf form adult females were examined from the leaves, and over 200 bark from adult females were seen from the stems.

An attempt was made to infest clean *Nyssa sylvatica* plants with crawlers produced by leaf-form females. Infested leaves were attached to uninfested, bag isolated *N. sylvatica* plants. These transfers were unsuccessful, apparently because the leaves dessicated too rapidly, and the crawlers died before they could reach the unifested plants.

The control plants were examined in November and were found to be without scale insects.

Because bark form females were the only scales introduced onto the uncontaminated *Nyssa sylvatica* plants, the presence of leaf and bark forms on these plants establishes conclusively that they are dimorphic forms of the same species, *Chionaspis nyssae*.

Determination of Life History in the Field

This species has 2 generations/yr and occurs on the bark and leaves of it host.

Life History on Bark

(Fig. 1)

The overwintering adult female occurs primarily on the previous year's growth and is typically heavily sclerotized along the body margin and pale yellow centrally. By the last week in March eggs are visible within the body of the adult. During the first week of April egg laying begins and an escape slit is formed at the posterior end of the scale cover which will serve as the exit for newly hatched crawlers. The number of eggs laid/female varies from 50-80 with an average of about 70. Adult females die soon after egg laying is complete.

Eggs are pink when first laid and turn purple just

before hatching. Each egg is covered with numerous tiny C-shaped wax structures that apparently are produced by the perivulvar pores. These C-shaped structures were reported by Hamon, *et al* (1975) on *Kermes kingi* Cockerell. Eggs are embryonated when laid and have 2 dark eye spots that are clearly visible through the transparent egg membranes.

Crawlers first appear in the middle of April and are pink when they hatch. After the crawlers settle and mature, they turn yellow. It is not possible to determine the sex of the crawlers without mounting them on a microscope slide. Crawlers tend to be thigmotactic, settling in areas such as under abandoned scale covers, next to buds, in cracks or crevices on the bark, under the mother's scale cover, or rarely on the open surface of the bark. After settling, each crawler develops a white, waxy covering composed of many fine filaments. Most crawlers molt by the end of June.

Sexes of mature 2nd instars are easily separated in the field. The cover of the female is pear shaped, is composed of smooth wax, is without carinae; the ventral cover is thin and nearly transparent; and the body is yellow. The cover of the male is elongate, has parallel lateral margins, is composed of filamentous wax, has 3 dorsal carinae; the ventral cover is absent; and the body is pink or purple.

The majority of the 2nd instars molt by the beginning of July. Prepupae, pupae, and adult males are present during the last part of June and the beginning of July. Both winged and wingless forms are present, but winged forms are predominant. Exuviae of the 2nd-instar males, prepupae, and pupae are pushed through the exit slit at the posterior apex of the scale cover.

Adult females begin to appear during the middle of June and are most abundant during the first weeks of July. The scale cover consists of the wax and dorsal exuviae of the crawler and 2nd instar, and the wax produced by the adult. Wax of the dorsal cover is extruded as a series of flat ribbons by the dorsal macroducts and as fleshy filaments by the gland spines. As the wax is produced, it is molded by the pygidium to form an elongate, oyster-shell appearing cover. Ventral microducts are apparently important in forming the thin ventral cover.

General features of the stages of the 2nd generation on the bark are the same as the 1st generation. Eggs first appear in early July and are present into early October. The rest of the life history of the 2nd generation on the bark should be evident from Fig. 1. Adult males are wingless late in the year, but a few winged males are produced early in the 2nd generation (Table 2).

Life History on Leaves

(Fig. 1)

Leaves appear on *Nyssa sylvatica* in the College Park area about the end of April, and by the middle of May most leaves have reached their maximum size.

Crawlers appear on the leaves in the middle of May and are present continuously until leaf drop in November. There is a noticeable difference between the sexes in their choice of settling sites. Males seem to prefer areas away from the midvein of the leaf, either in close proximity to a secondary vein, along the margin of the leaf, or in the space between the secondary veins. Most females settle in the small pocket formed by the junction of the mid- and secondary veins with their heads pointed into the junction. Because of pubescence on the veins, the space at the junction is covered by hair which almost completely encloses the settled female crawler. When all of the preferred sites are occupied on a leaf, female crawlers settle in protected areas near the mid- or secondary veins.

Figure 1 represents the life history on the leaf. Field features of the various stages on the leaf are the same as on the bark. Winged males are predominant in the 1st generation and wingless forms are most abundant in the 2nd (Table 2).

Comparison of Bark and Leaf Life Histories

There are a number of differences in the life history of *C. nyssae* on leaf and bark. (1) Overwintering forms do not occur on leaves. A careful search of fallen leaves in November and December revealed that all scales, including eggs, were shriveled and dehydrated and presumed dead. (2) Males are most abundant on leaves, and females are predominant on the bark. (3) On the leaf, females continue to lay eggs until the leaves fall in November; whereas on the bark, females stop laying eggs after the first week in October.

Intermediate and Aberrant Forms

Throughout the year, specimens collected on leaf petioles were often unusual. At least 10 specimens collected in this position had one side of the body with median lobes and with macroducts on segment VI typical of the leaf form, whereas structures on the other side were typical of the bark form. Other specimens collected on petioles and leaf buds exhibited lobes intermediate between the leaf and bark forms as illustrated by Takagi (1967).

In October, a small number of female 2nd instar and adults were collected on the leaves that were typical bark forms. At first these specimens were believed to be products

of laboratory mislabelling, but their appearance persisted until leaf drop. It now seems apparent that these forms are products of some physiological change in leaves approaching senescence. Crawlers that settle on the leaves during this time apparently are ingesting sap different from that of normal leaves. Stafford and Barnes (1948) recovered only leaf forms of the fig scale on leaves during the spring and summer, but after October bark forms were found.

Taxonomic Treatment of *Chionaspis nyssae*

Genus *Chionaspis* Signoret

Chionaspis Signoret, 1869. Type-species *Coccus salicis* Linnaeus, 1758, by subsequent designation of Cooley, 1899:3, 9-10.

Phenacaspis Cooley and Cockerell, *In* Cockerell, 1899. Type-species *Chionaspis nyssae* Comstock, 1881, by subsequent designation of Cooley, 1903: 38.

Fundaspis MacGillivray, 1921. Type-species *Chionaspis americana* Johnson, 1896, by original designation.

Marchaliella Bodenheimer, 1951. Type-species *Chionaspis lepineyi* Balachowsky, by original designation and monotypy.

Euvoraspis Mamet, 1951. Type-species *Chionaspis cordiae* Mamet, 1936, by original designation and monotypy.

Chionaspis nyssae Comstock

Sour-gum scale

Chionaspis nyssae Comstock, 1881: 316.

Phenacaspis nyssae (Comstock), Cooley, 1903: 48.

Chionaspis sylvatica Sanders, 1904: 95.

Type-material—We have chosen from the syntypes and marked as lectotype an adult female mounted alone on a slide labeled "629. *Chionaspis nyssae* Comst. Type." Paralectotypes: 12 specimens on 5 slides with above data. These are deposited in the U.S. National Museum of Natural History (USNM).

Specimens examined—135 specimens on 77 slides from 18 states and the District of Columbia, in addition to the specimens used in the life history and morphology studies described herein. Unless otherwise noted, all specimens examined were collected from *Nyssa sylvatica* and are in the USNM collection. Some specimens from hosts other than *N. sylvatica* showed unusual amounts of morphological variation. For example, the bark form from *Symplocos tinctoria* has one submarginal and one submedial dorsal macroduct on each segment VI, whereas, the bark form from *Lindera benzoin* has 3 microducts between the first interlobular space. Leaf forms from unusual hosts did not exhibit aberrant morphological variations.

Alabama: Mobile Co., Mobile, 24-X-1925. Arkansas: Washington Co., Fayetteville, 19-IX-1943. Connecticut: Fairfield Co., Fairfield, 29-IX-1954. Georgia: Cobb Co., Powder Springs, 21-I-1901; McIntosh Co., Darien, 23-XI-1943, on *Symplocos tinctoria*. Florida: Alachua Co., Gainesville, 8-II-1918; Columbia Co., Lake City, 16-V-1900. Maryland: Montgomery Co., Ashton, 15-X-1940; Prince Georges Co., Beltsville, 10-VIII-1972, Berwyn, 9-IX-1971, College Park, 10-VIII-1972, Hyattsville, 10-VIII-1972. Mississippi: Stone Co., 8-V-1929. New Jersey: Camden Co., Merchantville, 6-V-1931; Middlesex Co., Milltown, 22-VII-1916. New York: Nassau Co., N.Y. Botanical Garden, 29-VI-1921, on *Lindera benzoin*. North Carolina: Chatham Co., Siler City, 6-VIII-1969; Orange Co., Chapel Hill, 22-XI-1927; Wake Co., Raleigh, 4-VI-1927; Wilkes Co., Millers Creek, 29-IV-1923; Polk Co., Tryon, 14-VI-1904. Ohio: Fairfield Co., Sugar Grove, 21-X-1903; Franklin Co., Columbus, 3-II-1903, on *Crataegus*; Muskingum Co., Duncan Falls, 31-XII-1917; Perry Co., Somerset, 12-VIII-1903. Pennsylvania: Dauphin Co., Harrisburg, 23-VIII-1937; Schuylkill Co., 13-III-1907; Co. ?, Springbrook, 1-V-1945, 13-VII-1945. South Carolina: Charleston Co., 19-III-1930, on *Quercus* sp.; Oconee Co., Clemson, 20-I-1899, 1915. Virginia: Fairfax Co., Mt. Vernon, 20-IX-1912; Northampton Co., Cape Charles, 16-VIII-1945; Independent Cities, Charlottsville, 13-VIII-1909, Richmond, 18-VIII-1942; Shenandoah National Park, 13-IX-70. Washington, D.C.: 29-V-1901, 21-IX-1908, 9-VII-1946, 19-VI-1958. West Virginia: Barbour Co., Junior, 20-IV-1912; Hardy Co., Moorefield, 31-III-1959.

Literature Records—The following include host, state, and/or county records not noted above. Dietz and Morrison (1916), Indiana. Hollinger (1923), Missouri: Stoddard Co. Kosztarab (1964), Ohio: Franklin Co., Blacklick Creek, 20-V-1961, on *Celtis occidentalis*; Carroll Co., Carrollton, 14-III-1916; Guernsey Co., Quaker City, 1904; Hocking Co., 20-V-1961; Licking Co., Newark, 1904; Scioto Co., Portsmouth, 14-VIII-1917; Wayne Co., Wooster Cemetary, 3-IX-1913.

Description of Stages

First Instar

Males and Females (Fig. 8)

Pink except just prior to molting when yellow. Oval when mounted. Sexes identical except dorsosubmedial setae absent from segments II-VII on female. Antenna 6-seg-

mented; antennal segment 1 with 2 hairlike setae, segment 2 with 1 hairlike seta, and 1 porelike sensillum, segments 3-4 without setae, segment 5 with 2 fleshy setae, segment 6 with 1 hairlike seta, 4 fleshy setae, and 2 invaginated "sensory pegs". Segment 6 about equal to combined lengths of antennal segments 3-5, weakly annulate. Marginal eye with basal pigmentation in life, pigmentation absent from cleared, stained specimens. Coxae each with 2 setae, trochanters with 1 seta, 1 apparent setal socket, and 4 small, oval sensilla, femora and tibiae without setae, tarsi with 3 sensilla, tarsi and claws each with 2 capitate digitules. Anal opening present between posterior pair of 8-shaped ducts. Stylets coiled in loop to right in unsettled crawlers.

Body setae–Male as illustrated. Female dorsally without submedials on segments II-VII. Note 4 pairs of small setae near submargin of segments VIII and IX.

Tubular ducts–Dorsally, with 1 pair of 8-shaped ducts near base of antennae larger than other macroducts; pro-, meso-, and metathorax each with 1 pair of submedial ducts; area lateral of anal opening with 1 pair of 8-shaped ducts. Ventrally with 9 ducts on each margin from mesothorax to segment VII, dermal orifice of ducts usually protruding.

Lobes–Median lobes represented by a pair of pointed, platelike structures; 2nd lobes with 2 primary lobules, medial lobule normally twice notched, lateral lobule normally simple; 3rd lobes small, simple, once or twice notched; 4th lobes absent.

Spiracles–Anterior spiracles each with one associated trilocular pore; posterior spiracles without pores.

Discussion–The above description is based on over 100 specimens. The descriptions of *C. americana* Johnson and *C. kosztarabi* Takagi and Kawai in Willoughby and Kosztarab (1974) are similar to the above description of *C. nyssae*. *C. americana* appears to differ from *C. nyssae* by having one more seta on the dorsal surface on the head. *C. kosztarabi* differs by having the 2nd lobe undivided and 1-3 tubular ducts on the ventral surface of the thorax; *C. nyssae* has the 2nd lobe divided into 2 primary lobules and has 3 tubular ducts on the ventral thorax.

Second Instar

Bark Females (Fig. 9)

Yellow, except prior to molting when golden yellow to brownish yellow. Fusiform when mounted. Antenna 1–segmented with 1 large spur, 1 fleshy seta, and 2 invaginated "sensory pegs". Eye with circumocular pigmented area visible in live, newly molted specimens, not visible in live, mature specimens or cleared, stained specimens. Anal opening just anterior of pygidial center.

Body setae–Dorsally, head with 6-7 (6.4, 6), usually 6 marginals to level of eye, 1 submarginal anterior to level of eye, 2 submedials on medial axis, rarely with a 4th marginal or a single medial; prothorax with 2-3 (2.1, 2), mesothorax with 2, metathorax and segment I each with 2, segments II-VIII each with 1 marginal, segment IX with 1 small, submarginal sclerotized ring resembling a setal socket in which seta not visible. Ventrally, head with 2-4 (2.9, 3), usually 2 marginals posterior to antenna and 1 submarginal at level of eye, rarely with a 3rd marginal anterior to antenna or with the submarginal absent; prothorax with 0-2 (1.1, 1), mesothorax with 1-2 (1.6, 2), metathorax with 2, segment I with 0-2 (1.1, 1), segment II with 1-2 (1.9, 2), segment III with 2-3 (2.9, 3), segment IV with 3, segment V with 1-2 (1.8, 2), segment VI with 2-3 (2.9, 3), segment VII with 3, segment VIII with 1 marginal setal socket with seta rarely visible, segment IX represented by 1 medial setal socket without seta.

Microducts–Ventrally, head with 0-2 (1.0, 1); prothorax with 2-3 (2.7, 3), mesothorax with 0-1 (0.1, 0), metathorax with 0.5-2.5 (1.3, 1.5); segment I with 0-1 (0.2, 0), segments II and III without microducts, segment IV with 0-1 (0.7, 1), segments V and VI each with 1, segment VII with 0-1 (0.1, 0), segment VIII without microducts.

Macroducts–Dorsally, segment IV with 0.5-1 (0.9, 1), segments V-VII each with 1.

Gland spines–Ventrally, prothorax with 0-1 (0.7, 1), mesothorax with 0-2 (0.9, 1), metathorax with 1-3 (1.9, 2); segment I with 0-2 (0.9, 1), segment II with 0-1 (0.8, 1), segment III with 1-2 (1.1, 1), segment IV with 1-2 (1.6, 2), segments V-VIII each with 1.

Lobes–Median lobes well developed, fused for at least 2/3 of their lengths, broadly triangular, medial margin usually with 2 serrations, lateral margin with 6 or 7 serrations, yoked by rounded, basal zygosis with a transverse sclerosis at base. Second lobes conspicuous, bilobed, medial lobule normally with 4 lateral serrations, lateral lobule simple. Third lobes inconspicuous, reduced to small sclerotized projections, frequently with 2 or 3 serrations. Fourth lobes indicated by low sclerotized area normally with 3 serrations.

Spiracles–Anterior spiracle with 2-3 (2.1, 2) associated trilocular pores, posterior spiracle normally without trilocular pores, rarely with 1.

Discussion–The above description is based on over 50 specimens.

The description of *C. kosztarabi* in Willoughby and Kosztarab (1974) is similar to the above description of *C. nyssae*. *C. kosztarabi* differs by having 4 or 5 macroducts along each side of the pygidium, no transverse sclerosis at

the base of the median lobes, and the setae anterior of median lobes relative to the other pygidial marginal setae are noticeably different than on *C. nyssae. C. nyssae* has 3 or 4 macroducts on each side of the pygidium and a transverse sclerosis at the base of the median lobes. *C. americana* is very different from *C. nyssae*. In addition to the features mentioned in the comparison with *C. kosztarabi, C. americana* also has median lobes that are shaped differently from those of *C. nyssae* and there are more ventral gland spines than on *C. nyssae*.

Second Instar

Leaf Females (Fig. 10)

Same as 2nd-instar bark female except as follows: Generally antennae protrude from cephalic margin more, and anterior cephalic margin normally more flattened.

Body setae–Dorsally, head with 7-9 (7.7, 8) setae, usually 4 marginals to level of eye, 2 submarginals with 1 next to eye and 1 anteromedial of eye, 2 submedials on medial axis, sometimes without marginal or submarginal or with extra marginal or submarginal. Ventrally, head with 2-3 (2.3, 2); prothorax with 1-3 (1.5, 1), mesothorax with 1-2 (1.8, 2), metathorax with 2-3 (2.1, 2), segment II with 1-3 (2.0, 2), segments III-IV each with 3, segment V with 2, segments VI and VII each with 3.

Microducts–Ventrally, head with 0-1 (0.6, 1); prothorax with 1-5 (2.8, 3), mesothorax with 0-1 (0.2, 0), metathorax with 0.5-1.5 (1.2, 1.5); segment I with 0-2 (0.7, 0), segment IV with 0.5-1 (0.9, 1).

Macroducts–Dorsally segments IV-VII each with 1 marginal macroduct, anterior pair sometimes thinner than others.

Gland spines–Ventrally, prothorax with 0-2 (1.0, 1), mesothorax with 0-1 (0.6, 1), metathorax with 1-2 (1.6, 2); segment I with 0-1 (0.6, 1), segment II with 0-1 (0.9, 1), segment III with 1.

Lobes–Median lobes strongly divergent, long and narrow, medial margins each with over 10 serrations, lateral margins without serrations, yoked by small sclerosis, with a transverse sclerosis near anterior end of lobe. Second lobes with medial lobule normally with 3 or 4 serrations laterally; lateral lobule rounded or pointed. Third and 4th lobes inconspicuous, reduced to small, sclerotized projections.

Spiracles–Anterior spiracle with 2-3 (2.2, 2) associated trilocular pores; posterior spiracle without pores.

Discussion–The above description is based on over 50 specimens. Leaf forms of *C. americana* and *C. kosztarabi* are unknown.

Third Instar

(Adult) Bark Females (Fig. 11)

Yellow, except pinkish red during and after egg formation. Antenna 1–segmented with 1 large spur, 1 fleshy seta, and 2 invaginated "sensory pegs" (Fig. 2). Eye inconspicuous. Anal opening just anterior of pygidial center.

Body setae–Dorsally, head with 5-8 (6.8, 6 & 7 & 8); prothorax with 2-3 (2.2, 2), mesothorax and metathorax each with 2; segment I with 2, segments II-VIII each with 1, segment IX with 1 setal socket without visible seta. Ventrally, head with 3-6 (4.9, 5); prothorax with 1-4 (2.6, 3), mesothorax with 2-5 (3.1, 3), metathorax with 2-5 (3.1, 3); segment I with 3-4 (3.1, 3), segment II with 2-4 (3.0, 3), segment III with 3-4 (3.9, 4), segment IV with 4 setae, segment V with 2-5 (3.3, 3), segments VI and VII each with 3-4 (3.7, 4), segment VIII with 1 setal socket with seta rarely visible, segment IX with 1 submedial setal socket without visible seta.

Microducts–Dorsally, segment I with 0-2 (0.6, 0); segment II with 0-1 (0.7, 1), segment III with 0-2 (0.9, 0). Ventrally, head with 5-8 (6.2, 5); prothorax with 6-10 (8.0, 8), mesothorax with 0.5-5 (2.6, 2.5), metathorax with 3.5-7 (5.2, 3.5 & 6 & 7); segment I with 0-2.5 (1.2, 1), segment II with 1-2.5 (1.9, 2), segment III with 0-1 (0.7, 1), segment IV with 0-1 (0.9, 1), segment V with 1-2 (1.2, 1), segment VI with 0-2 (1.6, 2), segment VII with 1-2 (1.2, 1), segment VIII with 1 very small microduct.

Macroducts–Dorsally, metathorax with 0-2 (0.5, 0); segment I with 0-3 (1.1, 0), usually without, marginal when present, segment II with 0-3 (1.2, 1) marginals, segment III with 3-7 (5.1, 5), usually 2 marginals and 3 submarginals, segment IV with 5-8 (5.9, 6), 2 marginals and usually 4 submarginals, segment V with 6-9 (7.6, 8), 2 marginals, usually 4 submarginals, and 2 submedials, segment VI with 2-3 (2.1, 2) marginals, rarely with 1 or 2 submarginals (Fig. 3), and 1 or 2 submedials, segment VII with 1 marginal. Ventrally, metathorax with 0-4 (2.5, 3); segment I with 0-6 (4.3, 5); segment II with 0-6 (3.7, 4 & 4 & 5), segment III with 0-2 (0.9, 0).

Gland spines–Dorsally, with 1 on each of segments VII and VIII overlying ventral gland spines. Ventrally, head with 0-1 (0.2, 0); prothorax with 0-2 (0.3, 0), mesothorax and metathorax each with 0-3 (1.3, 1); segment I with 0-1 (0.2,0), segment II with 1-5 (2.4, 2), segment III with 3-5 (4.0, 3 & 3 & 5) (Fig. 4), segment IV with 3-5.5 (3.5, 4), segments V-VIII each with 1.

Perivulvar pores–Quinqueloculars (Fig. 5), median group with 0-14 (7.5, 8), anterolateral group with 0-28 (15.2, 14), posterolateral group with 0-24 (14.3, 15) (Fig. 6).

Lobes–Median lobes well developed, fused for at least 2/3 of their lengths, broadly triangular, medial margin normally with 1 or 2 serrations, lateral margin with 6-10 serrations, yoked by rounded, basal zygosis with a transverse sclerosis at base. Second lobes conspicuous, bilobed, medial lobule normally with 4-6 lateral serrations, lateral lobule simple. Third and 4th lobes inconspicuous, each reduced to 2-4 small scerotized projections.

Spiracles–Anterior spiracle with 5-12 (8.8, 6) associated trilocular pores (Fig. 7), posterior spiracle with 1-4 (2.1, 2) trilocular pores.

Discussion–The above description is based on over 100 specimens.

The bark form of *C. nyssae* is most closely related to *C. americana* in having median lobes which are fused almost to their apices. *C. nyssae* differs in lacking small-sized ducts interspersed with submedial groups of macroducts and in having submedial macroducts on segment V. *C. americana* has many small ducts associated with the submedial clusters and has submedial macroducts on segments II, IV, and V.

Third Instar

(Adult) Leaf Females (Fig. 12)

Same as 3rd-instar bark female except as follows:

Body setae–Dorsally, head with 6-8 (7.4, 8); prothorax with 2-4 (2.4, 2), mesothorax with 1-2 (1.9, 2), metathorax and segment I each with 2; segments II-VIII each with 1, segment IX with 1 submarginal setal socket with seta rarely visible. Ventrally, head with 3-6 (4.3, 4); prothorax with 1-4 (2.2, 2), mesothorax with 3-4 (3.2, 3), metathorax with 1-3 (2.6, 3); segment I with 1-3 (2.3, 2), segment II with 1-4 (2.4, 3), segment III with 3-4 (3.8, 4), segment IV with 3-5 (3.8, 4), segment V with 2-5 (3.1, 3), segment VI with 1-2 (1.9, 2), segment VII with 3-4 (3.9, 4), segment VIII with 1, segment IX with 1 setal socket.

Microducts–Dorsally, head with 0-1 (0.1, 0); segment I with 0-1 (0.3, 0), segment II with 0-2 (0.6, 0), segment III with 0-3 (0.9, 0), segment IV with 0-1 (0.1, 0). Ventrally, head with 1-6.5 (4.2, 3.5 & 5.5); prothorax with 3.5-10 (5.8, 4 & 6), mesothorax with 1-5.5 (2.9, 2 & 2.5 & 4.5), metathorax with 3.5-5.5 (4.3, 3.5); segment I with 1-3.5 (1.7, 1.5), segment II with 1-2.5 (1.7, 2), segments III-V each with 1, segment VI with 1-2 (1.5, 1 & 2), segment VII with 0-2 (1.1, 1), segment VIII without microducts.

Macroducts–Dorsally, metathorax with 0-2 (1.1, 1); segment I with 0-4 (2.2, 2) marginals; segment II with 1-5 (2.4, 1) marginals, segment III with 1-8 (4.7, 5), usually 3 marginals and 2 submarginals, segment IV with 4-9 (6.8, 7), 2 marginals and usually 4 submarginals and 1 submedial, segment V with 5-9 (8.1, 7), 2 marginals and usually 3 submarginals and 2 submedials, segment VI with 2-9 (6.5, 6), 2 marginals and usually 2 submarginals and 2 submedials; segment VII with 1 marginal macroduct; segment VIII without macroducts. Several macroducts sometimes on margin or venter of metathorax and segments I-III.

Gland spines–Ventrally, prothorax with 0-1 (0.2, 0), mesothorax with 0-2 (0.7, 0), methathorax with 0-2 (0.6, 0); segment I with 0-1 (0.1, 0), segment II with 0-3 (1.9, 2), segment III with 2-6 (3.6, 2), segment IV with 2-5 (3.6, 4), segments V-VIII each with 1.

Perivulvar pores–Quinqueloculars, median group with 2-8 (4.9, 4), anterolateral group with 5-14 (10.4, 10), posterolateral group with 5-16 (8.7, 8).

Lobes–Median lobes strongly divergent, long and narrow, medial margins each with 10-15 (11.1, 11) serrations, lateral margins normally without serrations, yoked by variably shaped sclerosis, with a transverse sclerosis near anterior end of lobe. Second lobes conspicuous, bilobed, medial lobule serrate laterally, lateral lobule rounded. Third and 4th lobes inconspicuous, reduced to small, sclerotized projections.

Spiracles–Anterior spiracles each with 5-12 (8.7, 9) associated trilocular pores, posterior spiracles with 0-2.5 (1.4, 1 & 2).

Discussion–The above description is based on over 100 speicmens.

The 2 marginal macroducts on segment VI separate the leaf form of *C. nyssae* from leaf forms of other species of *Chionaspis*.

Second Instar

Males (Fig. 13)

Reddish pink. Oval as mounted. Antenna 1–segmented with 1-3 small spurs, 1 fleshy seta, and 2 invaginated "sensory pegs". Eyes usually inconspicuous. Anal opening unusually large compared to ring of other instars, present near pygidial center.

Body Setae–Dorsally, head with 6-7 (6.9, 7), 4 marginals to level of eye, 1 anterosubmarginal, and 1 submedial each in middle and posterior regions of head; prothorax with 2-3 (2.3, 22), mesothorax with 1-2 (1.9, 2), metathorax with 2 (2.0, 2); segments I-III each with 1-2 (1.9, 22), segments

IV-VII each respectively with 2 (2.0, 2), 2-3 (2.2, 2), 2 (2.0, 2), 1-2 (1.8, 2), segments VIII and IX each with 1 seta. Ventrally, head with 4-7 (5.2, 4 & 6) setae, 3 marginals to level of eye and 2 submarginals in anterior region; prothorax with 0-2 (0.8, 1), mesothorax with 1-3 (1.5, 1), metathorax with 0-3 (1.5, 2), segment I with 0-2 (1.2, 1), segment II with 1-3 (1.7, 2), segments III-IV each respectively with 1-3 (2.3, 3), 2-3 (2.9, 3), segments V-VI each with 3 (3.0, 3), 2-3 (2.9, 3), segment VII with 1-2 (1.7, 2), segment VIII with 1; segment IX apparently with 1 setal base.

Tubular ducts–Variable in size from unquestionable microducts to undoubted macroducts with all intermediate forms. Because of this variation, ducts will not be distinguished as "micro-" or "macro-". Medial ducts on dorsum tend to be smallest and marginals tend to be largest; posterior ducts are normally larger than anterior ducts. Large marginal ducts, "cup-shaped ducts" of Boratynski (1953), on segments II-VII unusual in form, "C" shaped from above, with single bar at inner apex, those on segments III and IV unusually close together, also microduct on "2nd lobule" of each apparent lobe near dorsal marginal seta of segments V-VIII. Venter with several unusually large ducts on marginal and submarginal areas of thorax and segment I and with minute duct opposite anal ring. Dorsally, head with 0-2 (1.4, 2); prothorax with 0-4 (2.0, 1 & 3), mesothorax with 0-5 (2.8, 3), metathorax with 1-8 (5.1, 6); segments I-VII respectively with 2-7 (4.3, 5), 3.5-8 (5.2, 5), 4-7 (5.1, 5), 3-6 (4.8, 5), 3-7 (5.3, 5), 2-5 (4.6, 4), 1-3 (2.5, 2), segments VIII and IX without ducts. Ventrally, head with 1-4 (2.6, 3); prothorax with 0-7 (5.1, 4), mesothorax with 2-9 (5.0, 4), metathorax with 2-7 (5.7, 5); segments I-VII respectively with 2-7 (3.1, 3), 2-2.5 (2.0, 2), 2-3 (2.2, 2), 2 (2.0, 2), 1.5-2 (1.9, 2), 1.5-2 (1.5, 1.5), 0-1 (0.1, 0), without ducts on segments VIII and IX.

Gland spines–Dorsally segments IV-VIII each with 1, segment IX without. Ventrally, prothorax with 1-4 (2.2, 2), mesothorax with 0-2 (1.1, 1), metathorax with 1-3 (1.9, 2); segments I-III respectively with 0-6 (3.3, 5), 0-4 (2.4, 3), 1-1.5 (1.2, 1).

Pygidial margin–With series of plates and platelike lobes along margin of pygidium; plates distinguishable only by position of setae; plates and lobes normally toothed apically except 2nd lobule of lobes 2, 3, and 4 which frequently have a smooth apex.

Spiracles–Anterior spiracle with 2-3 (2.3, 2) associated trilocular pores, posterior spiracle with 0-1 (0.4, 0 & 0.5) trilocular pores.

Discussion–The above description is based on over 50 specimens. Examination of these specimens failed to disclose definitive morphological characters which might enable separation of the bark form and leaf form.

From the work of Takagi and Kawai (1967), it is evident that *C. kosztarabi* and *C. gleditsiae* Sanders are quite different from *C. nyssae*. The latter has an unusual, marginal macroduct on segments II-VII, whereas they are absent on *C. kosztarabi*. . On *C. gleditsiae* the unusual ducts occur on segments III, IV, and VII. Based on the illustration of Willoughby and Kosztarab (1974), *C. americana* appears to have unusual, marginal macroducts on segments II, III, V, VI, VII, whereas Takagi and Kawai (1967) place them on segments III-VII. Based on the paper by Tippins and Beshear (1970), *C. betulae* Tippins and Beshear has these ducts on segments IV, V, and VII. Perhaps the most closely related 2nd-instar male is *Chionaspis platani* Cooley, which has 6 unusual ducts on each side of the body similar to *C. nyssae*. We have been unable to examine 2nd-instar males of this species and base our statement on Takagi and Kawai (1967).

Third Instar, Winged

(Prepupal) Males (Fig. 14)

Pinkish red. Oval, elongate in outline as mounted; antenna extending posteriorly to mesothorax, weakly segmented, with 2 "sensory pegs" near apex; dorsal and ventral eyespots purplish in live specimens, not always visible in specimens mounted in Hoyer's mounting medium, legs short, weakly segmented, metathoracic legs extending beyond body margin, prothoracic legs with apex oriented towards meson, mesothoracic and metathoracic legs with apices oriented posterolaterally; 1 pair of wing buds, each extending posteriorly to segment I; developing penial sheath internal, extending anteriorly to segment V; anus dorsomedial near apex of abdomen.

Body setae–Dorsally, head with 5-7 (6.1, 6); prothorax with 1-2 (1.4, 1), mesothorax and metathorax each with 0-1 (0.1, 0) marginals and with 1 submedial; segments I-VII each with 2 setae, segment VIII with 1 marginal and 0-1 (0.6, 1) submarginals, segment IX with 0-1 (0.9, 1) marginal. Ventrally, head with 2; prothorax with 0-3 (0.3, 0), mesothorax, metathorax, and segments I-III without setae, segment IV with 1, segment V with 0-1 (0.1, 0) marginals and 0-1 (0.9, 1) submedials, segments VI-VII each with 1 marginal and 1 submedial, segment VIII with 1-2 (1.9, 1) marginals, segment IX with 0-1 (0.1, 0).

Discussion–The above description is based on over 15 specimens. The "sensory pegs" on the antennae of the pupae and prepupae have apparently not been observed before. They are homologous to the "sensory pegs" of adult males.

Prepupae of *C. nyssae, C. kosztarabi*, and *C. americana* appear similar.

Third Instar, Wingless

(Prepupal) Males (Fig. 15)

Same as winged prepupa except as follows: Antenna shorter, not extending beyond level of prothorax; wing bud absent; developing penial sheath extending anteriorly to level of segment V, rarely to level of segment IV.

Body setae—Dorsally, head with 5-6 (5.9, 6); prothorax with 2, mesothorax with 0-1 (0.9, 1) marginals, metathorax and segments I-VII each with 1 marginal, mesothorax, metathorax, and segments I-IV each with 1 submedial, segments V-VII each with 0-1 (0.8, 1) submedials, segment VIII with 1 marginal and 0-1 (0.9, 1) submarginals, segment IX with 1 marginal. Ventrally, head with 2 setae; prothorax, mesothorax, metathorax, and segments I-III without setae, segment IV with 1 submedial seta, segment V with 0-1 (0.6, 1) marginals, segments VI and VII each with 1 marginal, segments V-VII each with 1 submedial seta, segment VIII with 2 marginals.

Discussion—The above description is based on over 10 specimens.

The wingless prepupae of *C. nyssae* and *C. kosztarabi* are similar.

Fourth Instar, Winged

(Pupal) Males (Fig. 16)

Pinkish red. Oval, elongate in outline as mounted; antenna extending posteriorly to metathorax, weakly segmented, with 2 "sensory pegs" near apex; dorsal and ventral eyespots purplish in live specimens; all legs extending beyond body margin, with apices oriented outwardly and with 4 short spines; segment IX produced into penial sheath, tapering to blunt apex; dorsomedial anus at base of segment IX.

Body setae—Dorsally, head with 5-6 (5.1, 5), prothorax with 2, mesothorax with 0-1 (0.6, 1) marginals and 0-1 (0.9, 1) submedials, metathorax with 0-1 (0.1, 0) marginals and 1 submedial; segments I-III each with 1 marginal, segment IV with 1-2 (1.1, 1) marginals, segments V-VIII each with 1 marginal, segment I with 0-1 (0.9, 1) submedials, segments II-VII each with 1 submedial, segment VIII with 1 marginal and 1 submarginal, segment IX with 1 submedial. Ventrally, head with 1-2 (2.0, 2); prothorax, mesothorax, metathorax, and segments I-III without setae, segment IV with 1-1.5 (1.1, 1); segment V with 0.1 (0.4, 0) marginals and with 0-1 (0.9, 1) submedials, segments VI and VII each with 1 marginal and 0-1 (0.9, 1) submedials, segment VIII with 0-1 (0.9, 1) marginals and 0-1 (0.1, 0) submedials.

Discussion—The above description is based on over 10 specimens.

Winged pupae of *C. nyssae, C. kosztarabi*, and *C. americana* are similar.

Fourth Instar, Wingless

(Pupal) Males (Fig. 17)

Same as winged pupae except as follows: Wing bud absent.

Body setae—Dorsally, head with 5-6 (5.1, 5); prothorax with 2, mesothorax with 1-2 (1.9, 2) marginals and 0-1 (0.9, 1) submedials, metathorax with 1-2 (1.1, 1) marginals, segments I-VII each with 1 marginal, metathorax and segment I with 1 submedial, segment II with 0-2 (1.0, 1) submedials, segments III-VII each with 1 submedial, segment VIII with 1 marginal and 1 submarginal; segment IX with 1 submedial. Ventrally, head with 1-2 (1.9, 2); prothorax, mesothorax, metathorax, and segments I-III without setae, segment IV with 1; segment V with 0-1 (0.7, 1) marginal, segment VI with 0-1 (0.8, 1) marginals, segment VII with 1 marginal, segment V with 1 submedial, segments VI and VII each with 0-1 (0.9, 1) submedials, segment VIII with 1 marginal.

Discussion—The above description is based on over 15 specimens.

Wingless pupae of *C. nyssae* and *C. kosztarabi* are similar.

Fifth Instar, Winged

(Adult) Males (Fig. 18)

Setae—Head: With one pair of setae on midcranieal ridge at anterior apex of head; with remaining dorsal midcranial setae behind lateral arms of midcranial ridge, occasionally with 1 or 2 of these setae on ridge; with 1 pair of ventral midcranial setae not attached to ridge. One short genal seta on each gena. One seta on postoccipital ridge near each juncture of anterior and posterior arm; without setae behind posterior arm. With 4 or 5 interocular setae. Thorax: Prothorax with 3 small setae on each side of body on lateral or mediolateral part of dorsum. Mesothorax with 2 setae on each tegular bulge and 1 pair of short setae on scutellum. Metathorax with 1 small seta near each metapostnotal sclerite. Abdomen: Submarginal dorsal setae normally present on each side of segments I-VII, occasionally without setae on segment I; with 1 marginal seta on each side of segments I-IV, segment V with 1 or 2 setae, segments VI and VII each with 2 setae, segment VIII with 3 setae on

each side; submarginal ventral setae on segments IV-VII, present or absent on segment III.

Head—Midcranial, postoccipital, and postocular ridges well developed. Anterior arms of postoccipital ridge short or extending to near lateral arms of midcranial ridge. Preocular ridge produced dorsally beyond articulatory process of antenna. Postocular ridge fenestrated dorsally near eye. Preoral ridges absent. Ocular sclerites lightly sclerotized around eye; postocular sclerite present but indistinct. Ocelluslike spot on gena present, sometimes indistinct. Mouth tubercle with weak sclerotization. Posterior tentorial pits present, ventral plates represented by narrow area of sclerotization.

Thorax—Prothorax: Of pronotal sclerities, only lateral pronotal sclerities visible; pleural ridge, and pleural sclerite well developed; epimeron present; posternum with heavily sclerotized median ridge attached to lightly sclerotized transverse lateral ridges; triangular sclerite at junction of median and lateral ridges normally absent. Mesothorax: Mesophragma transversely elongate. Prescutum rectangular, with characteristic reticulation; prescutal ridges well developed, sometimes connected by sclerotized prescutal suture; median groove absent. Scutum with characteristic reticulation, medially divided by shallow groove, prealare separated by distinct suture with heavily sclerotized crescent-shaped triangular plate; sinuous suture weakly developed. Scutellum in form of elongate rectangle; with small foramen. Membranous triangular area behind scutellum with weak longitudinal striation. Basisternum divided by conspicuous median ridge; furca arms long, extending to near marginal ridge. Metathorax: Suspensorial sclerites small; metapostnotal sclerities represented by area of irregular sclerotization; pleural ridge well developed, marginal and precoxal ridges weakly sclerotized; metasternum sclerotized laterally only; episternum and epimeron small.

Abdomen—Sclerotization on segments I-VII weak or absent, segment VIII with small tergite on each side of abdomen. Penial sheath about 280μ long; basal ridge of penial sheath developed ventrally and laterally; basal rod and process of penial sheath conspicuous; subgenital plates heavily sclerotized.

Legs—Hind legs longest, middle legs equal to or longer than front legs, front legs shorter than hind legs. Setae on inner margin of tibiae divided near apex.

Antenna—Ten segmented, about 400μ long.

Wings—Front wings about 570μ long.

Discussion—The above description is based on 15 specimens.

From the description of *C. salicis* (L.) presented by Ghauri (1962), *C. nyssae* differs as follows: With dorsal midcranial setae on membranous area posterior of lateral arms of midcranial ridge; tegular bulge with 2 setae; triangular membranous area behind scutellum with fine longitudinal striations; antennae about 400μ long; penial sheath about 208μ long; front wings about 570μ long. *C. salicis* has: Dorsal midcranial setae on midcranial ridge; tegular bulge with 1 seta; triangular membranous area behind scutellum with longitudinal striations; penial sheath about 333μ long; antennae about 436μ long; front wings about 594μ long.

We have had great difficulty in making comparisons of *C. nyssae* with the descriptions of *C. americana* and *C. kosztarabi* presented by Willoughby and Kosztarab (1974), because there appear to be a number of inaccuracies in their descriptions, and because winged and wingless forms were not treated separately.

Fifth Instar, Wingless

(Adult) Males (Fig. 19)

Same as winged male except as follows:

Setae—Mesothorax: Tegular bulge with 1 seta. Abdomen: Submarginal dorsal setae present on each side of segments I-VII; with 2 or normally 3 setae on each side of segment VIII; submarginal ventral setae normally present on segments IV-VII, rarely present on segment III.

Head—Postocular ridge normally not fenestrated. Ocelluslike spot on gena indistinct but normally visible. Ventral plate sclerotization variable.

Thorax—Variable. Prothorax: Of pronotal sclerites, lateral sclerite and posttergite present. Triangular sclerite at junction of median and lateral ridges normally present. Mesothorax: Mesophragma apparently absent; prescutum and prescutal ridges absent; scutellum variable, frequently with anterior ridge partially developed, without foramen. Membranous area behind scutellum without longitudinal striations. Postnotal sclerites normally not connected medially thus not forming triangular membranous area. Basisternum with anterior portion of marginal ridge absent; basisternum sclerotized in lateral and posterior areas only. Pleural ridge not as long as on winged form.

Abdomen—Segment VII normally more constricted than on winged form. Penial sheath about 285μ long.

Legs—Hind legs longest, front legs smallest.

Antennae—Normally 9 segmented, rarely with 10, about 360μ long.

Discussion—The above description is based on 7 specimens.

From the work of Ghauri (1962), *C. nyssae* differes from *C. salicis* as follows: Setal pattern differences are the same as on the winged forms except *C. nyssae* has only one seta on each tegular bulge; *C. nyssae* lacks the prescutum and anterior ridge (marginal ridge) of the basisternum; these structures are present on *C. salicis*.

CONCLUSIONS AND SUMMARY

Chionaspis nyssae is a bivoltine species that occurs on the bark and leaves of its host. The species overwinters as mated, adult females on the bark; leaf forms are absent during the winter. Males are most abundant on the leaves and females on the bark. *Chionaspis nyssae* is known only from the eastern United States and is restricted primarily to *Nyssa sylvatica* and *N. aquatica*; specimens collected from the bark of other hosts are often aberrant.

This paper presents conclusive evidence that *Phenacaspis nyssae* is the leaf form of *Chionaspis sylvatica* because: (1) isolated plants of *Nyssa sylvatica* infested with *Chionaspis sylvatica* produced specimens of *C. sylvatica* on the stems and *P. nyssae* on the leaves; (2) intermediate forms were occasionally collected on the petioles of the host; (3) specimens were collected with lobes similar to *C. sylvatica* on one side and to *P. nyssae* on the other side; (4) details of the pygidial morphology of *C. sylvatica* and *P. nyssae* are remarkably similar; (5) the 1st-instar female and all stages of the male are identical for *C. sylvatica*, and *P. nyssae*; (6) life history studies indicate that *P. nyssae* completely disappears in the winter.

Because *Chionaspis* is the oldest available genus-group name and *nyssae* is the oldest available species-group name, the proper name of the species is *Chionaspis nyssae*, as stated by Takagi and Kawai (1967).

Differences between the leaf and bark forms of *C. nyssae* occur in the adult female and 2nd-instar female only. The adult female bark form (1) has median lobes that protrude beyond the apex of the pygidium and are fused medially over half of their lengths leaving no apical pygidial notch, (2) normally has no submarginal or submedial macroducts on segment VI, (3) has 2 gland spines in each 1st and 2nd interlobular space, (4) and normally has more perivulvar pores (Table 1). The leaf form has (1) median lobes that do not protrude beyond the apex of the pygidium and are separate medially forming a conspicuous "V" shaped apical notch, (2) normally has submarginal and submedial macroducts on segment VI, (3) has one gland spine in each 1st and 2nd interlobular space, (4) and normally has fewer perivulvar pores. Forms of the 2nd-instar females differ only in the shape of the median lobes.

Occurrence of aberrant and intermediate forms on the petioles, leaf buds, and fruit of the host, and the presence of bark forms on senescing leaves suggest the possibility that the factor affecting the morphological differences of these forms may be a chemical derived from the host. However, until more precise information is available relative to scale insect settling sites and plant tissue food sources, we can only speculate about causative factors.

Sex of 1st-instar crawlers can be determined by examining the dorsosubmedial setae on the abdomen. On the male, these setae are normally present on all abdominal segments; on the female, they are absent on segments II-VII.

Second-instar males are remarkably different from 2nd-instar females. Differences include the structure of the pygidial fringe, the size, shape, and abundance of the tubular ducts, and the size and shape of the antennae.

Winged and wingless adult males are reported. Winged forms are most abundant in the 1st generation, while wingless forms are predominant in the 2nd (Table 2). In late fall winged males are absent.

In comparing the various stages of *C. nyssae* with the same stages of other species of *Chionaspis*, apparent morphological relationships may vary greatly from one instar to the next, i.e., the crawler of *C. nyssae* is very similar to the crawler of *C. americana*; the 2nd-instar bark female is most similar to *C. kosztarabi*; the winged adult male to *C. salicis*; the wingless adult male is very different from *C. salicis*; the adult female bark form is similar to *C. americana*; the adult female leaf form is very different from all North American *Chionaspis* species. These comparisons may be somewhat misleading because detailed descriptions of all stages of all U.S. species of *Chionaspis* are not available; however, there are remarkable differences in relationships from one instar to the next.

ACKNOWLEDGMENTS

The senior author wishes to thank Manya B. Stoetzel, William F. Gimpel, Jr., Larry Stevens, Beth Merrell, and M. Lee Vernon for their encouragment and support during this study.

Scanning electron microscope (SEM) time was supported in part by the University of Maryland Center of Materials Research, Department of Mechanical Engineering, Electron Microscope Central Facility. We are grateful to Mr. Gene Taylor for his assistance with the SEM. We express our appreciation to Dr. Eugene Small, Zoology Department, University of Maryland, for allowing us to use the critical point apparatus under his jurisdiction.

Thanks are expressed to Manya B. Stoetzel, Arnold S. Menke, and Ronald W. Hodges Systematic Ent. Lab, 11B111, ARS, USDA, for their useful criticisms and comments concerning this manuscript.

This work is part of a thesis submitted by the senior author in 1976 to the Graduate School of the University of Maryland in partial fulfillment of the requirements of the M.S. degree.

Literature Cited

Anonymous. 1976. Plant Protection and Quarantine treatment manual. USDA, APHIS, Plant Prot. Quar. Programs.

Bartlett, B. R. and G. Kats. 1969. Inflated plastic bags as cages for insects on potted plants. J. Econ. Ent. 62: 524-525.

Bodenheimer, F. S. 1951. Description of some new genera of Coccidae. Ent. Ber. 13: 328-331.

Boratynski, K. L. 1953. Sexual dimorphism in the second instar of some Diaspididae. Trans. Roy. Ent. Soc. London 104: 451-479.

Borchsenius, N. S. 1966. A catalog of the armoured scale insects (Diaspidoidea) of the world. Akad. Nauk SSSR Zool. Inst., Leningrad. 448 p. (In Russian.)

Comstock, J. H. 1881. Report of The entomologist. Part II. Report on scale insects. *In* U. S. Dep. Agr., Comm. Agr. Rept., 1880: 276-349; also reprinted in 1916. Cornell Univ. Agr. Exp. Sta. Bull. 372: 425-500.

Cooley, R. A. 1899. The Coccid genera *Chionaspis* and *Hemichionaspis*. Spec. Bull., Mass. Agr. Exp. Sta. 57 p.

Cooley, R. A. 1903. A new diaspid genus. Can. Ent. 35: 48.

Cooley, R. A. and T. D. A. Cockerell. 1899. p. 398. *In* T. D. A. Cockerell. A check-list of the Coccidae. Bull. Illinois State Lab. Natur. Hist. 4: 318-339.

Danzig, E. M. 1970. Synonymy of some polymorphous species of coccids. Zool. Zh. 49: 1015-1024.

Dietz, H. F. and H. Morrison. 1916. The Coccidae or scale insects of Indiana. Indiana State Ent. Ann. Rep. 8 (1914-1915): 195-321.

Ebeling, W. 1938. Host-determined morphological variations in *Lecanium corni*. Hilgardia 11: 613-631.

Ferris, G. F. 1953. Report upon scale insects collected in China. Part IV. Microent. 18: 59-84.

Ferris, G. F. 1955. The genus *Phenacaspis* Cooley and Cockerell. Part I. (Insecta: Homoptera: Coccoidea). Microent. 20: 41-82.

Ferris, G. F. 1956. The genus *Phenacaspis* Cooley and Cockerell. Part II. (Insecta: Homoptera: Coccoidea). Microent. 21: 67-83.

Ghauri, M. S. K. 1962. The morphology and taxonomy of male scale insects. Brit. Mus. (Natur. Hist.), London. 221 p.

Hamon, A. B., P. L. Lambdin, and M. Kosztarab. 1975. Eggs and wax secretion of *Kermes kingi*. Ann. Ent. Soc. Amer. 68: 1077-1078.

Hollinger, A. H. 1923. Scale insects of Missouri. Missouri Agr. Exp. Sta. Bull. 58, 71 p.

Johnson, W. G. 1896. Preliminary notes on five new species of scale insects. Ent. News 7: 150-152.

Komosinska, H. 1975. Studies on the biology of *Mytilaspis conchiformis* forma *conchiformis* (Gmelin) in Poland. Pol. Akad. Nauk, Ann. Zool. 33: 127-148.

Kosztarab, M. 1964. The armored scale insects of Ohio. Ohio Biol. Surv. Bull. 2 (1963). 120 p.

Linnaeus, C. 1758. Insecta Hemiptera. Coccus. Systema Nat. (ed. 10) 1: 455-457.

Lupo, V. 1943. Il *Mytilococcus ficifoliae* (Berlese) e una forma estiva del *M. conchiformis* (Gmelin). Boll. Lab. Zool. Gen. Agr. R. Inst. Superiore Agr. Portici 5: 196-205.

MacGillivray, A. D. 1921. The Coccidae. Scarab, Illinois. 502 p.

Mamet, R. 1936. New species of Coccidae from Mauritius. Proc. Roy. Ent. Soc. London, Ser. B, 5: 90-96.

Mamet, R. 1951. Notes on the Coccoidea of Madagascar.–II. Mem. Inst. Sci. Madagascar, Ser. A., 5: 213-254.

Marchal, P. 1908. Notes sur les cochenilles de l'Europe et du nord de l'Afrique. Ann. Soc. Ent. France 77: 223-309.

Sanders, J. G. 1904. Three new scale insects from Ohio. Ohio Natur. 4: 94-98.

Sanders, J. G. 1909. The identity and synonymy of some of our soft scale-insects. J. Econ. Ent. 2: 428-448.

Signoret, V. 1869. Essai sur les Cochenilles. (Part 2). Ann. Soc. Ent. France (1868) 8: 829-876.

Stafford, E. M. and D. F. Barnes. 1948. Biology of the fig scale in California. Hilgardia 18: 567-598.

Stannard, L. J. 1965. Polymorphism in the Putnam's scale, *Aspidiotus ancylus*. Ann. Ent. Soc. Amer. 58: 573-576.

Stoetzel, M. B. and J. A. Davidson. 1971. Biology of the obscure scale, *Melanaspis obscura* (Homoptera: Diaspididae), on pin oak in Maryland. Ann. Ent. Soc. Amer. 64: 45-50.

Takagi, S. 1961. A contribution to the knowledge of the Diaspidini of Japan. Part II. Insecta Matsumurana 24: 69-103.

Takagi, S. 1967. An additional note on dimorphism in *Chionaspis nyssae*. Insecta Matsumurana 30: 55-56.

Takagi, S. and S. Kawai. 1966. Some Diaspididae of Japan. Insecta Matsumurana 28: 93-119.

Takagi, S. and S. Kawai. 1967. The genera *Chionaspis* and *Pseudaulacaspis* with a criticism on *Phenacaspis* (Homoptera: Coccoidea). Insecta Matsumurana 30: 29-43.

Takahashi, R. 1952. Descriptions of five new species of Diaspididae from Japan, with notes on dimorphism in *Chionaspis* or *Phenacaspis*. Res. Inst. Natur. Resources, Misc. Rep. No. 27: 7-15.

Takahashi, R. 1953. Dimorphism in some species of *Chionaspis* or *Phenacaspis*. Portici Boll. Lab. Zool. Gen. Agr. "Filippo Silvestri" 33: 48-56.

Tinker, M. E. 1957. Effect of DDT on the bionomics of Putnam's scale *Aspidiotus ancylus* (Putnam). Ph.D. Dissertation, Univ. Ill., Urbana. 69 p.

Tippins, H. H. and R. J. Beshear. 1970. A new species of *Chionaspis* from *Betula nigra*. Ann. Ent. Soc. Amer. 63: 1022-1023.

Voukassovitch, P. 1930. Sur la polyphagie de la cochenille *Lecanium corni*. Compt. Rend. Soc. Biol. Paris 104: 1065-1068.

Willoughby, P. A. and M. Kosztarab. 1974. Morphological and biological studies on two species of *Chionaspis*. Va. Polytech. Inst. Res. Div. Bull. 92: 1-83.

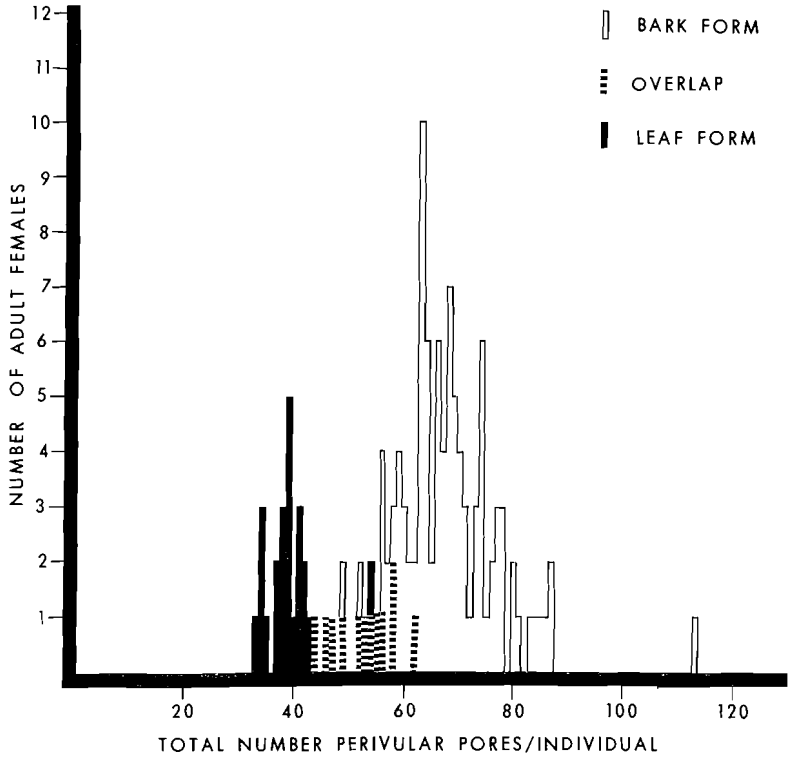

Table 1. Frequency histogram showing total number of perivulvar pores present in individual bark and leaf form adult females of *C. nyssae*. Checkered bars indicate that the same number of perivulvar pores is found in both bark and leaf form females. Statistics measured for bark form females include: n (total number of individuals measured) = 106, $\overline{X}$ (mean) = 66.8 ± 10.2, and range = 44-113. Statistics measured for leaf form females include: n = 35, $\overline{X}$ = 43.7 ± 8.0, and range = 33-62.

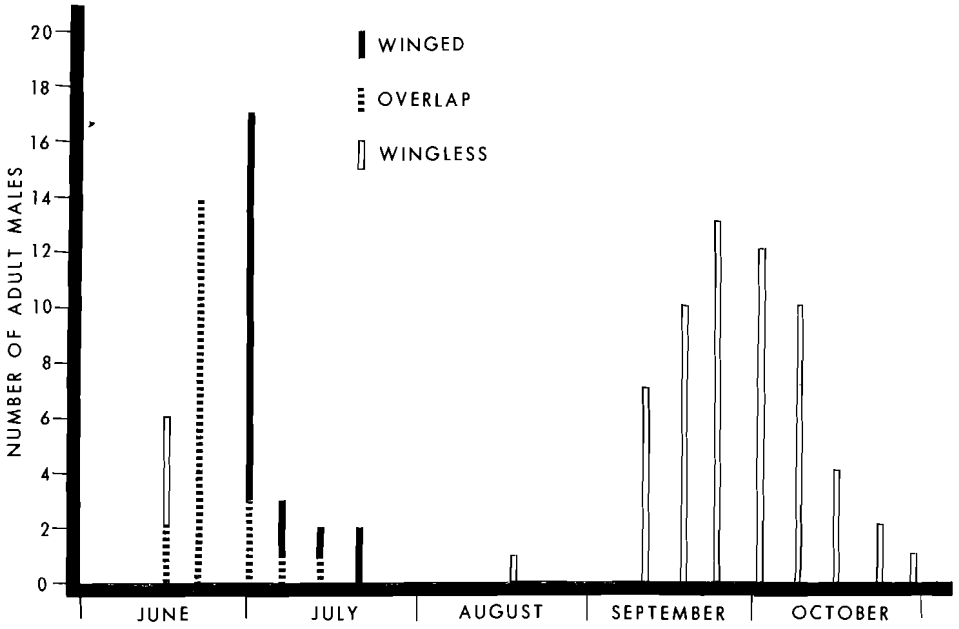

Table 2. Frequency histogram showing number of winged and wingless males of *C. nyssae* sampled on various collection dates in 1972 at Hyattsville, Maryland. Note that checkered bar indicates both winged and wingless males were present on that date. Males measured represent pooled samples of 3rd, 4th, and 5th instar males.

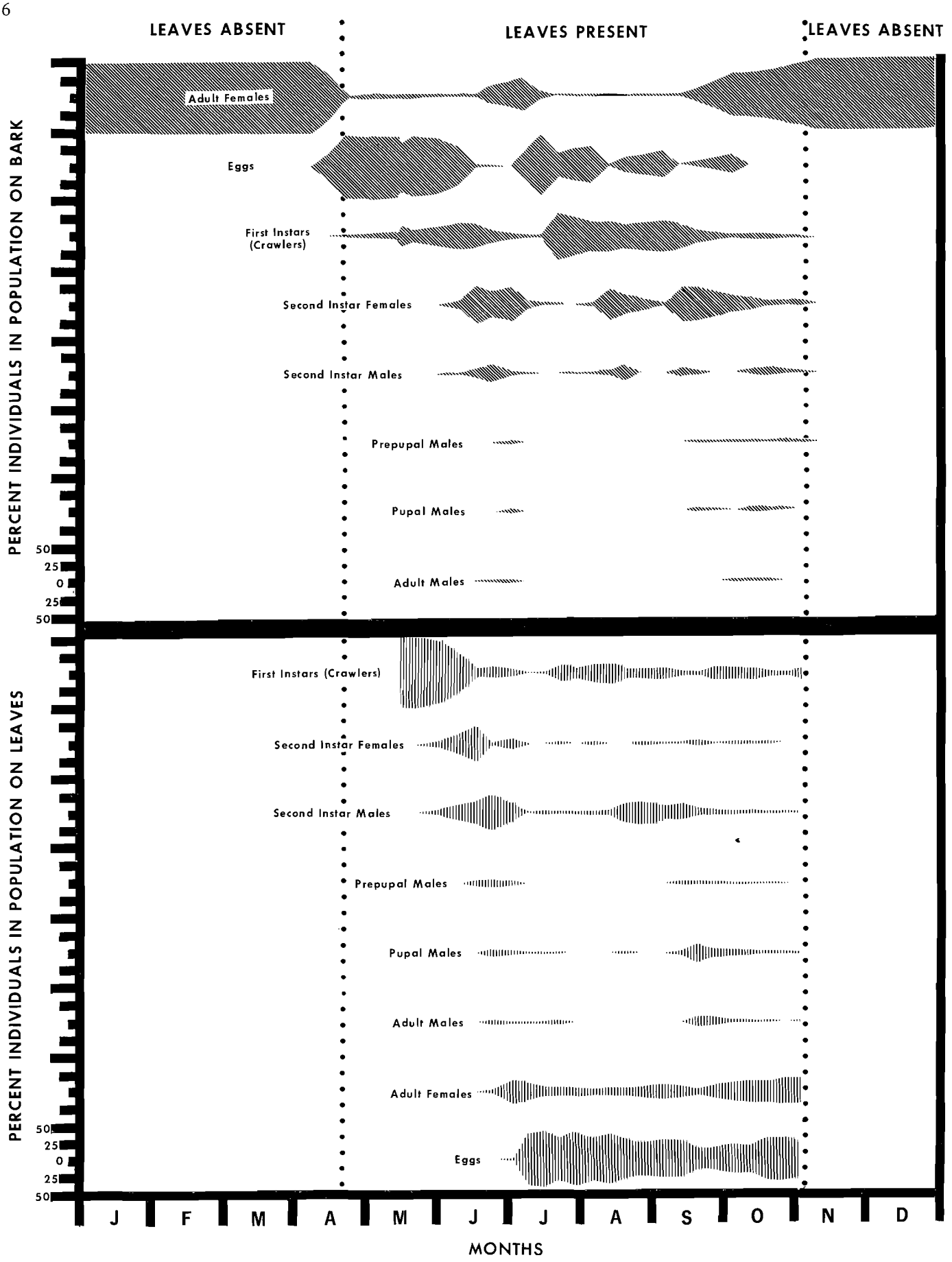

Figure 1. Life history chart of *Chionaspis nyssae* on *N. sylvatica* (black or sour gum) in Hyattsville, Maryland, 1972-1973.

Figure 2. Adult Female–SEM micrograph of antenna taken at 2,500X.

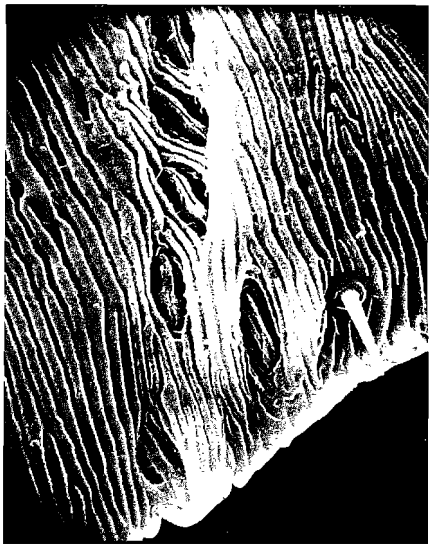

Figure 3. Adult Female–SEM micrograph of dorsal marginal and submarginal macroduct orifices on segment V taken at 2,000X.

Figure 4. Adult Female–SEM micrograph of gland spines on margin of segment III taken at 1,800X.

Figure 5. Adult Female–SEM micrograph of perivulvar pore taken at 12,000X.

Figure 6. Adult Female–SEM micrograph of vulva and perivulvar pore clusters taken at 1,350X.

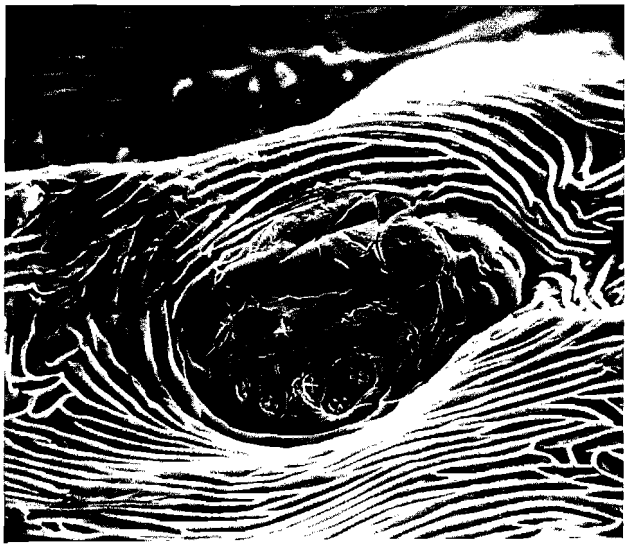

Figure 7. Adult Female–SEM micrograph of spiracular opening and associated trilocular pores taken at 1,100X.

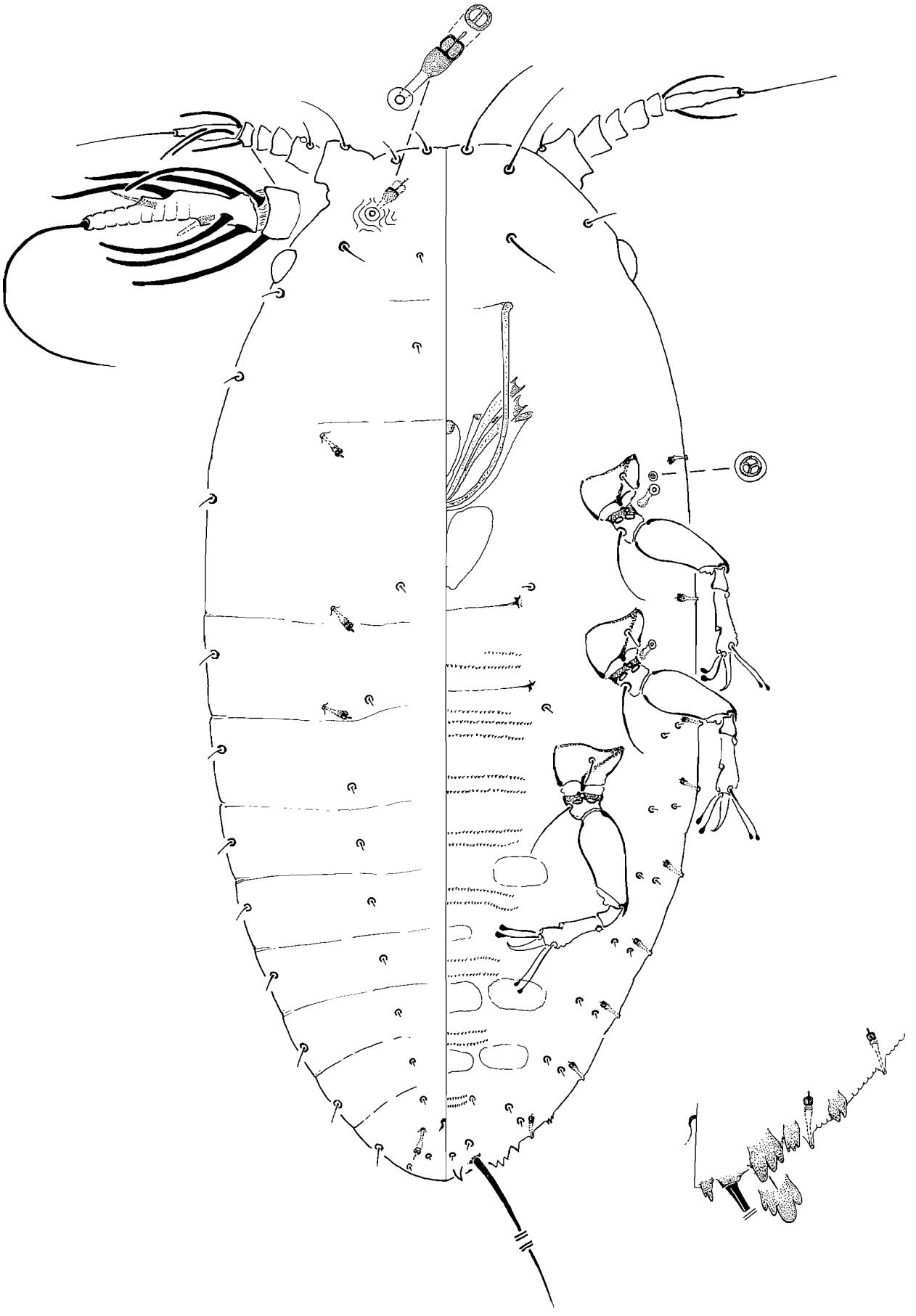

Figure 8. 1st instar (crawler) male of *C. nyssae*.

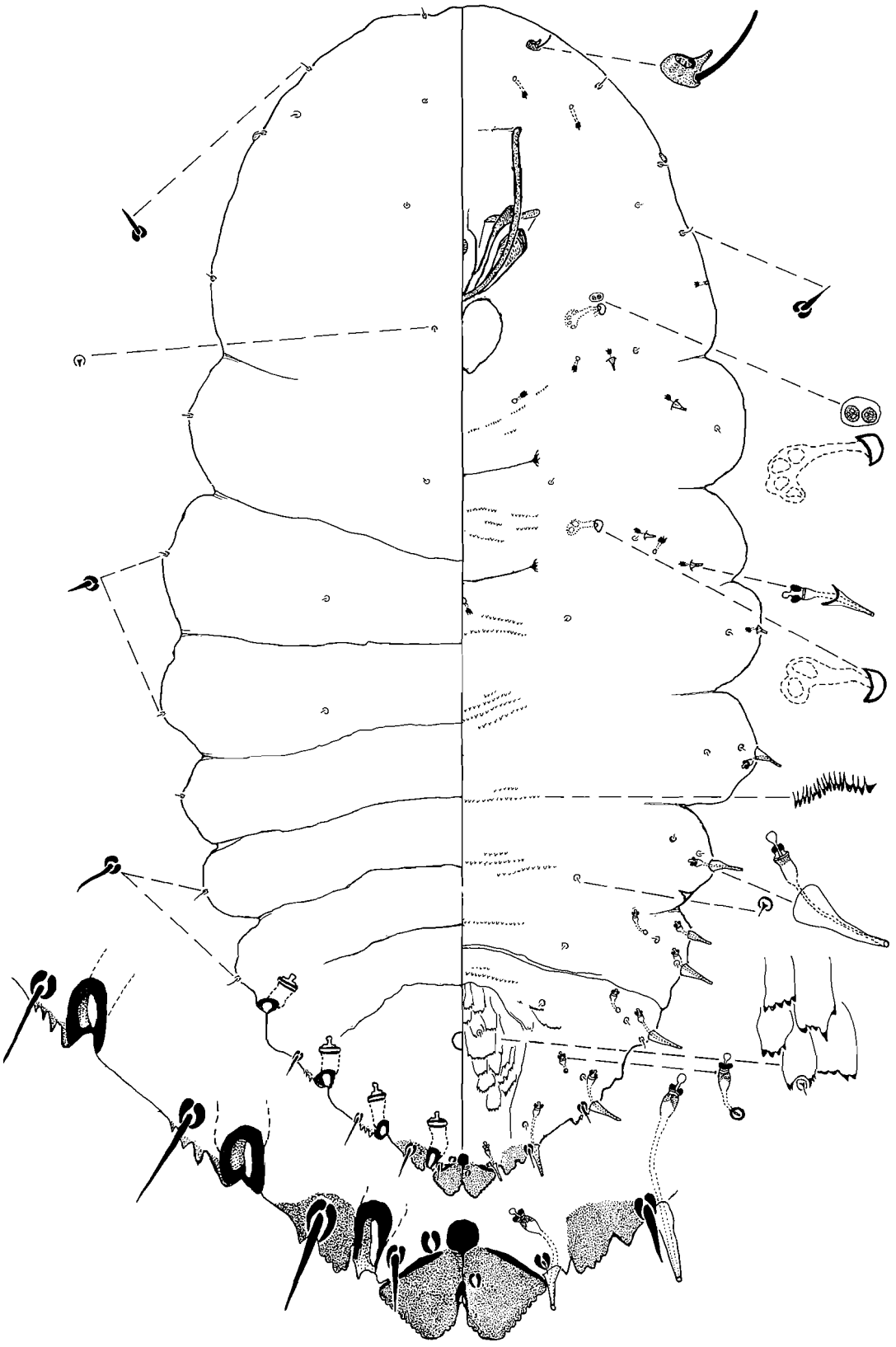

Figure 9. 2nd instar bark form female of *C. nyssae*.

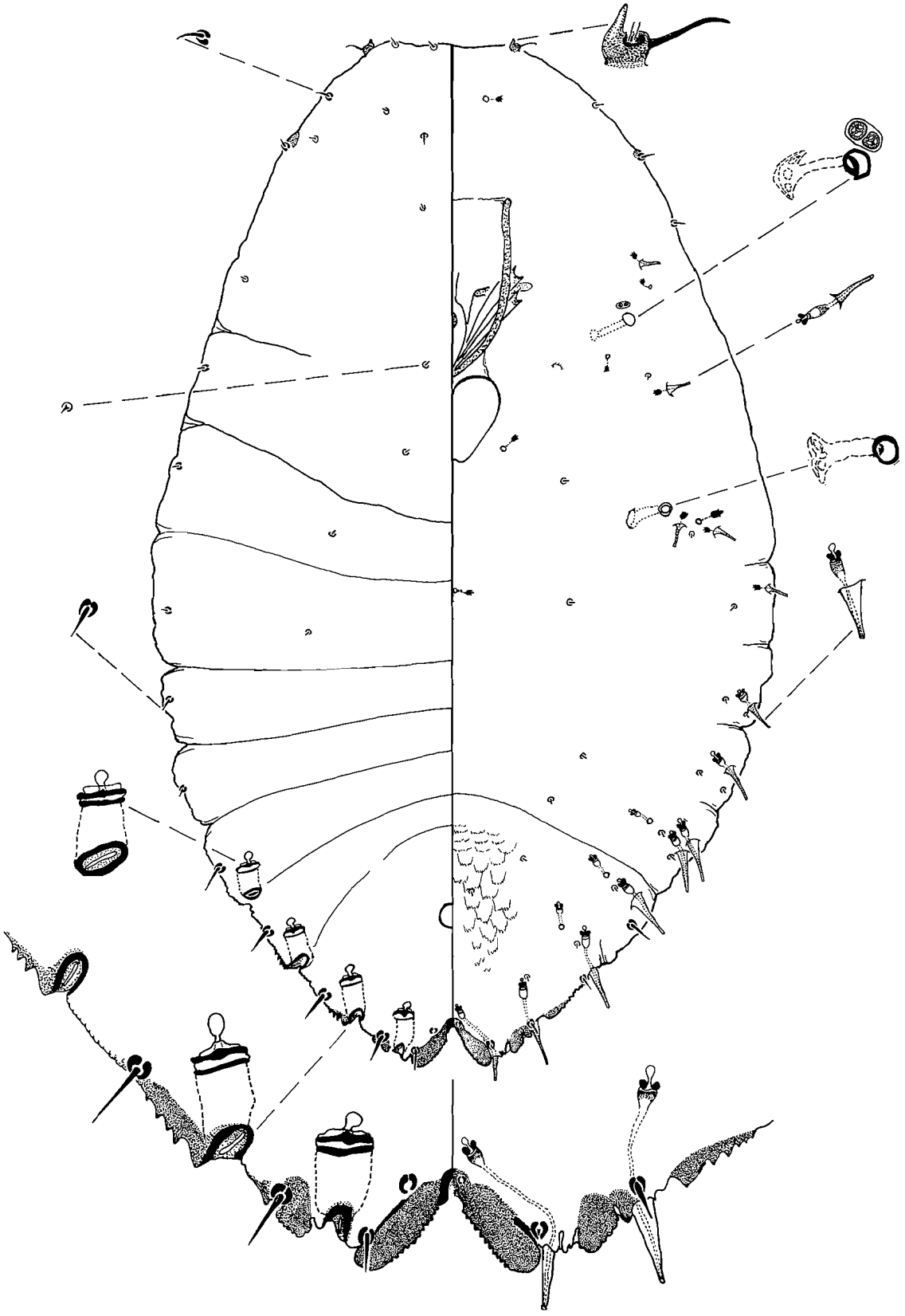

Figure 10. 2nd instar leaf form female of *C. nyssae*.

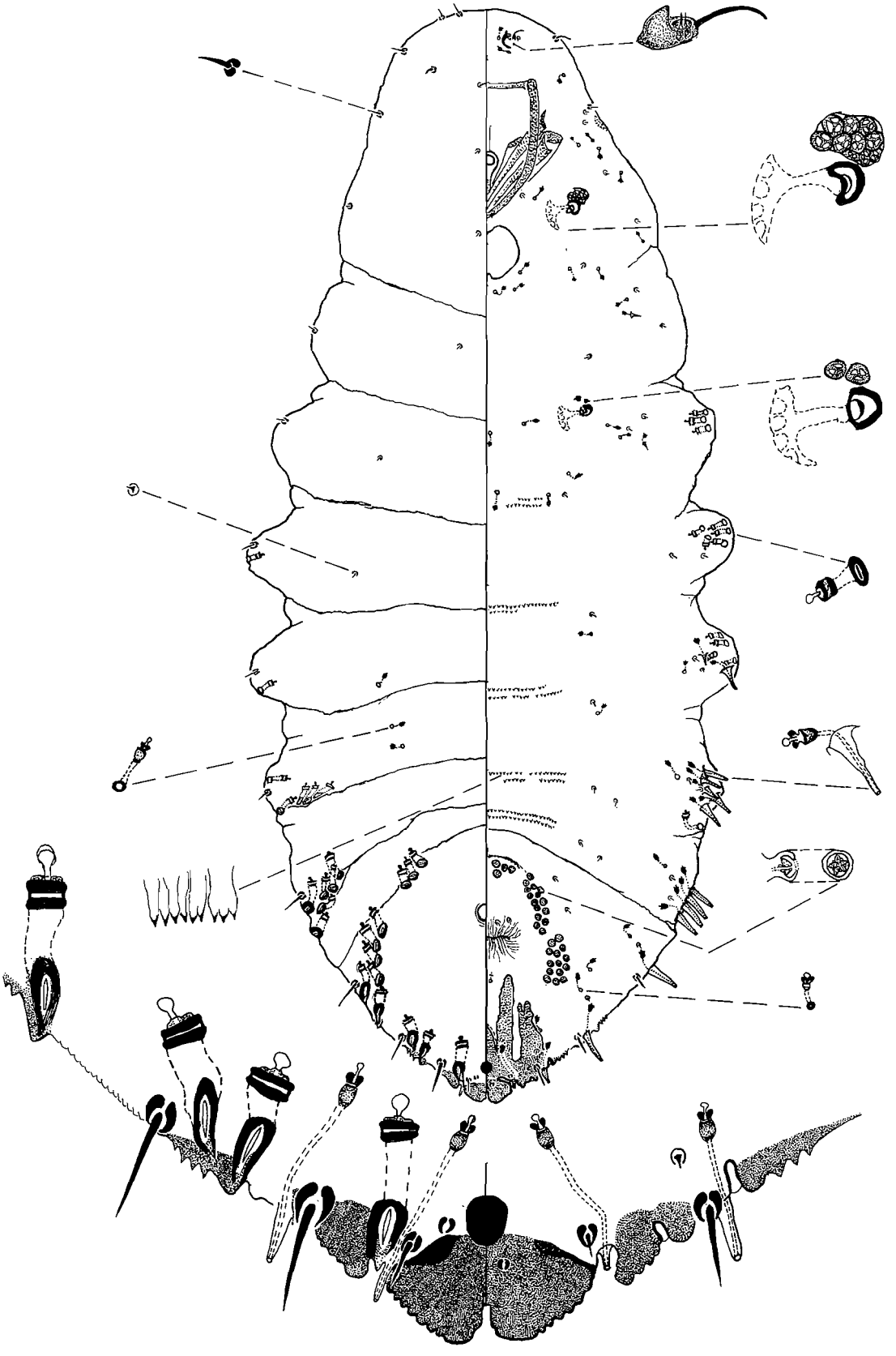

Figure 11. 3rd instar (adult) bark form female of *C. nyssae*.

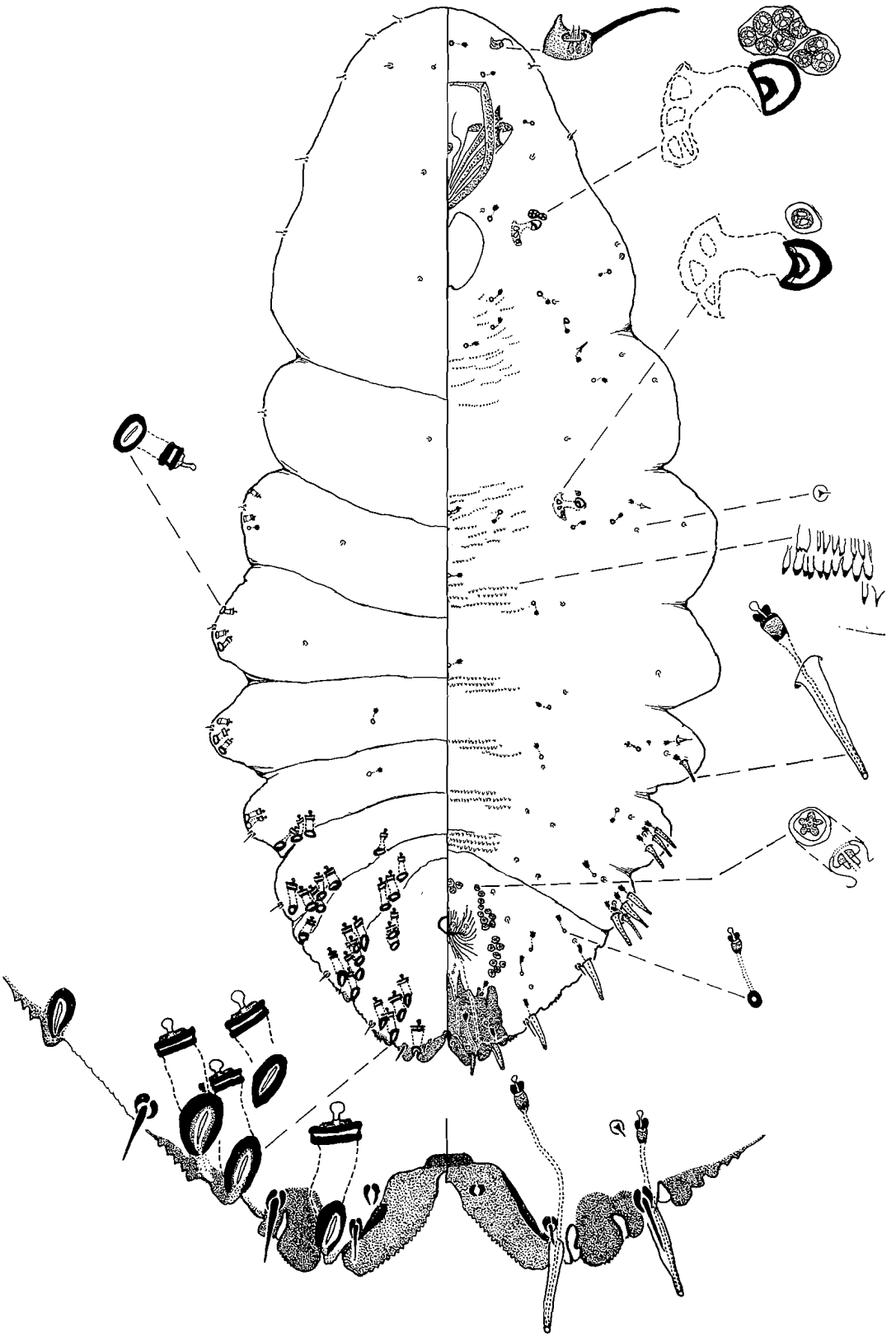

Figure 12. 3rd instar (adult) leaf form female of *C. nyssae*.

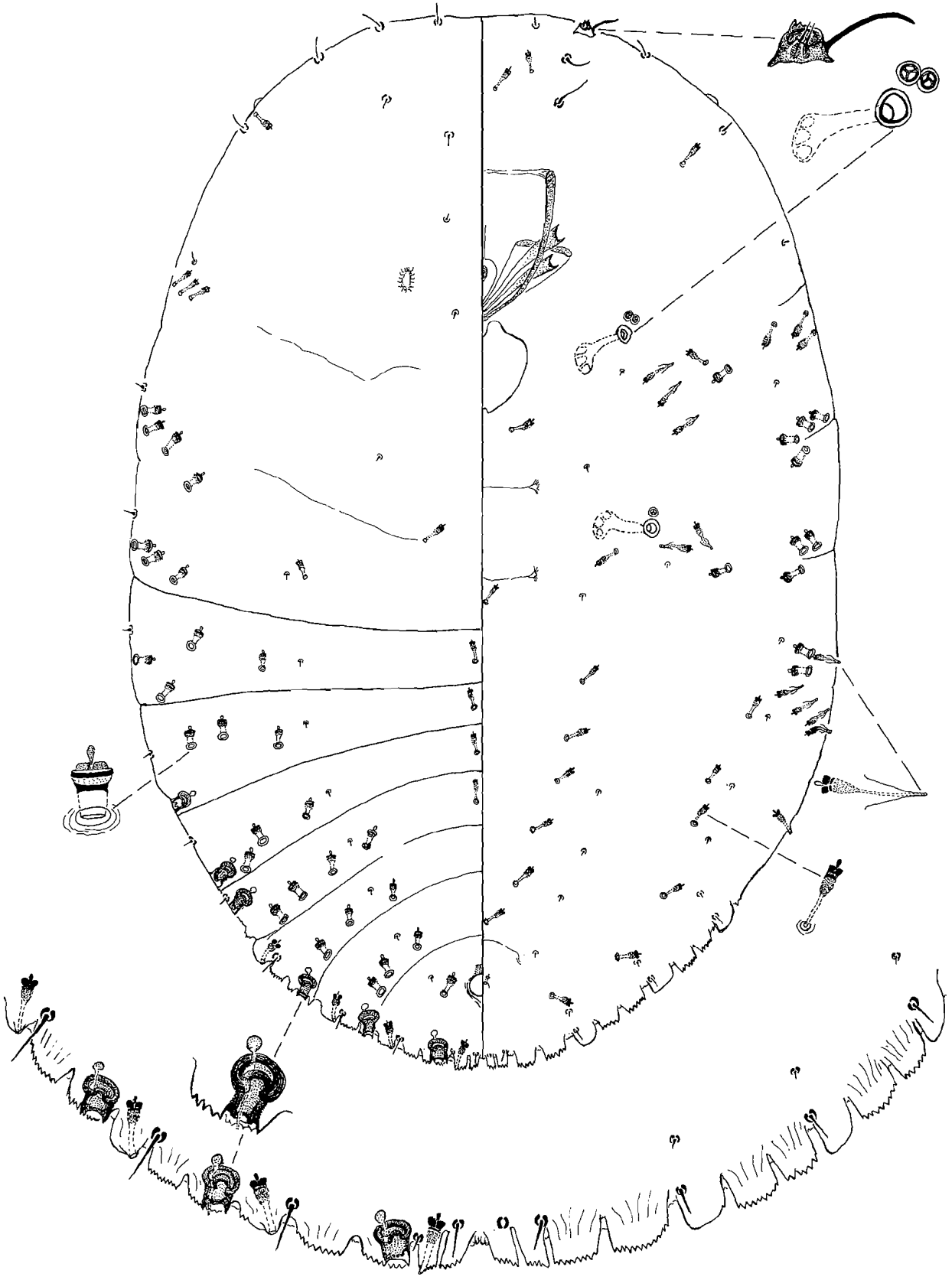

Figure 13. 2nd instar male of *C. nyssae*.

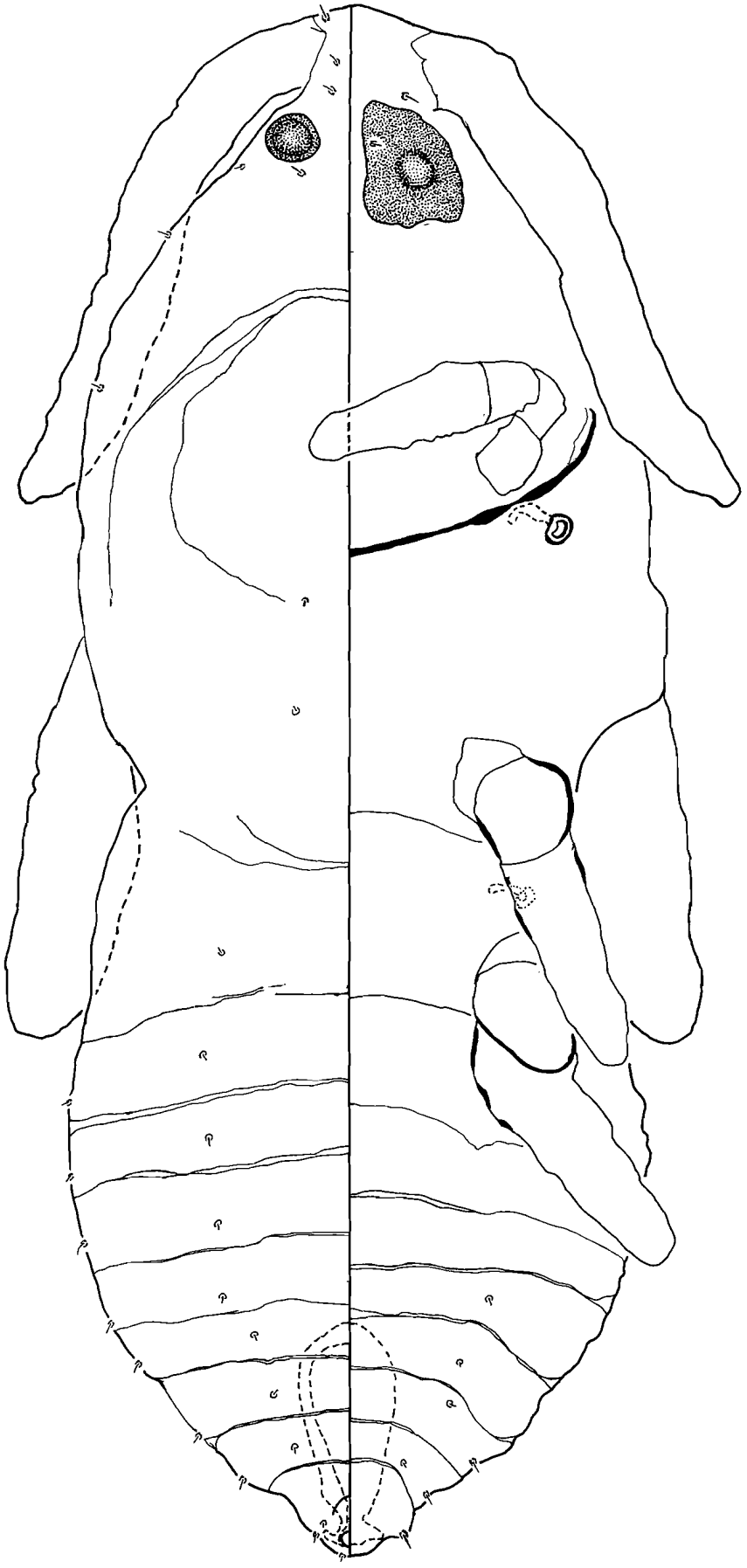

Figure 14. 3rd instar (prepupal) winged male of *C. nyssae*.

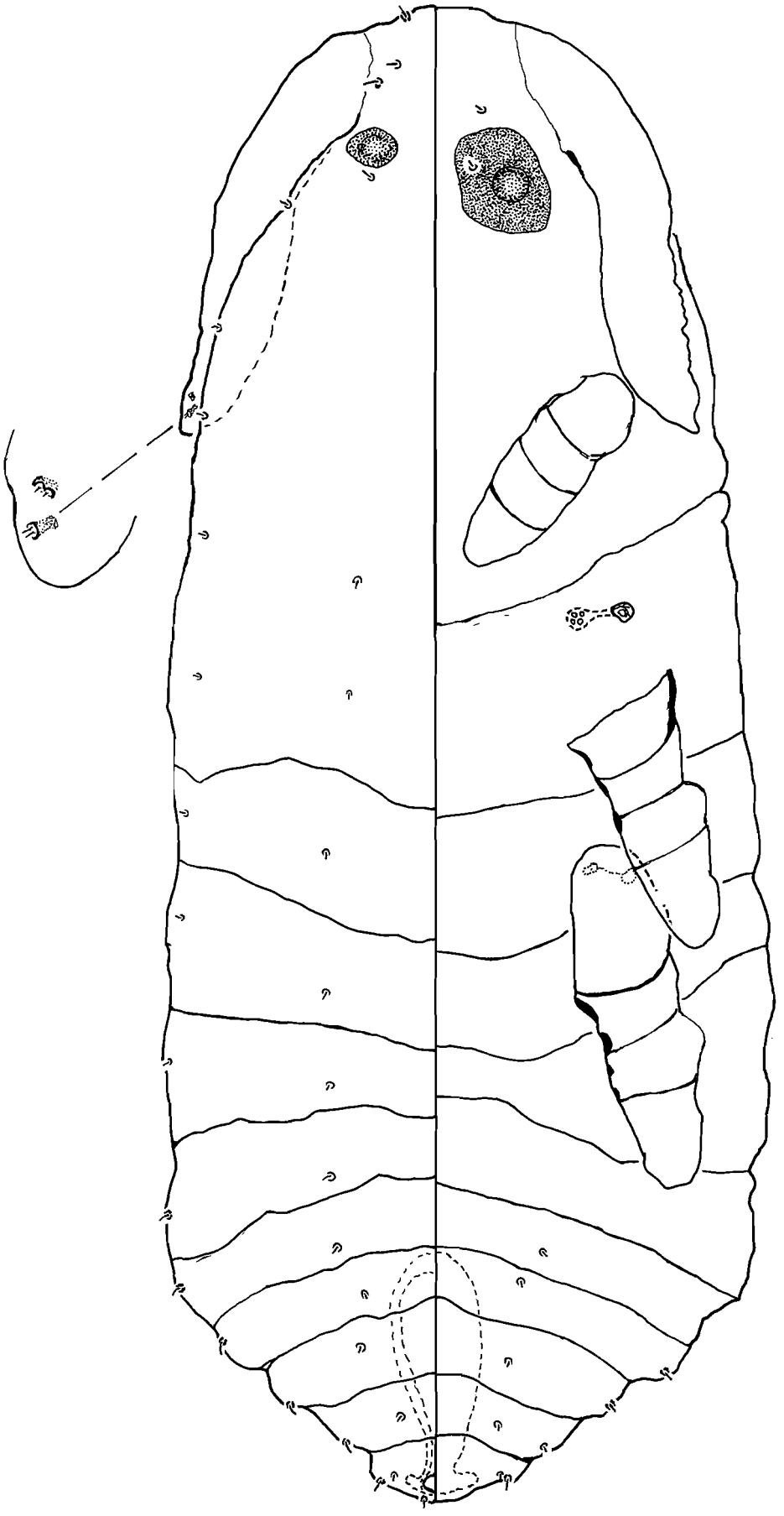

Figure 15. 3rd instar (prepupal) wingless male of *C. nyssae*.

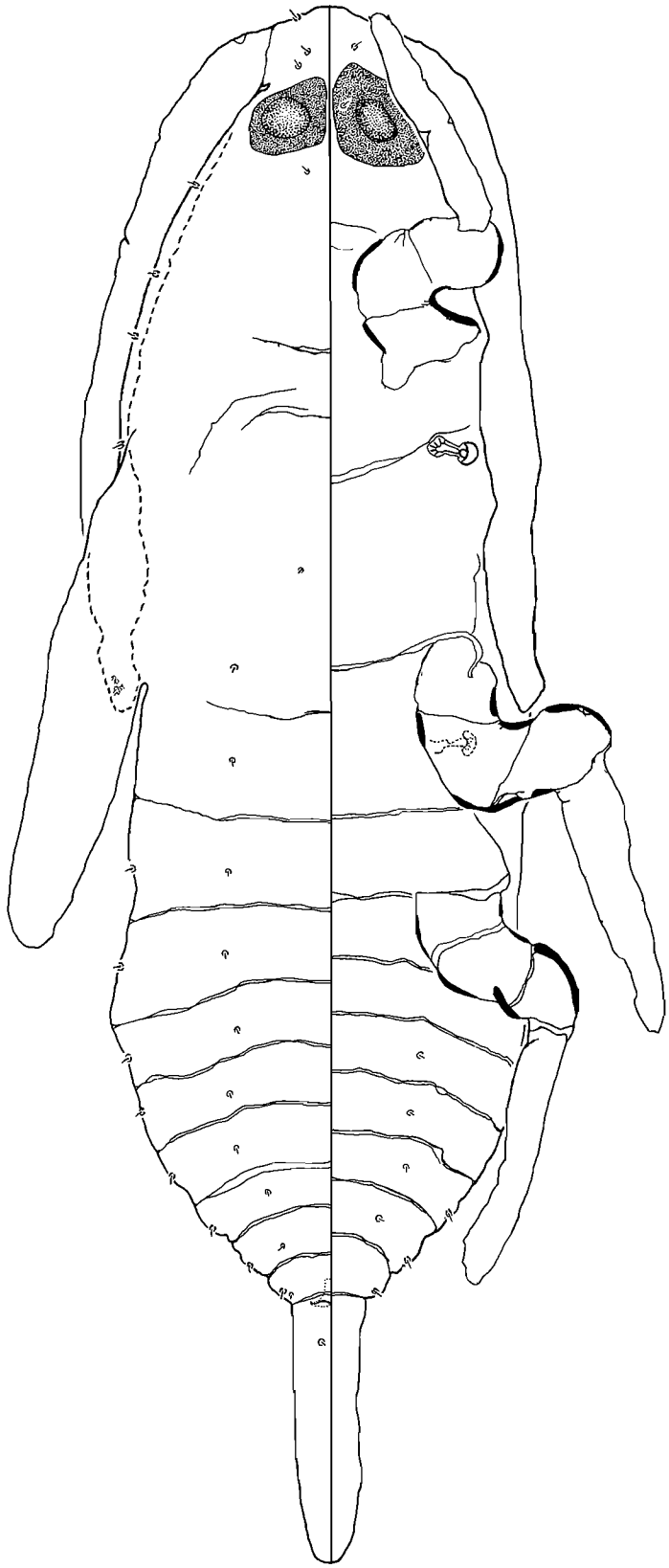

Figure 16. 4th instar (pupal) winged male of *C. nyssae*.

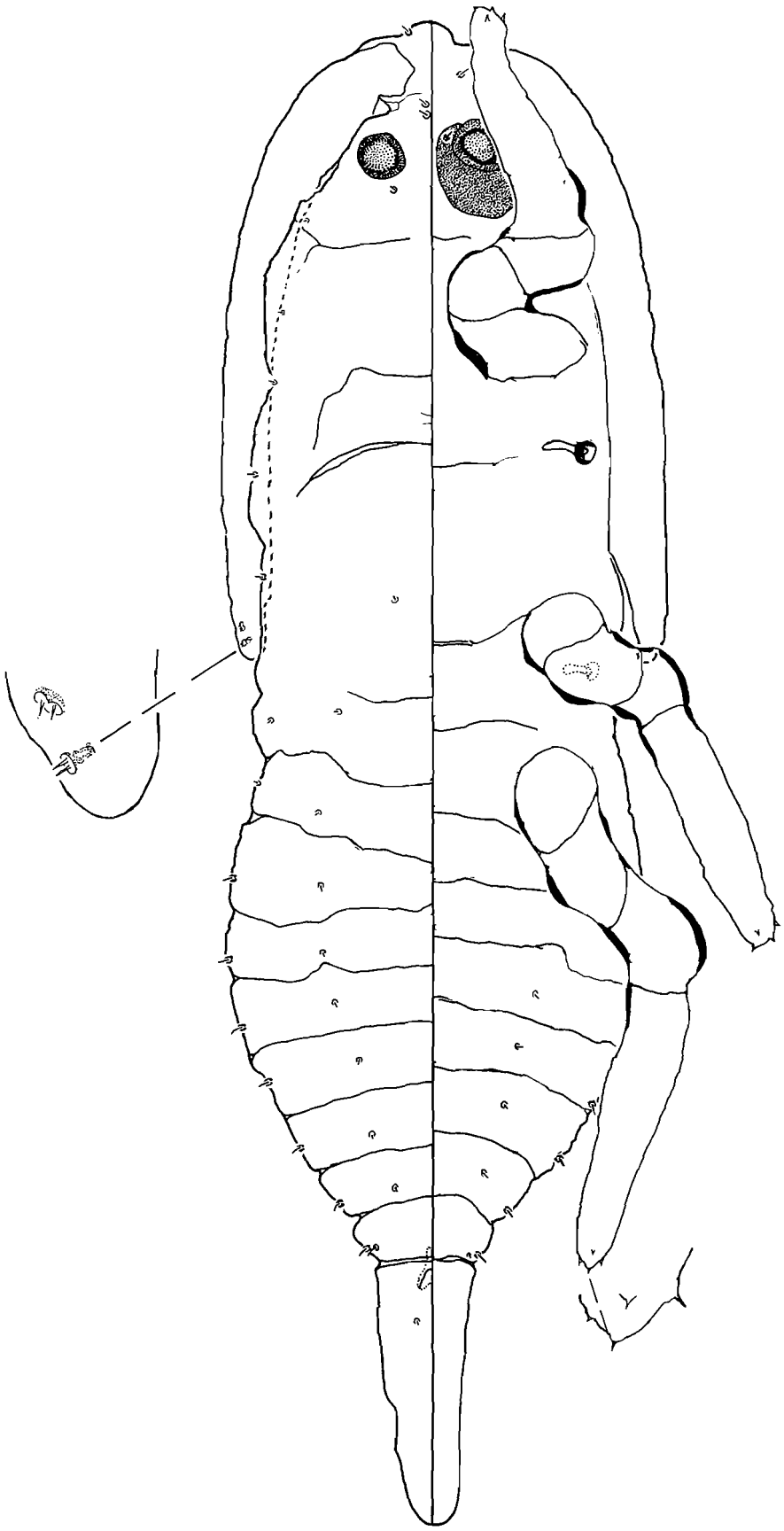

Figure 17. 4th instar (pupal) wingless male of *C. nyssae*.

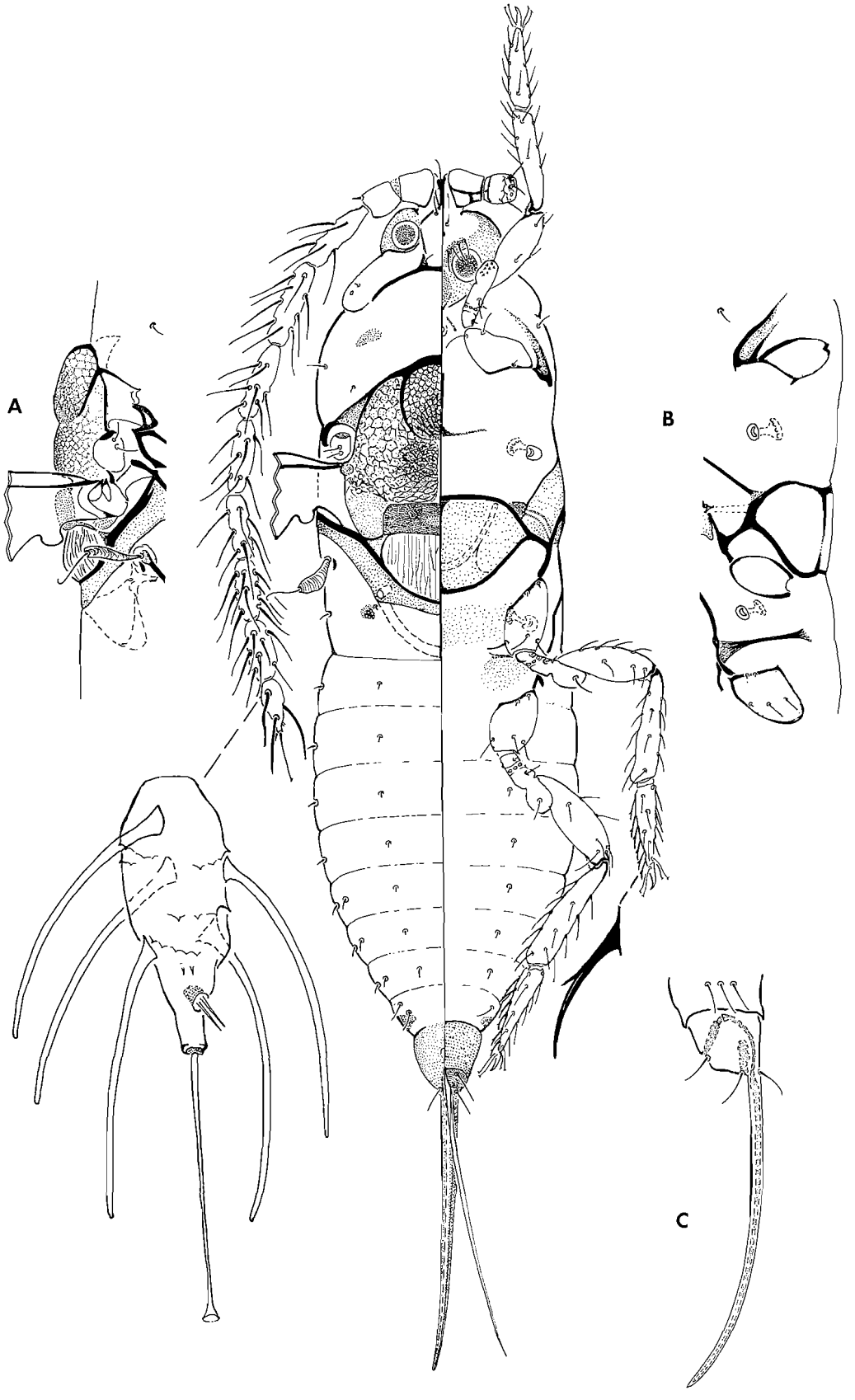

Figure 18. 5th instar (adult) winged male of *C. nyssae*.

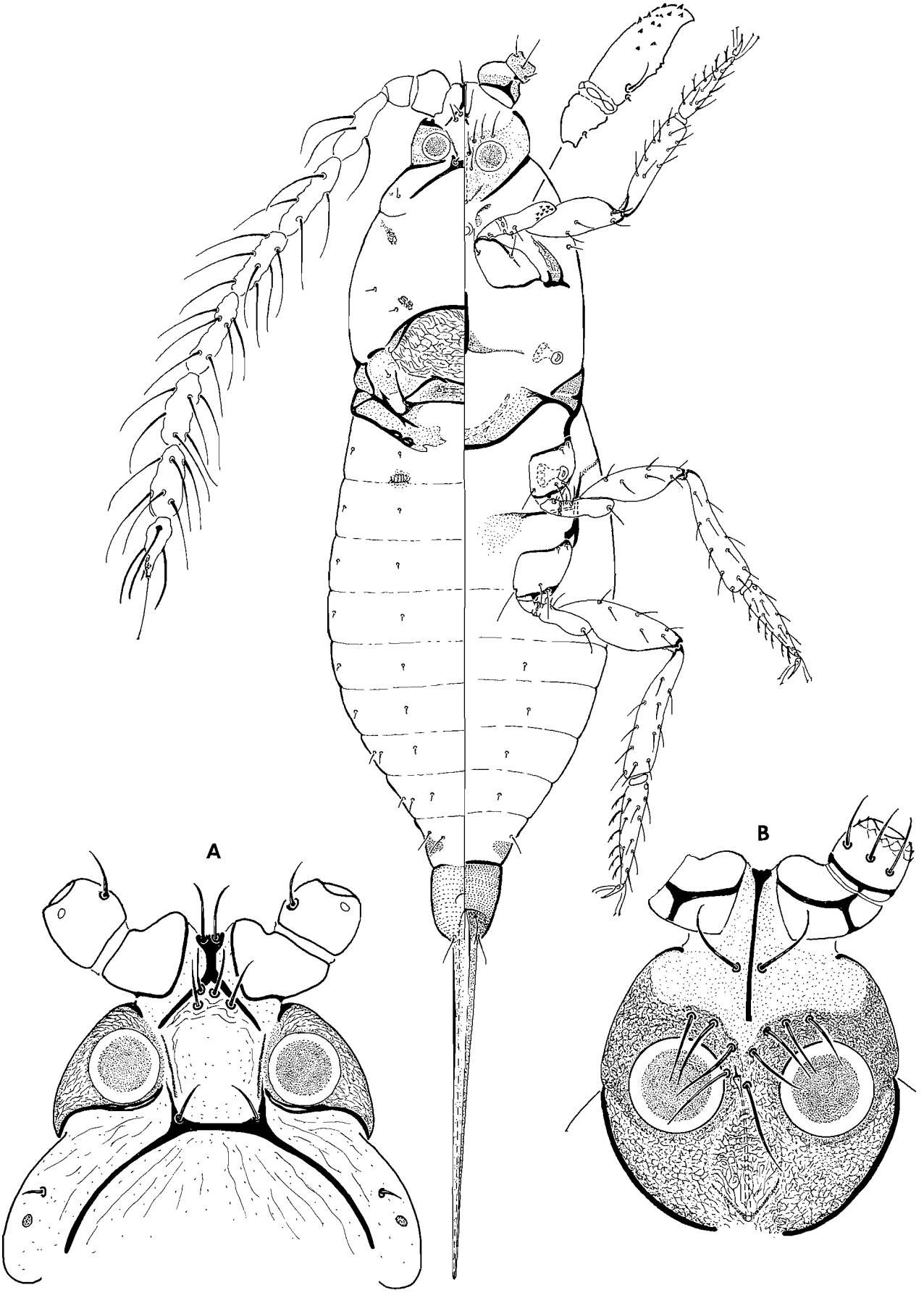

Figure 19. 5th instar (adult) wingless male of *C. nyssae*.