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Biological and Taxonomic Studies of *Signiphora borinquensis,* New Species, (Hymenoptera: Signiphoridae), a Primary Parasite of Diaspine Scales

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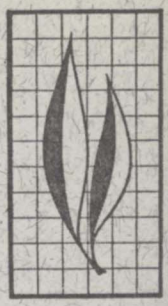

Synonymy of *Thysanus* and *Signiphora* is discussed as well as classification of species of *Signiphora.* A new species, *Signiphora borinquensis* Quezada, DeBach, and Rosen, is described and its morphology, biology, behavior, and ecology treated in detail. *Signiphora borinquensis* is a thelyotokous, primary endo-ectoparasite of certain diaspine scale insects. Size of parasites as well as size of hosts influence both total number and size of resulting progeny. Host-feeding is prerequisite to oviposition, and both occur within one hour after adult emergence. Over half of the total egg production occurs during the first three days. Honey (carbohydrate) and hosts (protein) are constantly necessary to insure optimum longevity and progeny production. High host specificity is indicated. Males are extremely rare and unnecessary for reproduction, but their incidence can be greatly increased by subjecting female pupae to 90°F for 48 hours. The resulting adult females tend to produce males. Ovisorption occurs under stress, but does not operate to maintain maximal progeny production. Effects of parasite density on longevity, progeny production, and on host survival are discussed.

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Biological and Taxonomic Studies of *Signiphora borinquensis,* New Species, (Hymenoptera: Signiphoridae), a Primary Parasite of Diaspine Scales[1]

I. INTRODUCTION

EXCEPT FOR THE INFORMATION given by Clausen (1924) and by DeBach, Kennett, and Pence (1958), little is known about the biology and habits of the members of the family Signiphoridae (Thysanidae). Though previously commonly regarded as being hyperparasitic in their habits, certain species of *Signiphora* have been found to be primary parasites of diaspine scale insects (DeBach, Kennett, and Pence, 1958), and it is likely that further studies will enlarge the list. The purpose of this study was to add to and clarify the limited amount of information previously obtained about this small but interesting parasitic group, especially since no thorough investigation has been made of any species which is a primary parasite.

These studies were begun in September, 1965, with a colony of *Signiphora* sp., a newly imported primary parasite of diaspine scales which was being maintained in the insectary of the Department of Biological Control of the University of California, Riverside, for biological control studies.

II. MATERIALS AND METHODS

The species of *Signiphora* we were studying was soon determined to be an undescribed new species. It is described later herein as *S. borinquensis* Quezada, DeBach, and Rosen and had been reared at DeBach's request by T. W. Fisher in Guayama, Puerto Rico (June 3, 1965), from coconut scale, *Aspidiotus destructor* Signoret, on banana (*Musa* sp.). It was propagated in the insectary at Riverside on cactus scale, *Diaspis echinocacti* (Bouche), maintained on pads of two species of cactus, *Opuntia elata* and *O. ficus indica.*

Except for certain observations, specified in appropriate sections of this report, all the work was done under controlled insectary conditions where the temperature was maintained at 80 ± 2°F, and the relative humidity at 55 ± 5 per cent.

Culture of host material and parasites

The method of Argyriou (1965) was followed. A population of adult *Diaspis echinocacti* suitable for experimental studies is obtained in about 35 days after cactus pads are infested with the scale crawlers. The parasites reproduce

[1] Submitted for publication July 5, 1972.

very well on adult scales which are about to produce eggs.

A continuous culture of the parasites was maintained by starting one subculture every week. One-gallon battery jars were used as containers in which a medium-sized cactus pad infested with scales was placed. Honey streaks were applied on the inside of the jar to provide food for the adult parasites. This was done in all tests even if not specifically mentioned hereafter. The initial number of parasites used depended on the density of the scale population, but 100 per jar was average. After sufficient information on the life cycle of the parasite had been gathered during the initial phases of study, it was possible to obtain any desired stage (i.e., newly emerged females, different larval stages or pupae) at any given time.

Handling the parasites

To handle small numbers of insects, or transfer a single one from one small rearing cell into another, a fine camel's hair brush was used, the tip of which was slightly moistened. By gently touching the parasite's dorsum with the tip of the brush, it could be picked up and transferred without injury.

Newly emerged females were often needed for certain tests. They were obtained from appropriate cultures by lifting the scale covers with a dissecting needle and carefully removing the dark pupae, i.e., mature ones, and isolating them in one-fourth dram vials with a little honey as food for the adults as they emerged. Unemerged females which were still motionless under the scale cover or in the process of chewing their way out of it were similarly obtained and isolated. A camel's hair brush was used to transfer the pupae or adults.

Test cells

Several of the experiments and observations reported herein required the confinement of one or more parasites in small cells superimposed over the cactus scale materials and held in place by means of a sticky material, Tree Seal[2]. Two sizes of cells were used—a small one, 22 mm diameter and 13 mm high, and a larger type, 37 mm diameter and 13 mm high. When one or more parasites were transferred into either of the cells, the screen was partly lifted to allow enough room for the transfer and then pressed back into place in the Tree Seal, which is harmless to the parasites. The large cells were modified for certain experiments by cutting out the center of the plastic caps of the vials so that they could be used as lids to hold the covering screens. Figure 1[3] shows the different types of cells used.

Microtechniques and measurements

Dissections of adult females were done in order to isolate their ovaries for ovisorption studies. The specimens were dissected in saline solution, the sternum being held with a fine needle, while the ovipositor was pulled with very fine forceps. With some practice the whole reproductive system could be drawn out. The ovaries were stained with a drop of acetocarmine for one minute and then mounted in Hoyer's medium.

The procedure for studying the life history of *S. borinquensis* was as follows: a medium-sized cactus pad, infested with adult scales, was exposed to a suitable density of adult parasites for six hours in a battery jar. After oviposition the cactus pad was kept in the battery jar for the duration of the developmental time required by the parasite species. Beginning 24 hours after oviposition, ten host scales were dissected daily in order to follow closely the development of the parasites. Cer-

[2] Manufactured by Bishop Co., Whittier, California.

[3] Figures start on page 577.

tain microscopic observations were best made of material in saline solution on slide mounts. To differentiate between the larval stages, it was necessary to record the size and shape of the mandibles. This required special preparation. The larvae were boiled in a 10 per cent KOH solution for one minute and then mounted ventral side up in Hoyer's medium. The mandibles were clearly seen under a Zeiss phase contrast photomicroscope (10× ocular, 40× objective), and measured in microns by means of a 10× calibrated ocular micrometer. The number and duration of larval stages was accurately determined by careful daily measurements. Whenever possible, several measurements of specimens and structures were taken and an average figure obtained. A similar procedure was used to study the head structure of the mature larva. Cleared, slide-mounted adult specimens were studied under the same Zeiss photomicroscope. Dried adult specimens were studied under a Joelco SEM-II scanning electron microscope.

III. TAXONOMY: Signiphoridae (=Thysanidae)

Relatively little attention has been given to the taxonomy of this family. The names Signiphoridae and Thysanidae seem to be used interchangeably in the literature. The first family-group name applied to this group was Signiphorinae (then a subfamily of Encyrtidae), based on the genus *Signiphora* (Howard, 1894; Girault, 1913). The genus *Thysanus* was then included in the Eulophidae, subfamily Aphelininae (see Ashmead, 1904).

Subsequently, *Signiphora* was considered to be a synonym of *Thysanus;* hence, the family name Thysanidae was adopted by some authors. Such a change would not be made today (see Article 40, International Code of Zoological Nomenclature) even if the synonymy were retained. However, *Signiphora* is now considered to be a valid genus, distinct from *Thysanus.*

Had the name Thysanidae become, in the meanwhile, generally accepted, according to the Code it should be retained in the interests of stability. We do not consider such to be the case, but if agreement among workers cannot be reached, the case should be referred to the International Commission on Zoological Nomenclature. We favor the name Signiphoridae because it has precedence and should not have been changed in the first place.

Mercet (1916, 1917) and Kerrich (1954) established certain genera in the family. Nikol'skaya (1952) made a significant contribution by establishing better criteria for the separation of the genera. Recently, Rozanov (1965) has given more detailed information on the family, separating the genera with additional characters. In relation to the species we have been studying, the separation of the genera *Thysanus* Walker and *Signiphora* Ashmead is particularly important, since there are good reasons to refer our species and several related ones to the genus *Signiphora* rather than to *Thysanus,* as has been done in the past.

The genus *Thysanus* was established by Walker (1840), who used *Thysanus ater* as the type species. Later, Ashmead (1880) established the new genus *Signiphora* with *S. flavopalliatus* (subsequently amended to *flavopalliata*) as the type species. Kerrich (1954) gives a good account of how other workers interpreted the problem. According to him, Howard (1894) and Ashmead (1900) placed *Signiphora* in a subfamily of its own (Signiphorinae) in the Encyrtidae. Mercet (1917) and Silvestri (1918) independently brought together *Signiphora* Ashmead and *Thysanus* Walker, a genus that until then had been placed with the Aphelinidae. Mer-

cet treated them as separate genera within a single tribe (Signiphorini). Silvestri considered that some *Signiphora* species should be placed in *Thysanus;* for example, all the species placed by Girault (1913) in the group of *Signiphora nigra* Ashmead. Other authors considered these genera to be synonymous (see, for instance, Peck, 1963).

The separation of the genera by Mercet (1917) is followed, with additional details, in the works of Nikol'skaya (1952) and Rozanov (1965). Rozanov suggested dividing the family into five genera: *Thysanus* Walker, *Signiphora* Ashmead. *Chartocerus* Motschulsky, *Clytina* Erdos, and *Kerrichiella* Rozanov. The key characters given by the Russian workers, especially Rozanov, place our Puerto Rican species in the genus *Signiphora.*

Although most earlier authors classified the signiphorids as a subfamily of the Encyrtidae, Domenichini (1954), in a detailed study of comparative morphology, has shown that the Signiphoridae are in some respects more closely related to the Aphelinidae. We agree with that conclusion. However, Domenichini used the genus *Prospaltella* Ashmead as a representative aphelinid for his comparisons. The affinities between the Signiphoridae and Aphelinidae become all the more apparent if comparisons are made with the aphelinid genus *Aphytis* Howard. The peculiar antennae, with reduced funicular segments and a long, undivided club; the structure of the metanotum, with two oblique sutures on the sides and a small anteromedian apodeme; the relatively long propodeum, with a cut-off, triangular median salient (see description of *S. borinquensis* in the following pages)—all these typical characters of the Signiphoridae have similar counterparts in *Aphytis.* In our view, the Signiphoridae are more closely related to the Aphelinidae than to any other family in the Chalcidoidea.

The main differences separating the genus *Signiphora* from *Thysanus* are summarized here:

Genus *Signiphora* Ashmead	**Genus *Thysanus* Walker**
Body compact, somewhat flattened	Body slender, elongated, thorax convex
Occipital margin acute, concave	Occipital margin rounded, straight
Mandibles bidentate (fig. 2A)	Mandibles tridentate (fig. 2B)
Antennal club twice as long as scape or less, with only a few sensilla in both male and female (fig. 3A)	Antennal club 3 or 4 times as long as scape, with as many as 30 sensilla in the male, much fewer in the female (fig. 3B)
Funicle 3-segmented (fig. 4A)	Funicle 4-segmented (fig. 4B)
Pronotum transverse, considerably shorter than the mesoscutum	Pronotum elongated, about as long as the mesoscutum or longer
Propodeal triangle with a V-shaped process (fig. 5A)	Propodeal triangle without a process (fig. 5B)
Phallobase of male genitalia without a process (fig. 6A)	Phallobase of male genitalia with a slender process (fig. 6B)
Host records: primary or secondary parasites of coccids and aleyrodids	Host records: Primary parasites of dipterous pupae or secondary parasites

Girault (1913) separated the species of *Signiphora* into six groups, mostly on the basis of their coloration and the pattern of distribution of dark and clear areas on the body. The Puerto Rican species, *S. borinquensis,* with its pre-

dominantly yellow color, fits in the *aleyrodis* group of Girault. However, since coloration may be subject to some variation, this species may also fit in his closely related *flavopalliata* group. *Signiphora borinquensis* was therefore compared directly with the types of all the species of these two groups preserved in the U. S. National Museum. Those loaned to us for study were: *aleyrodis* Ashmead, *aspidioti* Ashmead, *basilica* Girault, *coquilletti* Ashmead, *fax* Girault, *flava* Girault, *flavella* Girault, *flavopalliata* Ashmead, *louisianae* (Dozier), *lutea* Rust, *mexicana* Ashmead, *thoreauini* Girault, and *townsendi* Ashmead. One of these species, *S. mexicana,* was found to be morphologically much more closely related to Girault's *rhizococci* group than to the *flavopalliata* group in which Girault originally placed it. *Signiphora rhizococci* Ashmead was therefore also included in this study.

Very little is known about the range of variation of morphological characters in these species, and some of them may eventually prove to be synonyms of one species or another. Also, most of the types are only partially or not at all cleared, and important characters sometimes cannot be seen. Nevertheless, *S. borinquensis* was found to be distinctly different from all these species and is therefore described below as a new species. The validity of this species was kindly confirmed by Dr. Barnard D. Burks of the U. S. National Museum.

The following key, based on a study of the types, may help in the identification of *borinquensis* and related species of *Signiphora.*

KEY TO THE SPECIES OF THE *RHIZOCOCCI, FLAVOPALLIATA* AND *ALEYRODIS* GROUPS OF *SIGNIPHORA* FEMALES[4]

1. Forewing broad, bearing a discal bristle, marginal fringe shorter than width of disc, submarginal vein bearing two setae; hind wing broad, not parallel-margined, bearing a discal bristle; lobes of second abdominal tergite[5] not pronounced (fig. 7); largely dark brown 2

   Forewing narrower, marginal fringe longer than width of disc, submarginal vein bearing a single seta; hindwing narrow, parallel-margined, without a discal bristle; second abdominal tergite with pronounced lobes (fig. 5A) 3

2(1). Hindwing widest at apex of venation, tapering somewhat distad; posterior margin of mesoscutum, scutellum, and metanotum white; entire abdomen, including the propodeal triangle, dark brown *rhizococci* Ashmead

   Hindwing widening considerably distad of venation; posterior margin of mesoscutum, scutellum, metanotum, and most of propodeal triangle dusky orange yellow; rest of abdomen dark brown *mexicana* Ashmead

3(1). Forewing bearing a discal bristle (fig. 8) 4

   Forewing without a discal bristle 5

4(3). Abdomen brown, propodeum mostly yellow, posterior tergites sufused with yellowish on sides; midtibial spur about as long as the corresponding basitarsus; ovipositor sheaths relatively long, about

[4] *Signiphora louisianae* (Dozier) was described from males only and is not included in this key. It differs markedly from the uniparental *borinquensis* in being much more extensively infuscated and in having a relatively longer midtibial spur, about nine-tenths length of the corresponding basitarsus.

[5] Propodeum counted as first abdominal tergite.

three-fifths the length of the midtibia ..... *flavopalliata* Ashmead

Abdomen uniformly dark brown, including the propodeum except triangle which is yellow; midtibial spur distinctly shorter than the corresponding basitarsus (0.75–0.85); ovipositor sheaths relatively short, about two-fifths the length of midtibia ..... *fax* Girault

5(3). Mesoscutum transversely striated; at least some gastral tergites yellow 6

Mesoscutum transversely reticulated; gaster entirely brown; abdominal tergites II–V dark brown, posterior tergites paler brown *townsendi* Ashmead

6(5). Thorax and abdomen yellow, without any dark brown areas except ovipositor sheaths 7

At least pronotum centrally, mesoscutum anteriorly, and cross-band at base of gaster dark brown 8

7(6). Abdomen entirely yellow; antennal pedicel slender, about 4¾ times as long as wide (fig. 9) ..... *flava* Girault

Basal half of gaster faintly suffused with brownish; antennal pedicel about two to 2¾ times as long as wide ..... *flavella* Girault

8(6). Seventh abdominal tergite with distinct dark brown blotches on sides, sometimes with a complete cross-band 9

Seventh abdominal tergite yellow or faintly suffused with fuscous, without distinct blotches 10

9(8). Band at base of abdomen short, covering the posterior parts of second and third tergites and the entire fourth tergite, not extending into fifth tergite, with straight anterior and posterior margins; blotches on sides of seventh tergite large, roughly rounded, widely separated by yellow centrally; midtibial spur relatively long, about nine-tenths the length of the corresponding basitarsus (fig. 10); ovipositor sheaths about one-half length of midtibia ..... *basilica* Girault

Band at base of abdomen longer, covering the posterior parts of second and third tergites, the entire fourth tergite, and the anterior part of fifth tergite, with convex anterior and posterior margins; blotches on sides of seventh tergite transverse, usually connected by a faintly fuscous cross-band; midtibial spur relatively short, about three-fourths the length of the corresponding basitarsus (fig. 28); ovipositor sheaths about two-fifths the length of midtibia *borinquensis*, n. sp.

10(8). Antennal club pale on proximal half, distinctly dark-brown on distal half (fig. 11) 11

Antennal club pale or uniformly dusky (fig. 3A) 12

11(10). Band at base of abdomen extensive, almost black on sides, apparently covering second and third tergites except on sides, the entire fourth and fifth tergites, and the anterior part of sixth tergite; midtibial spur about four-fifths the length of the corresponding basitarsus *aspidioti* Ashmead

Band at base of abdomen less extensive, fading or suffused with yellowish on sides, sometimes just a central brown blotch, at most covering the posterior parts of second and third tergites and the entire fourth and fifth tergites; midtibial spur about as long as the corresponding basitarsus (fig. 12) ..... *lutea* Rust

12(10). Antennal club faintly dusky or yellowish 13
Antennal pedicel, funicle and club uniformly dark brown; seventh abdominal tergite faintly suffused with fuscous on sides; midtibial spur about as long as the corresponding basitarsus; ovipositor sheaths nearly one-half the length of midtibia ..... *thoreauini* Girault

13(12). General color orange yellow; anterior half of mesoscutum dark brown; band at base of abdomen covering the posterior parts of second and third tergites and the entire fourth and fifth tergites; seventh abdominal tergite faintly suffused with fuscous centrally; antennal club faintly dusky; midtibial spur about three-fourths to four-fifths the length of the corresponding basitarsus; ovipositor sheaths a little over half length of midtibia ..... *coquilletti* Ashmead
General color pale lemon yellow; a little more than anterior third of mesoscutum dark brown; band at base of abdomen shorter, covering the posterior part of third tergite, the entire fourth tergite, and the anterior part of fifth tergite; seventh abdominal tergite yellow; antennal club yellowish; midtibial spur about nine-tenths the length of the corresponding basitarsus (fig. 13); ovipositor sheaths a little over half the length of midtibia ..... *aleyrodis* Ashmead

Signiphora borinquensis,[6] NEW SPECIES
(Figures 2A–6A, 14–32)

Distinguishing characters: Crossband at base of abdomen with convex anterior and posterior margins, covering the posterior parts of second and third tergites, the entire fourth tergite, and the anterior part of fifth tergite; second band on seventh tergite; antennal club uniformly dusky; pedicel 2¼ to nearly three times as long as wide; mesoscutum transversely striated; midtibial spur short, about three-fourths the length of the corresponding basitarsus; ovipositor sheaths about two-fifths the length of midtibia; forewing without discal bristle.

Female: Length 0.30–0.85 mm. Form robust, integument polished. General coloration lemon-yellow with dark brown markings; eyes and ocelli dark red. Face and cheeks suffused with fuscous, clypeus black, back of head blackish; mandibles brown, the apical teeth black (fig. 2A). Central part of pronotum dark brown; three black spots on tum and anterior one-third of mesoscuthe axillary sclerites on each side of thorax; tegulae fuscous distally. A dark-brown, roughly oval, tranverse band across base of abdomen, covering the posterior parts of second and third tergites, the entire fourth tergite, and the anterior part of fifth tergite, with both the anterior and posterior margins convex; seventh tergite with a transverse dark-brown blotch on each side, connected by a transverse, faintly fuscous band; ninth and tenth tergites, ovipositor sheaths, and posterior parts of outer ovipositor plates, dark-brown; a pair of black spots at base of ovipositor; margin of endophragma posteriorly blackish. Venter of body pale yellow, except for a pair of brown spots on mesopleura. Antennal scape pale yellow, pedicel and funicle faintly dusky, club wholly dusky (fig. 3A). Legs entirely yellow, apical tarsal segment faintly dusky. Forewing (fig. 29) hyaline, with a conspicuous dusky band across the middle, below marginal and stigmal vein; proximal margin of band concave posteriorly; under phase contrast the distal part of the band appears to be composed of separate spots. Hindwing hyaline, marginal vein dusky.

Head lentiform (fig. 14, 17) about as

[6] *Borinquen* is the vernacular name of Puerto Rico.

wide as the thorax; occipital margin acute, concave; occipital foramen close to occipital margin. Eyes (figs. 14, 15) rather small, their longitudinal diameter about as long as the cheek, nearly glabrous, bearing a few minute setae between facets. Frontovertex (fig. 17) wide, transversely striated; ocelli in an obtuse triangle, the posterior pair about their own diameter from eye margin, about two diameters from occipital margin. Mandibles (fig. 2A) bidentate; maxillary palpi two-segmented, labial palpi one-segmented. Antennae (figs. 3A, 4A, 16) six-segmented (1,1,3,1), inserted near oral margin. Scape reaching to about middle of eye, rather thick, 3½ to 4½ times as long as wide. Pedicel obconical in lateral view, pyriform in dorso-ventral view, 2¼ to nearly three times as long as wide, about two-thirds the length of scape and at apex about as wide as the scape. Funicle (figs. 4A, 16) somewhat less than half the length of pedicel, the three segments increasing slightly in width from first to third, the third being about two-thirds the width of pedicel; first funicular segment very small, symmetrical, 2¼ to 2¾ times as wide as long; second segment trapezoidal, ventral margin the longest, considerably longer than the first segment, about 1½ times as wide as long, bearing a short seta; third segment somewhat trapezoidal, distinctly longer than the second, usually less than 1⅖ times as wide as long, twice to nearly three times longer than the first segment. Club long, four to six times as long as wide (usually over five times), 1½ to 1¾ times longer than the scape and about 2⅓ to 2⅔ times longer than the pedicel, as long as or somewhat shorter than the scape and pedicel combined; club bearing five to eight longitudinal sensilla, each being about one-third the length of club.

Thorax robust, transversely striated. Pronotum (figs. 17, 18) short, overlapping the anterior part of mesoscutum, bearing a transverse row of fine setae along posterior margin and one spiracle more or less concealed near each lateral corner; when flattened in slide-mounted specimens, the pronotum is about 4½ times as wide as long, about half the length of mesoscutum. Mesoscutum (fig. 18) about twice as wide as long, bearing a pair of fine, sublateral setae; no indication of parapsidal sutures. Scutellum (figs. 18, 19) short, transverse, 4¾ to 5½ times as wide as long, about one-third the length of mesoscutum, bearing a transverse row of four fine setae along posterior margin, usually with a pair of submedian circular sensilla anterad of the setae. Axillae small, triangular, bearing a single seta at the posterior corner, extending antero-laterad of the scutellum and separated from the latter by internal ridges which can be readily seen in cleared specimens (fig. 20) but are not evident on the dorsal surface (figs. 18, 19). Metanotum (figs. 18, 19, 21) short, transverse, about three-fifths the median length of scutellum, bearing a minute antero-median apodeme, which apparently fits beneath posterior margin of scutellum; a triangular, nearly smooth lobe is cut off by an oblique suture on each side of metanotum. Prepectus undivided; between it and the prosternum, beneath the fore coxae, is a broad, transverse membrane bearing numerous minute, stout spines (fig. 22).

Propodeum long, (figs. 5A, 19) bearing a large spiracle at each antero-lateral corner, and a conspicuous central triangular area, pointing caudad, about 1¼ to 1⅓ times as wide as long. The suture delimiting this area on the propodeum is trapezoidal, and runs inside the margin of the triangle, leaving an overhanging, V-shaped ledge or process (fig. 5A). The suture, which can be seen only in cleared specimens, is in direct continuation of the oblique sutures on the sides of the metanotum. The V-shaped process overlaps the posterior margin of the propodeum and the short

median section of the second abdominal segment. The posterior margin of the propodeum, i.e., the line separating it from the second abdominal tergite, is a very fine, arched suture that can hardly be detected in cleared specimens (fig. 5A) but is readily visible under the scanning electron microscope (fig. 19); it runs under the V-shaped process of the propodeal triangle. Triangle included, the propodeum is nearly as long as the mesoscutum, 2⅔ to three times longer than the scutellum, and about 4½ to five times longer than the metanotum. Propodeal triangle transversely reticulate-striated, other parts of propodeum smooth except for some slight transverse striation mesade of spiracles.

Gaster (fig. 23) sessile. Second abdominal tergite (figs. 5A, 19, 23) smooth, composed of two conspicuous, sublateral, rounded lobes, connected by a short, transverse median section that is overlapped by the V-shaped process of the propodeal triangle. Third tergite the longest, extending anteriorly lateral of the lobes of second tergite and reaching the posterior margin of the propodeum, reticulated on the sides and, more strongly, just lateral of the lobes of second tergite, with some transverse striation between the lobes. Tergites III–VII subequal in length, VIII shorter. Fourth tergite reticulated on sides, smooth with faint transverse striation centrally; fifth tergite reticulated on sides, transversely striated posteriorly across center; tergites VI–VIII reticulated across, fading anteriorly. Tergites III–VII bearing one to several setae in a short transverse row on each side, and a circular sensillum anterad of the setae. Eighth tergite bearing five to eight setae in a transverse row between the spiracles, and four circular sensilla in a transverse row anterad of the setae. Ninth abdominal tergite (fig. 24) is composed of a short, transverse, smooth plate, bearing a pair of circular sensilla, and two small side plates projecting backwards on both sides of tenth tergite; the latter is small, triangular, bearing five to six setae in a transverse row. Pygostyles small, embedded in the membrane on each side of the base of tenth tergite (i.e., between the tenth and the surrounding ninth tergite), each bearing two long setae and one short seta. Sternites of first and second abdominal segments not discernible as distinct sclerites, those of segments III–VII exposed in unmodified form on ventral surface of gaster. Third sternite bearing no setae, fourth sometimes with one seta, fifth and sixth with two to five setae in a transverse row; seventh sternite with two submedian groups of four setae each, and a small, median triangular projection near posterior margin (fig. 25). Outer ovipositor plates about five times as long as wide, bearing four setae along inner margin on the exposed posterior part. Ovipositor slightly extruded, its base at base of fifth tergite, about 1¾ times to nearly twice as long as midtibia. Ovipositor sheaths rather stout, about two-fifths length of midtibia (0.39–0.41), each bearing two fine setae near apex. Endophragma distinctly longer than wide, rounded, extending from the axillar region to about the base of ovipositor.

Legs strong, rather long, all tarsi five-segmented. Foreleg with a well-developed strigil (fig. 26). Trochanter of middle leg (fig. 27) long, curved; midfemur thick, about three times as long as wide, bearing a long, stout ventral spine near apex and two rows of short bristles along dorsal margin. Midtibia longer than the femur, about 4½ to 5½ times as long as wide, bearing several short bristles, and four strong dorsal spines: one short and one long spine at base, one long spine a short distance from base, and one long spine about the same distance from apex. Midtibial spur (fig. 28) a little longer than the subapical spine, about two-fifths the length of midtibia, about three-fourths the length

of the corresponding basitarsus (0.71–0.77), bearing four to six lobes in two rows on posterior aspect (i.e., facing the basitarsus): a main row of three to four long lobes, attached obliquely (i.e., not in comb-like fashion), and another row of one to two lobes of about same size, as well as several smaller, appressed lobes on anterior and lateral aspects. Hind tibia long, rather slender, about 1½ times as long as midtibia, bearing a short, stout apical bristle.

Forewing (figs. 29–31) 3¼ to 3⅓ times as long as wide; marginal fringe long, with 26–43 setae, the longest ones about 1⅓ to 1½ times width of disc (up to 1¾ times in smallest specimens). No dorsal discal bristle or setae; a single ventral seta in proximal one-fourth of costal cell, one minute ventral seta below submarginal vein, three to five minute ventral setae below junction of submarginal and marginal vein (fig. 30). Costal cell long, triangular, tapering toward apex. Submarginal vein long, slender, distinctly longer than the thick marginal vein into which it gradually merges, bearing one seta on proximal one-third and nine to 14 bullae along posterior margin. Marginal vein bearing three to four coarse setae along anterior margin, the distal one considerably longer than the rest, two along posterior margin; when measured along anterior margin of wing, the marginal vein is about 1½ times longer than the stigmal vein. Postmarginal vein absent. Stigmal vein (fig. 31) broad at base, without a distinct stalk, narrowing toward apex, curved, the posterior margin parallel to anterior margin of wing; two small papillae (circular sensilla ?) at apex of stigmal vein, with a larger one, about three times their diameter, adjacent to them proximad; a coarse seta near apex of vein. An oblique crease crosses the wing at the dusky band, from stigmal vein to posterior margin of wing.

Hindwing (fig. 32) narrow, parallel margined, slightly longer than the forewing, about 7½ to 8½ times as long as wide; marginal fringe nearly as long as that of forewing, with 28–49 setae, the longest ones about 3 to 3½ times width of disc (up to 3⅔ times in smallest specimens). Vein with a thick proximal part, a short slender portion bearing 9–13 bullae along posterior margin, and a long, thick distal part, about 2½ times longer than the slender portion, bearing a fine seta on anterior margin proximally, another on posterior margin distally; vein reaches margin of wing only at apex, bearing two hooks and one straight bristle. No discal setae, except a single, minute dorsal seta below slender portion of vein.

Male: Essentially similar to the female in structure, chaetotaxis, sculpture, and coloration. The two black spots at base of ovipositor obviously are absent in the male, and the dark brown spots on sides of seventh abdominal tergite are somewhat larger than in the female. Antenna as in the female. Genitalia (fig. 6A) about 100 microns long, and about 35 microns at maximum width of phallobase. Digiti with a strong curved apical spur. The phallobase, although narrow at its rounded proximal end, lacks a distinct process.

Habitat and hosts. Reared by T. W. Fisher from *Aspidiotus destructor* on banana (*Musa* sp.) in Guayama, Puerto Rico, June 3, 1965, and imported into Riverside, California (UCR, Division of Biological Control accession number R65-55). Colonies were maintained at the Riverside insectary, using *Diaspis echinocacti* grown on cactus plants (*Opuntia elata* and *O. ficus indica*). Described from numerous insectary-reared specimens.

Types. Holotype ♀ and paratypes deposited in collection of Division of Biological Control, University of California, Riverside. Paratypes deposited in U. S. National Museum and British Museum (Natural History).

Notes. *Signiphora borinquensis* can be rather easily separated from most related species by the characters presented in the key. It appears to be most closely related to *S. thoreauini* Girault and *S. basilica* Girault. It can be separated from *thoreauini* by the presence of distinct infuscation on seventh abdominal tergite, by the shorter midtibial spur, and by the somewhat shorter ovipositor sheaths. *Signiphora basilica* was described from a small specimen, about 0.45 mm long. Specimens of *borinquensis* of comparable size tend to be even more extensively infuscated than large specimens, considerably more so than *basilica*. The shape of the abdominal band, and the relatively shorter midtibial spur and ovipositor sheaths are considered valid differences between *borinquensis* and *basilica*. It is noteworthy that the host from which *basilica* was reared [latania scale, *Hemiberlesia lataniae* (Signoret)], is not suitable for development of *borinquensis*, as shown by our host preference experiments, which is another indication that these represent two different species.

IV. GENERAL BIOLOGY

Signiphora borinquensis is a thelyotokus species in which the presence of males is extremely rare. Microscopic examination of 500 adults collected at random from seven laboratory cultures revealed no males. However, on rare occasions males were found in cultures. Male production of any consequence has only been attained by means of high temperature treatment of pupae (see "Male Production," p. 568). Under favorable conditions the female lays an average of 25 eggs internally in the host. The adult parasites apparently have the ability to discriminate between parasitized and unparasitized scales, since they normally do not attempt oviposition in hosts already parasitized. Development is usually solitary, but occasionally two, or even more, individuals may develop on one host. The larva of *S. borinquensis*, after starting development as an endoparasite, migrates out of the body of the host scale and takes an external feeding position, becoming a typical ectoparasite. This habit was first reported by DeBach *et al.* (1958) for *Signiphora merceti* (then recorded as a *Thysanus*), and may represent, according to their view, "a link between the ecto- and endoparasitic habit." In the present study, the first and second instar larvae were found to be endoparasitic and the last two instars ectoparasitic. A great proportion of the host body content is consumed by the externally feeding larva. This endo-ectoparasitic type of development apparently is unique within the Hymenoptera. In addition to signiphorids, it is known to occur in certain specialized aphelinid parasite species such as *Encarsia pergandiella* Howard (Gerling, 1966), whose males develop as hyperparasites in the female pupae of their own species, and have the endo-ectoparasitic habit. External feeding is common in certain endoparasitic Braconidae (see Clausen, 1924, p. 34).

The average duration of the life cycle of *S. borinquensis* at 80°F) is 25 days. The first instar larva hatches by rupturing the egg chorion with its mandibles. Though it may float freely in the host's body fluids, it is usually found among the eggs in the ovary of the host. The host does not show any visible reaction to the larva. The first instar larva has been observed feeding on the host's ovarian eggs (figure 33). In doing so, it anchors itself to an egg by the posterior end and by contracting movements it draws its head against the same egg, vigorously rasping the membrane with its mandibles. Some of the egg material becomes visible in the gut, which

shows rhythmic movements. According to Argyriou (1965), the average number of eggs in normal cactus scale is 113. Just how many eggs a first instar larva eats was not determined directly, but dissections indicated that an average of 87 eggs were consumed per larva.

By the time the first larval instar molts into the second, the scale contents turn milky white. The host integument is at first pale-green and the parasite larva is visible inside. Then the host integument turns light brown, which becomes darker by the end of the parasite's second larval instar. The second stage larva displays activity similar to the preceding instar; though none was observed feeding on scale eggs, they may possibly do so. Their mandibles are in constant motion and the foregut shows rhythmic pulsations that may indicate the swallowing of host fluids.

The third instar larva soon starts working its way out of the scale body. It always does this at the lateral margin of the scale body, apparently using its mandibles in combination with muscular contractions to rupture the host's cuticle. Once the head is out, it is directed along the edge of the scale body toward the posterior end. At this point in the process the body of the host is still turgid and its integument has become more opaque and has a light purple color. The larva does not interrupt feeding while getting out of the host, to which it remains attached. The salivary glands, difficult to see in previous instars, are clearly seen when dissecting this instar as well as the mature larva. Their enlargement may be a response to the intense feeding that takes place in the ectoparasitic stages.

The fourth larval stage, or mature larva, consumes the remainder of the host contents completely in about two days, after which it casts the first meconia. The meconia will be completely voided on the third day. After this, the larva turns its body so that its ventral side faces the scale cover. It remains quiescent and enters the prepupal stage. In about 24 hours the pupa is formed.

The gradual changes in the color of the pupa will be described later (see Morphology and Development of Immature Stages, p. 556. The pupal stage requires seven days, after which the adult begins to emerge. The adult spends about 24 hours under the scale cover. During this period, it shows occasional stretching movements of the legs, movements that become more frequent as time passes. When the insect is ready to emerge from under the scale covering, it uses its mandible for about 20 minutes to cut a round opening in the scale cover. If the scale cover happens to be loose from the plant host at any point, the parasite may crawl out under the edge instead. Newly emerged females have been seen to defecate about four times after emerging. They do this while walking and dragging the abdomen, leaving a fine strip of whitish material behind them up to 1 mm long. This defecation probably represents the excretory materials accumulated during the intense metabolic activity of the pupal stage.

Signiphora borinquensis females will start ovipositing about 45 minutes after emerging from the host. Though they have a complement of mature eggs (six to eight) that can be laid immediately, they almost invariably feed on the host before laying the first egg. The process of host feeding is described in detail later (p. 559). The female normally lives about 25 days at 80°F and will lay eggs almost throughout her adult life span. However, about 75 per cent of her eggs will be laid during the first eight days.

Morphological and Biological Variation

A great deal of variation in size has been observed to occur among *S. borinquensis* individuals cultured in the laboratory. They range in length from tiny individuals (0.30 mm) to relatively large ones over twice as large (0.85 mm). Since this species is uniparental (the rare males presumably not contributing to gene flow), the insects in a laboratory culture are presumably very similar in their genetic makeup. Hence, morphological variation probably largely results from phenotypic response to different environmental situations. One of the causes of variation in size could be the size of the host, since this will determine the amount of food available for the developing parasite.

Experiments were conducted to see what effect host size might have on the size of the parasites. Two medium-sized cactus pads infested with cactus scales were used. One had a uniform population of large scales (av. 1.90 mm diameter), the other a population of smaller scales (av. 0.865 mm diameter). Three pairs of small plastic cells (see Materials and Methods), with honey streaks included for food, were attached to each cactus pad. Adult parasites of three sizes were obtained from a culture in which they were just emerging. Their sizes were designated as "small" (about 0.30 mm long), "medium" (about 0.55 mm long), and "large" about 0.75 mm long). Two parasites of each size category were confined in each of two cells, one with large hosts and one with small hosts. Parasites in all cells were observed feeding and ovipositing. Each combination was duplicated with the following results.

Emergence of offspring occurred first in the "medium" parasite and "large" parasite cells after 22 days, while progeny of "small" parental parasites appeared three days later regardless of host size. The eggs of small parasites have been observed to be smaller than those of large parasites. Measurements showed that all three sizes of parental parasites, whether ovipositing in large or small scale hosts, produced offspring that again displayed the size differences of the parents, though not in exact proportion. The progeny production per female of small parasites was definitely low, regardless of the host size. Small parasites may find difficulties in piercing the scale covers with their ovipositors. It is also known that small parasites tend to have a lower fecundity than large ones (Salt, 1941).

The larger the host, the larger was the average size of the parasites. Small hosts will obviously limit the maximum size of the resulting parasite progeny. There is also the possibility of intrinsic factors that may affect the size of progeny. It was noticed that small individuals are more likely to be found in old *S. borinquensis* cultures. This may be due to a decrease in the size of the eggs as a result of fewer hosts being available for host-feeding. Since this parasite usually host-feeds as soon as it emerges, and before the first oviposition takes place, the first eggs laid might be better endowed nutritionally than the succeeding ones, especially if protein food derived from host-feeding becomes less and less available for the adult parasites.

Despite the wide range of variation in size, the specimens of *S. borinquensis* appear to be rather remarkably uniform in most morphological characters. The form, relative proportions, and sculpture of most parts of the body are essentially the same in all specimens at hand. In very small specimens, the antennal club may be somewhat shorter, the forewing slightly narrower, and the ovipositor relatively somewhat longer than in large specimens. One female specimen had one abnormal antenna,

with only two funicular segments (fig. 34); the other antenna of that specimen was normal. The chaetotaxis of mesonotal sclerites appears to be constant, and that of abdominal tergites and sternites is subject to only minor variation. Very small specimens usually have fewer setae in the marginal fringe of the forewing, and these setae tend to be relatively somewhat longer than in large specimens. General coloration and wing pattern are essentially uniform. The vertex of the head, which is usually yellow, is occasionally dusky. In very small specimens, the fuscous band at base of abdomen tends to be more extensive, covering most of the third and fifth tergites, with straight rather than convex margins, and the band on seventh abdominal tergite is more nearly complete, more extensive than usual.

Rust (1913) and others recorded a wide range of variation in coloration in certain species of *Signiphora*, sometimes ranging from specimens with an entirely yellow abdomen to specimens with an extensive fuscous band. Certain series of undetermined species in the collection of the Division of Biological Control, Riverside, exhibit a similar range of variation in abdominal coloration. We do not know whether such field-collected series actually represent species considerably more variable than *borinquensis,* or a mixture of several species. At any rate, our extensive series of insectary-reared specimens of *borinquensis* are remarkably uniform in coloration as well as in structure.

Morphology and Development of Immature Stages

The egg (fig. 35)

It is enlongate, cylindrical, slightly convex dorsally, with the ends rounded, the cephalic end being broader. The color is opaque white and there is a clear area at each end. At deposition the egg averages 0.180 mm in length, and 0.075 mm at its greatest width. It will float free when the host scale is dissected in saline solution. A recently laid egg shows a yellow elongated internal mass enclosed in a thin membrane. This mass corresponds to the mid-intestine, which is clearly seen when the egg is about 72 hours old and ready to hatch (fig. 36). The first larval instar is distinctly seen enclosed in the chorion when the egg is about 48 hours old. The segments are clearly defined, as are the mandibles, which are used to rupture the chorion.

First instar larva

The larva hatches about 72 hours after egg deposition, and when newly hatched is just about the length of the egg, but soon becomes bigger upon feeding. The larva (fig. 37) is translucent except for an elongate, median opaque area which is due to the presence of food in the alimentary tract. Its form is that of the normal chalcidoid larva, with a prominent retractile head and 13 segments. The head is more or less semicircular in outline and superficially inserted in the prothorax, its color being similar to that of the body. The mandibles are anteroventral and surrounded by a short tubular structure formed by the integument. They (fig. 38) are small, sickle-shaped, and lie in the preoral cavity, their bases being as wide as their length. They average 2.9 microns in length. Supporting the mandibles and encircling the preoral cavity are the thickened ventral margins of the epicranium, which can only be clearly seen in cleared specimens.

The alimentary tract is only slightly visible through the transparent cuticle. A narrow esophagus extends through the prothoracic segment. Then the canal gradually widens into an elongated sack-like mid-intestine, which terminates in the region of the seventh abdominal seg-

ment. A short proctodeal invagination is hardly visible. The tracheal system is composed of two lateral longitudinal trunks united anteriorly in the prothorax and posteriorly in the eighth abdominal segment by transverse commissures. There are also extensions of the longitudinal trunks that pass anteriorly into the head and posteriorly into the caudal abdominal segments. Four pairs of spiracles are clearly seen: one pair on the mesothoracic segment and one on each of the first three abdominal segments. Before molting, the first instar larva attains considerable growth, the full-grown larva measuring an average of .380 mm long and .125 mm at its maximum width. The first larval instar lasts about 24 hours.

Second instar larva

This instar resembles the full-grown first instar, but is slightly more curved. It can be distinguished from the first instar by the size and shape of the mandibles, which measure 5.8 microns, have a narrower base, and are more elongate and only slightly curved (fig. 38). The appearance of the midgut and the spiracular arrangement are the same as those of the first instar, except for the darker color shown by the midgut. The second instar larva, when full-grown, averages 0.50 mm in length, 0.15 mm at its maximum width. This instar lasts three days.

Third instar larva

As soon as the second instar larva molts into the third, it uses its mandibles to rupture the host's integument, taking about 24 hours to move out of the host. It assumes an ectoparasitic existence until its development is completed. At this stage, the larva clearly shows a pair of elongated salivary glands, the ducts of which converge into a common duct which empties into the preoral cavity. The mandibles measure 11 microns in length, resembling those of the second instar in shape, although their bases are not so smooth and show some prominences (fig. 38). The full-grown third instar larva measures an average of 0.85 mm in length and 0.20 mm at its greatest width. The intestine is greatly enlarged and occupies about three-fourths of the body cavity. The spiracular arrangement is the same as in previous instars. The third instar lavra molts after three days.

Fourth instar larva

This stage is similar in appearance to the third instar, except that the size increases up to 1.00 mm in length and 0.30 mm at its greatest width (fig. 39). The mandibles are 20.3 microns long, with strong, wide bases, which show some prominences (fig. 38). The spiracular arrangement is the same as in the other instars, though the spiracles now appear to be open. The hind intestine is connected to the midintestine. When the fourth instar larva is two days old, it casts the first meconia in the form of small reddish-brown pellets. By this time the body contents of the host have been completely consumed. All the meconia seems to be excreted within the next 24 hours, after which the larva enters the prepupal phase.

The larval head structures are best seen in cleared specimens of the fourth instar larva (fig. 40). In the following description of these structures the terminology of Vance and Smith (1933) and the order of description followed by Crandell (1939) are used.

The lateral epicranial margin, or pleurostoma, on either side of the preoral cavity, produces at its anterior or dorsal extremity the superior pleurostomal ramus. This ramus articulates with the mandibular acron, the upper basal portion of the mandible which is provided with a slight depression or concavity. A similar branch, the inferior pleurostomal ramus, is given off at the posterior or ventral extremity of the

pleurostoma, where the relatively large mandibular condyle articulates. The inferior pleurostomal rami are united by a sclerotized rod and present the appearance of a continuous band passing below the preoral cavity. The hypostoma is that portion of the epicranial margin which begins at the posterior extremity of the pleurostoma and extends below and laterad to the preoral cavity. The hypostomata diverge slightly as they proceed posteriorly and their posterior extremities are united by a long semi-circular schlerotized band, the tentorium, which slightly extends into the prothoracic segment. The epistoma, or the epicranial margin above the mouth, begins near the base of the superior pleurostomal ramus and extends over the preoral cavity to a similar point on the other side.

Prepupa

The excretion of the larval meconia and the attainment of the prepupal stage is accompanied by a decrease in size. The prepupa averages 0.66 mm in length and 0.15 mm at its maximum width. It is ivory white and differentiated into a relatively wide anterior region and a narrow posterior region which corresponds to the abdomen. The prepupal stage lasts about 24 hours.

Pupa

The pupa (fig. 41) is of the typical naked chalcidoid type. It lies on its dorsum, facing the scale covering. At first, it is ivory white and only by careful observation can various parts of the body be distinguished. After three or four days it starts showing some pigmentation. The eyes are then pale-brown, and a typical dark abdominal band begins to appear. In the next four or five days the pupa gradually darkens, the body changing from light- to dark-yellow, the eyes to reddish-brown, and the abdominal band to blackish. The ocelli also become visible, and the adult emerges in about two more days.

When the female pupa is about seven days old and has attained its dark coloration, two small dark spots are clearly seen on the middle of the ventral side of the abdomen. Such spots, which correspond to the second valvifers and phragmata of the ovipositor in the genital structures of the female, are absent in the male pupa.

V. ETHOLOGY AND ECOLOGY OF THE ADULT FEMALE

Host finding

Soon after emerging, the female spends a brief time cleaning its body and then starts an active search for hosts. While searching, the antennae are held vertically, tapping and inspecting the objects found with the tips. In one observation, a female was placed on a cactus pad with a very light cactus scale population. The nearest host, located about six centimeters away from the parasite, was found in less than three minutes. That *S. borinquensis* may be good searchers was also confirmed on an occasion when it accidentally contaminated cactus scale cultures in the insectary. Such cultures were being used to rear *Aphytis* parasites in plastic cells superimposed on the cactus scale material, and were located about four meters from the *S. borinquensis* culture jars—from which these parasites escaped and invaded the *Aphytis* cultures. They not only oviposited in scales not confined in the plastic cells, but they also managed to enter through the organdy mesh covering the cells and oviposit in the confined scales. The potential of these parasites may be enhanced by their ability to restrict oviposition in unsuitable

hosts, as well as by their capacity to survive for relatively long periods of time (seven days) without food or water.

Nutrition, host-feeding, and oviposition

Most adult female hymenopterous parasites require a certain amount and quality of food in order to prolong their life and to achieve substantial reproduction. To accomplish this, the female usually host-feeds before it lays its first egg in the host, unless subjected to stress conditions. Host-feeding may not be of immediate need for initial oviposition, since a complement of about six fully developed eggs is already present in the newly emerged female. However, host-feeding is believed to stimulate the initiation of oviposition as well as to provide protein nutrients for rapid development of additional eggs. Host-feeding takes place from time to time throughout the life span of the adult and only stops about a week before the parasites die, when they have apparently laid all the eggs that they are capable of producing.

TABLE 1
TIME SPENT BY NEWLY EMERGED *S. borinquensis* IN SEQUENTIAL HOST-FEEDING AND OVIPOSITION EVENTS

Female No.	Minutes spent:					
	Cleaning	Exploring with ovipositor	Constructing feeding tube	Feeding	Ovipositing	Total
1	4	4	14	18	9	49
2	3	6	12	14	10	45
3	5	5	13	12	10	45
4	5	4	12	17	12	50
5	5	3	13	16	11	48
6	4	3	14	13	10	44
7	6	5	15	11	10	47
8	5	5	13	10	11	44
9	5	4	11	10	11	41
10	4	5	12	16	10	47
Av.	4.6	4.4	12.9	13.7	10.4	46

Observations were made individually on ten newly emerged females, and their behavior was recorded during the first two hours after emergence and exposure to hosts. Each female was put on a small cactus pad infested with cactus scales. The parasites are not easily disturbed and are readily observable on the host substrate. After host-feeding and oviposition appeared to have occurred, the scale was marked and dissected later in saline solution to verify the presence of the egg. An account of what was generally typical for all the females follows, and the data are presented in table 1.

After it has chewed its way out of the scale cover, a newly emerged female spends about five minutes cleaning its body, especially the antennae and wings. In the presence of fresh host material it then starts exploring the scales, stops at one of them, climbs on it and explores it with the tips of its antennae for a few seconds. If the host is suitable, exploration with the ovipositor tip takes place for a little over four minutes, until a desired spot is located. Then the parasite starts drilling and forms a feeding tube, which is completed in about 13 minutes. The ovipositor is slowly withdrawn, the parasite turns around, or simply walks backwards, and after locating the feeding tube with the tips of its antennae, begins to feed. This con-

tinues for about 14 minutes. During the construction of the feeding tube, as well as during host-feeding, the antennae are completely still.

Signiphora borinquensis was also observed to host-feed on male cactus scale pupae and unemerged adults, which are quite "different" hosts than the females of this species. The feeding tube was formed in about 13 minutes and the parasites took from 14 to 18 minutes to feed.

Tests were performed to learn if oviposition and development would also occur in this host. Although the parasites lived up to 21 days when confined with male scales only, dissections did not show any evidence of oviposition having taken place, and no progeny were obtained from male scales.

Oviposition sometimes follows immediately after feeding on female hosts. At other times, however, the parasites spend a few minutes without apparent activity. But in most cases they briefly explore a nearby scale with the tips of their antennae, locate a suitable spot, drill for about ten minutes and lay an egg. However, it is not uncommon to see a parasite depositing an egg in the same scale on which it has just fed. Feeding, if done by a single parasite, does not kill the host, which will continue to produce eggs.

The time spent by the adult parasites from post-emergence cleaning through host-feeding and oviposition averaged 42 minutes. Up to three eggs were laid by a single female during the first hour. During the next hour the behavior of the insects varied; some were seen resting, others exploring the hosts, or feeding on honey. These observations confirm that there is no preoviposition period in *S. borinquensis.*

If females are held in the absence of hosts for about 72 hours after emergence, they change the sequence of the described events when put in contact with their hosts, and oviposit without previous feeding.

As indicated elsewhere, the parasites can live an average of 25 days in the presence of their cactus scale host and honey. Honey is a source of energy, and with it alone they are able to live up to 16 days. In the presence of hosts, but without honey, they live up to 15 days, which is an indication of the importance of honey in their diet. When the parasites are held in the absence of both hosts and honey, and only offered water, they only live up to seven days. Under high humidity conditions and in the complete absence of hosts, honey, or water, the parasites can also live up to seven days, with a rare instance of one that lived eight days. Thus water alone does not help much in the prolongation of the life span, but honey and hosts are nutritionally highly important. Progeny production is affected very similarly to longevity. A constant supply of honey (carbohydrate) and hosts (protein) is necessary for optimal progeny production (Ovisorption Studies, see page 565).

Host preference

Signiphora borinquensis was successfully cultured on cactus scales grown on cactus pads when it was first obtained, but its possible preference for hosts, other than the coconut scale, *Aspidiotus destructor,* from which it was obtained in Puerto Rico, needed checking in order to ascertain possible usefulness in biological control of various scale pests. Therefore, a series of tests was designed to find out if the parasites would attack other scale species. The scales tested were California red scale, *Aonidiella aurantii* (Maskell); oleander scale, *Aspidiotus hederae* (Vallot); latania scale, *Hemiberlesia lataniae* (Signoret); and greedy scale, *Hemiberlesia rapax* (Comstock). The first two hosts were grown on lemon fruits and the last two on potato tubers.

In the first test, the individual host plants, each infested with about 300 of its respective scales, were placed in one-pint jars with honey added for food. Twenty newly emerged female parasites were introduced into each jar. An additional jar containing cactus scales grown on a small cactus pad served as a check. Inspection for progeny production was made after one generation. Only the parasites confined with the cactus scale produced progeny. A total of 552 adults were recovered in the cactus jar, with an average progeny production of 27.3 per female.

In order to check these results and attempt to ascertain why no reproduction occurred on the other host species tested, observations were made on the behavior of the parasites when closely confined with the different hosts, as well as with the different host plants. In these tests the insects were confined in small plastic cells with the host material (Materials and Methods, p. 543). The adult parasites were all newly emerged and were provided with honey. Again cactus scale was used as a check. Three parasites and about 60 scales were used per cell. When the cells were checked after one generation, progeny again had been produced only in the cactus scales where 48 adult parasites, an average of 16 per female, emerged. During this test it was observed that all the parental parasites placed on latania and California red scales died within ten days, those on greedy scale lived up to 18 days, whereas the life span was normal (22 to 27 days) when confined with either oleander or cactus scales. The parasites tended to avoid California red and latania scales, spending most of their time on the screen on top of the cells. Restlessness was observed in both situations. They did not show much interest in greedy scale, but no restlessness was observed. On the contrary, they were seen exploring the oleander scales in the same behavioral pattern as they did the cactus scales.

In order to examine host preference further, the parasites were given a simultaneous choice between a preferred host, the cactus scale and one of the others under test. The same type of cell was used with some modifications. Sections of the cell wall were removed and covered with muslin to assure better ventilation for the parasites in case adverse volatile substances might be involved with the lemons or potatoes. Simultaneous choice tests were devised as follows. A cactus pad infested with cactus scales was connected to a potato infested with latania scales by means of one cell. The potato in turn was connected to a lemon infested with oleander scale by means of another cell. A second cell on the cactus pad connected it to a lemon infested with oleander scale. In this way the parasites, confined three to a cell, were offered a choice between two different hosts, with two different host plants in three situations. They were provided with honey and allowed to oviposit until they died. The results of this experiment are presented in table 2, which again shows that only cactus scale on cactus was suitable for the parasite.

Since *S. borinquensis* has been observed to be negatively geotactic, it was thought that this tendency might affect in some way the host preference results. A similar test was designed; this time the whole set of connected host plants was placed on a wooden holder and turned upside down every 24 hours to give the parasites an equal opportunity to contact all hosts. Again the results were the same, cactus scale being the only suitable host, although interest was shown in oleander scale.

Additional tests on host preference were made by confining 25 adult female parasites in one-pint jars with a surplus of each of the different hosts used before. The intention was to get data on the behavior, longevity, and progeny

TABLE 2

PROGENY PRODUCTION OF *S. borinquensis* WHEN SIMULTANEOUSLY OFFERED A CHOICE OF TWO HOST SPECIES IN THREE DIFFERENT COMBINATIONS

Host situation for *S. borinquensis*	Effects on *S. borinquensis*		
	Maximum longevity of parents (days)	Total progeny on:	Progeny per ♀
1. Cactus scale on cactus and oleander scale on lemon	18	Cactus scale: 49 Oleander scale: 0	16.3 0
2. Cactus scale on cactus and latania scale on potato	16	Cactus scale: 37 Latania scale: 0	12.3 0
3. Latania scale on potato and oleander scale on lemon	17	Latania scale: 0 Oleander scale: 0	0 0

TABLE 3

PROGENY PRODUCTION AND LONGEVITY OF *S. borinquensis* ON DIFFERENT HOSTS AND HOST PLANTS

Host	Host plant	Av. longevity (days)	Total progeny	Progeny per ♀
California red scale	lemon	6	0	0
Oleander scale	lemon	24	0	0
Latania scale	potato	7	0	0
Greedy scale	potato	14	0	0
Cactus scale	cactus	27	620	24.8

production of the parasites under the conditions of ample space as exists in a one-pint jar, as opposed to that existing in the small cells, in which interference may have occurred. Honey was provided for the parasites, daily observations were made on their movements, and the progeny production was recorded a month later. The results are shown in table 3.

The fact that the parasites died soon after confinement with California red and latania scales apparently cannot be ascribed to repellency or toxic effects of either potato or lemon, because the same host plants were used as hosts of oleander and greedy scales, with which the parasites lived a number of days longer. Careful observation of the insects when exposed to each host again revealed restlessness in those exposed to California red and latania scales, so that the parasites spent most of their time away from the host substrate. The failure of *S. borinquensis* to reproduce on latania scale, incidentally, first led to our views concerning its taxonomic distinctness (see Taxonomy, III).

Though host-feeding was never observed on greedy scale, the parasites lived some 14 days when in contact with it. Greedy scale, although closely related to latania scale, did not seem to produce as much stress on the parasites as the California red and latania scales did, for reasons that were not determined.

In this test series, aside from the cactus scale, the parasites were only seen to drill in oleander scale, making a feeding tube and then host-feeding on it. The parasites appear to "prefer" this host as much as the cactus scale, even though they produce no progeny on it. They also have a normal life span when in contact with oleander scale. Several instances of two adult parasites feeding on the same oleander scale were recorded.

Dissection of oleander scales after an apparent oviposition had taken place

yielded two scales out of 30 having one parasite egg each. Why some oviposition takes place, but no development, is a question upon which we can only speculate. Under stress conditions (lack of suitable hosts, crowding, and the like) the parasites may be induced to oviposit, especially in hosts that are suitable for adult host-feeding, and have a relatively soft scale cover as does oleander scale. Lack of development may be due to encapsulation of the eggs or newly hatched larvae by the blood cells of the host. It may also be due to nutritional deficiences.

Since the host plant may at times affect the development of immature parasites in their hosts, experiments were conducted to find out if *S. borinquensis* would develop in oleander scale raised on squash (*Cucurbita maxima*) instead of on lemons. Host-feeding was observed to occur almost immediately after exposure to the hosts. Dissections revealed that oviposition did occur, though quite infrequently. However, larvae were never observed to develop. The adult parasites lived for about 20 days.

Signiphora borinquensis, therefore, is rather host-specific; it actually appears to be repelled by some species of armored scales. It may host-feed on other species, presumably if a preferred suitable host is not available, but not utilize them otherwise. On some species it may host-feed to a considerable extent and oviposit sparingly, but no larval development will occur. Such oviposition probably results from stress due to the lack of suitable hosts. Larval development is probably prevented by phagocytosis or some other manifestation of host unsuitability.

Daily oviposition and progeny production

Adult females had been routinely observed to host-feed and oviposit almost throughout their usual 25-day life span, but exact details on daily and total lifetime oviposition were lacking. With this in mind, the following experiment was conducted. Four large cactus pads infested with cactus scales were obtained and 25 small plastic cells, each enclosing about 70 scales, were superimposed on each pad. One newly emerged female parasite was confined in cell No. 1 of each pad. The parasites were transferred every 24 hours to the next cell during a 25-day period (or until they were dead or lost). In the first test, injury or loss of parasites became serious after the tenth day. In a second test in which the handling techniques were refined, only one of the parasites was lost. The remaining females lived long enough to satisfy the needs of the experiment. They were permitted to stay in the twenty-fifth cell until they died. The results are presented in table 4.

Data from table 4 confirmed previous observations that most eggs are laid during the first few days after emergence. The cumulative percentages of eggs laid indicate that over 50 per cent of the eggs are laid during the first three days, and that during the first eight days the parasites lay about 73 per cent of the total. This is supported by dissection data, which show that the newly emerged female has a complement of about six mature eggs ready to be laid. Ovisorption studies discussed later also show that new egg development is very rapid following deposition of those eggs contained in the newly emerged female. After about 21 days, egg deposition did not occur even though the parasites lived a few days longer. The figures become very low toward the end of the insect's life span and there is always a period of no egg deposition before death. Observations of the parasites confined in their cells reveal that they are, in general, more active during the first week, but they occasionally host-feed or oviposit a few days before death.

Total progeny and longevity

The experiments designed to obtain data on daily oviposition also provided information on longevity and total progeny, as seen in table 4. However, it became desirable to confirm this information on longevity and fecundity when the adults were not subjected to the possible disturbances involved in the daily transfers necessary in the last mentioned studies. Ten newly emerged females were each confined individually in separate cells fixed to a cactus pad

TABLE 4

LIFETIME PROGENY PRODUCTION (EGGS) OF *S. borinquensis* FEMALES ON CACTUS SCALE

Day	Female no.				Daily oviposition		Cumulative percentage of total eggs
	1	2	3	4	Total	Average	
1	5	9	9	7	30	7.50	29.9
2	2	3	2	4	11	2.75	40.8
3	3	3	3	2	11	2.75	51.9
4	0	1	1	0	2	0.50	53.8
5	1	1	2	1	5	1.25	58.7
6	2	0	1	2	5	1.25	63.9
7	1	0	1	3	5	1.25	68.7
8	1	1	1	1	4	1.00	73.2
9	0	0	0	1	1	0.25	73.6
10	0	0	1	2	3	0.75	76.8
11	2	1	1	0	4	1.00	81.6
12	0	2	0	0	2	0.50	82.8
13	0	1	0	0	1	0.25	83.9
14	0	0	0	0	0	0.00	83.9
15	1	0	2	2	5	1.25	88.8
16	1	0	1	1	3	0.75	91.0
17	1	1	0	0	2	0.50	92.9
18	0	0	0	0	0	0.00	92.9
19	1	1	1	1	4	1.00	96.2
20	1	0	1	0	2	0.50	98.0
21	0	0	1	0	1	0.25	100.0
22	lost	0	0	0	0	0.00	
23		0	1	0	1	0.00	
24		0	1	0	1	0.00	
25		0	1	0	1	0.00	
Totals	22	24	28	27	101		

infested with about 70 cactus scales per cell. The parasites were held in the cells until they died, so no handling disturbances or injuries were involved. Daily observations were made to record their longevity. Total progeny production, as shown in table 5, was recorded after all the parental parasites were dead. Total progeny per female averaged 26.1, and longevity averaged 25.4 days. These results are very similar to the ones obtained in the daily oviposition studies. This indicates that careful daily transfer did not affect longevity and progeny production, and that the figures in tables 4 and 5 probably represent close to optimal survival and reproduction by this species. These results also indicate that no appreciable environmental contamination was caused by the female

TABLE 5
PROGENY PRODUCTION AND LONGEVITY OF *S. borinquensis* ON CACTUS SCALE

Replicate no. (1 ♀ per test)	Longevity (days)	Progeny produced
1	25	24
2	27	21
3	29	36
4	23	24
5	25	29
6	24	22
7	23	25
8	25	27
9	28	22
10	25	31
Average	25.4	26.1

when confined with scales for its entire lifetime.

Effect of temperature on progeny production and longevity

Various factors have been found to affect progeny production and longevity to a greater or lesser extent. Those discussed elsewhere include host and parasite size, host suitability, food and host-feeding, and crowding effects.

Experiments were conducted to determine the effect of sub-optimal temperatures on development, progeny production and longevity. The test temperatures were 50°F, 65°F, and 90°F, and the results were as follows: At 90°F, the life cycle was accelerated and completed in 16 days, but average progeny production per female was reduced to 14. At 65°F development was prolonged to 53 days and the progeny per female reduced to 18. At 50°F, no development occurred. This was inferred from the observation that no eggs hatched during a 90-day period, although dissections of these scales showed the presence of parasite eggs whose contents were intact but whose development had not started. The host scales were apparently healthy and not affected by the low temperature, except for slowing of their development.

Newly formed female pupae exposed to 90°F for 48 hours will cause the subsequently emerged adult females to produce some males. This is discussed in more detail later in this chapter (Male Production Experiments).

Temperature, within reasonable limits (75 to 85°F), does not greatly affect the longevity of the parasites, provided that relative humidity is kept to at least 60 per cent. Females held at 50°F will live only 14 days, and holding at 90°F will permit them to live only nine days.

Ovisorption studies

De Wilde (1964) defines ovisorption as "... the capacity of the follicle cells to dissolve and absorb the oocyte." According to the same author, "... several factors can contribute to the production of this phenomenon, in which vitellogenesis is interrupted and the oocyte, wholly enveloped in its follicle, may die. Follicle cells cease to participate in alimentary egg formation, may divide amitotically, and absorb the dead oocyte. Their nuclei become pynocytic, the cells breaking down and being absorbed through the ovarian sheaths." Thomsen (1952) states that ovisorption is brought about by the integration of several neurosecretory, physical, and chemical factors.

From the biological control viewpoint, this physiological characteristic could be very important in parasite species whose effectiveness as natural enemies of pests may depend in part on the conservation of reproductive material, which is correlated with a high searching capacity, as pointed out by Doutt (1964).

The question of whether ovisorption occurs in *S. borinquensis* was investigated by holding the parasites under different dietary conditions, and then observing how the progeny production was affected. Concurrently, dissections and staining of ovaries were done to get the necessary histological information

to complement the progeny production data. The techniques of Flanders (1935) and Edwards (1954) were followed in making these observations.

Dissections of pupae, unemerged adults (about one hour before emergence), as well as of newly emerged females, showed that some eggs are already fully developed before the insects emerge. The eggs in pupae appear to have more fat than those in unemerged adults. The eggs in the unemerged adults appear identical to those laid a little later in the scale body. The stained ovaries of older females which were absorbing their eggs showed that developing eggs have a distinctive shape and content, in contrast with eggs being resorbed, which show increasing disorganization of their shape and content.

Both egg development and ovisorption seem to occur very rapidly, and host-feeding, which has been observed to take place almost at any age of the adults under normal conditions, provides the nutrients for such rapid egg development.

It is noteworthy that the three ovarioles in each ovary (rarely four) do not show the long chain of developing eggs which is more usual in parasites. They only show one developing egg, or a mature one, followed by a small thin germarium. This contrast we believe to be due either to the rapid development or rapid absorption of the eggs.

The different experiments on ovisorption were as follows:

a) **No food or water.** Fifty newly emerged females were obtained and held for one to eight days without any food or water in groups of five in each of ten small vials. Every day for eight days the parasites of one vial were put in five small cells superimposed over ample cactus scale material. One parasite was used per cell. Three additional cells with a newly emerged female confined in each were used as checks which were provided with ample hosts and honey. The results of this experiment are shown in table 6.

TABLE 6

EFFECTS OF INITIAL WITHHOLDING OF FOOD AND WATER ON SUBSEQUENT PROGENY PRODUCTION AND LONGEVITY OF *S. borinquensis*

Time with no food, water	Replicated/ group (1 ♀/cell)	Av. progeny/ ♀	Av. longevity
Days	*No.*	*No.*	*Days*
1	5	16.0	21
2	5	15.0	22
3	5	13.6	20
4	3	16.0	25
5	2	0.5	4
6	2	0.0	2
7	1	0.0	2
8	1	0.0	2
Check*	3	21.3	30

* Check group was provided with ample hosts and honey.

Longevity and progeny production were somewhat affected in females held without food from one to four days. However, beginning with the fifth day, both longevity and progeny production were affected to a marked degree. Daily dissections of females kept under the same conditions served to correlate the progeny data with the conditions of the ovaries. Ovisorption was found to start after the third day in females held without food. This indicates that the number of resorbed eggs by the fourth day may account for the sharp decline in progeny production of females held without food for five days (table 6). Though some parasites lived up to eight days without food, they did not produce any progeny from the sixth day onward. Apparently host-feeding stops at about the fifth day if carbohydrate food is not provided, by which time exhaustion of all mature eggs through ovisorption has occurred and the germarium is no longer able to form new eggs due to the lack of the needed protein which is normally obtained from the host body fluids.

b) Honey as only source of initial food. The design of this test was that of (a), except that the females were continuously supplied with honey as food. The results are presented in table 7.

TABLE 7
EFFECT OF HONEY AS ONLY INITIAL SOURCE OF FOOD ON SUBSEQUENT PROGENY PRODUCTION AND LONGEVITY OF *S. borinquensis*

Days with honey only	Replicated/ group (1 ♀/cell)	Av. progeny/ ♀	Av. longevity
No.	*No.*	*No.*	*Days*
1	3	18.0	28
2	3	17.6	23
3	3	17.3	23
4	3	17.0	22
5	3	15.6	20
6	3	14.6	21
7	3	11.6	20
8	3	9.6	20
9	3	6.6	19
10	3	3.6	18
11	3	3.3	19
12	3	2.0	16
13	3	0.3	16
14	3	0.0	15
15	3	0.0	15
Check	3	19.0	29

Daily dissections of females held under this diet regime showed ovisorption to start on the third day of absence of hosts. Longevity was affected somewhat after withholding hosts for only one day and it slowly but steadily declined thereafter. Progeny production was nearly normal in the case of females withheld from hosts up to four days, after which it showed a steady decline. Table 7 demonstrates that carbohydrate food such as honey enables the parasites to stay alive much longer and produce many more progeny than otherwise. For example, after four days without any food or hosts, parasites produced virtually no progeny when placed with hosts (table 6), whereas when honey was available but hosts were withheld for four days, parasites produced 15.6 progeny per female when placed with hosts (table 7). In nature, this would help the parasites to conserve their egg supply and maintain adequate longevity while searching for their hosts with the energy provided by the honey. In the field, the source of energy may be nectar or honeydew secreted by coccids.

It is noteworthy, however, that the process of ovisorption never noticeably compensated to insure the equal replacement of ovisorbed eggs by newly developed ones, as has been postulated by some (Flanders, 1950). In fact, there is no indication from these data that ovisorption acted at all to conserve total lifetime progeny production. Some other explanation than the general one proposed for this phenomenon must be sought.

c) Effect of a nonsuitable host. This test was similar to (a) and (b) but was conducted in order to determine if the contact with a host that has proven to be unsuitable, as California red scale, would induce ovisorption. It had been observed previously that the parasites not only failed to host-feed and produce progeny in this scale, but also showed a great deal of restlessness when in contact with it (see page 561). Twenty females were confined in a large cell attached to a lemon infested with about 150 California red scale. The parasites were newly emerged and honey was available for them at all times. Individuals were removed for dissection every hour and ovisorption was found to occur beginning about four hours after confinement with the scale. To obtain progeny production records, one female was taken out of the cell containing California red scale every day and confined for life in a small cell with the preferred hosts, cactus scale, and honey. The results are tabulated in table 8.

Data in table 8 clearly show that previous confinement with California red scale has an immediate and drastic effect on subsequent progeny production

TABLE 8
EFFECTS OF VARIOUS PERIODS OF CONFINEMENT WITH A NONSUITABLE HOST (CALIFORNIA RED SCALE) ON SUBSEQUENT TOTAL PROGENY PRODUCTION AND LONGEVITY OF *S. borinquensis* ON CACTUS SCALE

Time with Calif. red scale	Replicated/ group (1 ♀/cell)	Av. progeny/ ♀	Av. longevity
Days	*No.*	*No.*	*Days*
1	3	13.6	18
2	3	10.0	18
3	3	6.6	17
4	3	6.6	12
5	3	3.6	11
6	3	2.0	9
7	3	1.3	5
8	3	1.0	....
9	3	0.0	1
10	3	0.0	1
Check (cactus scale only)	3	20.3	27

following transfer to a preferred host. This may be an additional indication that ovisorption takes place very rapidly under such unfavorable conditions. As indicated before, ovisorption starts about four hours after contact with California red scale, and the progeny data indicate that such resorption may proceed at a high rate, since subsequent progeny production on cactus scale is relatively low from the first day and sharply declines until none is produced following nine days of confinement with California red scale. The life span of the parasites was also gradually reduced, and no live insects were observed after ten days. This had been observed before in host preference tests. The shortening of the life span may be caused by some unknown influence of an unsuitable host which stimulates intense activity resulting in expenditure of a great amount of energy, which is not replenished adequately because the females do not spend much time feeding on honey, nor do they host-feed.

In general, data from all these ovisorption studies show that initial withholding of females from suitable hosts definitely increases the rate of ovisorption and adversely affects the progeny production, which was never normal even after short periods of absence of preferred hosts. These results indicate that ovisorption is not as important an adaptive mechanism for conservation of egg production in parasitic Hymenoptera as has been postulated by Flanders (1947).

Male production experiments

Normally, males do not occur in *S. borinquensis*. The induction of male production in certain synovigenic uniparental species of Hymenoptera has been demonstrated (Wilson and Woolcock, 1960; Flanders, 1965) by manipulating the environment of either the adults or developmental stages, especially by exposure to high temperature. This procedure was followed in order to test the induction of male production in *S. borinquensis*. Immature stages were exposed to 90°F for 48 hours. Representative stages included eggs, larvae, prepupae, early (clear) and late (dark) pupae. If any of these stages were affected by the high temperature so as to cause the formation of haploid eggs in the adult females, which developed from the treated immature stages, males should occur in the adult females' progeny. In order to obtain the different stages for simultaneous exposure to 90°F, five large plastic cells were superimposed on a cactus pad infested with cactus scales. These were parasitized in sequence as follows. Fifty female parasites were allowed to oviposit for eight hours in cell No. 1, after which they were removed. Five days later the same operation was repeated in cell No. 2, with cell No. 3 eight days later, 11 days later with cell No. 4, and 15 days later with cell No. 5. By this time the stages of the parasite present in the cells were as follows: eggs in cell No. 5; larvae in

No. 4; prepupae in No. 3; early pupae in No. 2, and late pupae in No. 1. The time interval for the stinging of the scales in each cell was determined by previous knowledge of the life cycle of the parasite. These stages were ascertained to be correct by dissecting five scales from each cell. When the adult females emerged following the 90°F exposure they were placed in another set of cells on another cactus pad, where the F_1 generation progeny were reared at normal temperatures and any males recorded.

Adult females were also exposed to 90°F for 48 hours and their progeny recorded. Two groups of female adults were tested: those emerged in regular cultures, that is, females already ovipositing; and a group of newly emerged females, isolated before emergence.

The only females that produced any males in all these tests were those previously subjected to 90°F as early pupae. These yielded a total of only 12 progeny, but five (42 per cent) were males.

Failure to obtain males from treated stages other than early pupae may be an indication either that oögenesis in this species does not start until the prepupa is formed, or that the critical meiotic divisions are more numerous at this stage because of rapid cell proliferation. Dissections of late pupae show the presence of a complement of 6 to 8 well developed eggs that would be ready for deposition by the newly emerged female. However, oögenesis may continue at least during the first week of the adult life, during which about 75 per cent of the eggs are laid (see section on nutrition, host-feeding and oviposition on page 559). Thus, it is difficult to understand why males were not obtained by treating dark pupae or newly emerged females.

Behavior. When confined with a female in a small vial, the male immediately responds to her presence by continually vibrating his antennae. In one instance, the male, which had only recently emerged, attempted copulation 10 minutes after being confined with the female. Raising his wings and vibrating his antennae, he approached the female and suddenly mounted her. His antennae kept vibrating, their tips touching those of the female. At the beginning, the female was not receptive to courtship and the copulation attempts failed after the male had mounted for about five seconds. After about 15 minutes of courting and failure to copulate, the male was accepted by the female. He then remained mounted for about 25 seconds, his abdomen bent and touching that of the female for a short time. When a male was confined with more than one female, he responded to their presence by attempting copulation with each. Dissections of three females which were left with two males for a period of 24 hours showed their spermathecae filled with "particles" that moved, as do spermatozoa. The "particles" were later seen spinning very rapidly around the inner wall of the sperm capsule. After some time they migrated to a small pouch in the spermathecal wall, where they kept moving rapidly and at random. When the spermathecae were opened in physiological saline solution, sperms were definitely recognized as rapidly moving tadpole-like structures. Thus, males appear to be functional.

Longevity. After being confined with three females for 24 hours, with apparent copulation having taken place, a male was isolated in a small one-fourth dram vial provided with honey. The vial was placed in a chamber having a high moisture content (about 60% RH) and held at 80°F. The male lived for 20 days. If the source of food of males in nature is nectar or honeydew it should permit them to live for a similar period and, in the case of normal males from arrhenotokous species, help insure the finding of females.

Males occasionally occur in regular cultures. One male was accidentally found in one of the cultures when trying to obtain newly emerged females. When confined with two females, he responded as others did, attempting copulation. This male lived 18 days with a honey diet. Although thelyotokous, therefore, *S. borinquensis* may on rare occasions, produce males. Several times the regular cultures have been inspected for the presence of males without finding any. As a further check, the dead parasites from old cultures were collected, boiled in 10 per cent KOH for about five minutes, then mounted in Hoyer's medium on slides. No males were found in more than 3,000 insects inspected. The phenomenon of male production in this species evidently is highly unusual. Just how extrinsic or intrinsic factors operate to cause the formation of haploid eggs is an interesting problem which remains to be investigated.

VI. PARASITE DENSITY EFFECTS

Behavior

When host density is more or less fixed and the parasite density varies, parasite behavior is also known to vary. Tests in the same cells as were used in the experiments on the behavior of the adult parasites were conducted to ascertain crowding effects (table 9).

When parasites were confined in seven situations ranging from one to 160 per cell, behavior ranged from normal (exploring hosts, ovipositing or feeding, remaining quiescent for long periods—either among scales or at the edges of the cells)—to behavior that appeared to be highly restless and interfering.

In the two cells containing five and 10 parasites, respectively, activity was stepped up but still normal—with encounters producing quiescent periods. Thereafter, encounters and interference increased, sometimes causing a jumping response and a tendency to gather on the screen on top of the cells. In cells containing 20 or more parasites, two and, in the end, as many as four parasites were seen drilling in the same scale.

As crowding progressed, parasite mortality increased until only 4 per cent were alive after 20 days in the cell containing 160 parasites; mortality began after five days with 50 per cent.

Density

In order to obtain quantitative information concerning the effect of crowding on fecundity of *S. borinquensis*, the

TABLE 9

EFFECTS OF PARENTAL PARASITE DENSITY ON PROGENY PRODUCTION OF *S. borenquensis*

Parental parasites/ cell	Replicates	Scales/ cell* (av.)	Parasite count		Fate of scales		
			Av. progeny/ cell	Av. F_1 adult progeny/♀	Av. parasitization	Av. dead (not para.)†	Av. surviving
No.	*No.*	*No.*	*No.*	*No.*	*Per cent*	*Per cent*	*Per cent*
1	4	179	14	14.0	7.8	4.0	88.2
5	4	164	128	25.6	77.7	14.4	7.9
10	5	210	159	15.9	75.7	17.8	6.5
20	5	191	134	6.7	69.8	22.0	8.2
40	2	191	128	3.2	67.2	26.1	6.7
80	1	184	88	1.1	47.8	46.2	6.0
160	1	199	16	0.1	9.5	88.4	2.1

* A "constant" host density of approximately 190 scales per cell was used for each parasite density tested.
† Scales dead from host-feeding, overstinging or unknown causes.

following experiment was conducted. Cactus pads with a rather uniformly distributed population of adult cactus scales were used. A series of large plastic cells (see Materials and Methods, Chapter II) was superimposed over an estimated 190 scales per cell, so that host density differences were insignificant. Different numbers of parental adult parasites were confined in a series of cells. The densities of parasites tested were 1, 5, 10, 20, 40, 80, and 160 per cell. Parasites were allowed to oviposit for 20 days, essentially their maximum reproductive period. The subsequent total F_1 adult offspring were recorded. The numbers of dead and surviving scales were also recorded. The results are presented in table 9 and a graphic representation of the effect of density on progeny production per female is given in figure 42. The per cent parasitization was calcu-

TABLE 10

EFFECTS OF PARENTAL PARASITE DENSITY UPON NUMBER OF PARASITE EGGS DEPOSITED PER HOST BY *S. borinquensis*

No. parasites/cell/no. hosts dissected (3 replicates)*	No. hosts parasitized with following no. eggs							Total no. eggs	Av. no. eggs/host
	1	2	3	4	5	6	7		
1/30	9	0	0	0	0	0	0	9	0.30
5/30	13	0	0	0	0	0	0	13	0.43
10/30	13	0	0	0	0	0	0	13	0.43
20/30	16	3	0	0	0	0	0	22	0.73
40/60	17	11	8	0	0	0	0	63	1.05
80/60	14	10	12	8	12	0	0	163	2.72
160/180	7	10	22	34	22	29	34	751	4.17

* A constant host density of approximately 190 scales per cell was used for each parasite density tested.

lated on the basis of the actual initial number of scales per cell and the respective total parasite progeny. The per cent of dead scales includes those resulting from host-feeding, "overstinging" (ovipositional probing) or other reasons. Table 9 and figure 42 will be discussed later in conjunction with the complementary test that follows.

Duplicates of all the preceding test density series were dissected daily in order to correlate initial egg deposition with number of larvae hatching and with final production of F_1 adults in relation to parental adult parasite densities. In effect, this is a measure of superparasitization. Two replicates of each density were used. In order to remove the scale for dissection, CO_2 was applied through the covering screen of the cells for about one minute to anesthetize the parental adult parasites. The cells were then uncovered and the desired number of scales were removed at random and dissected in saline solution.

The first dissections were made by removing scales from one representative cell of each density after the parasites had been in contact with their hosts for 24 hours. This operation was repeated each 24 hours during three consecutive days. This represents an accurate index (about 50 per cent) of the total lifetime fecundity. Ten scales were dissected daily from the densities 1, 5, 10, and 20; 20 scales were taken from densities 40 and 80; and 60 from the 160 density. All scales were removed at random. Results are presented in table 10, which will be discussed along with table 9 after the following section.

The remaining replicate cells of each density were left undisturbed for five days, so that when dissections were made during the fifth through the eighth days, the number of hatched larvae would be counted and correlated with the number of eggs laid. The number of

scales removed from the cells representing the different densities was the same as before, and again the scales were picked at random.

In order to determine if the numbers of pupae that developed under crowded conditions were closely correlated with the number of adults that would subsequently emerge from such pupae, four additional cells were assembled to make observations on the 80 and 160 parasite densities. Two cells were used for each density; one to determine the number of pupae by dissection of the scales at the proper time, and the other left undisturbed to record the subsequent emergence of adults. In one of the 80-density cells 92 pupae were found and left under the scale covers. Eighty-seven adults emerged. The other 80-density cell left undisturbed yielded 82 parasites. In one of the 160-density cells, 23 pupae were found, out of which 21 adults emerged. The other cell left undisturbed yielded 25 parasites. It is evident that once pupae develop, a very high proportion will emerge, regardless of high parental adult densities.

We will now review, discuss and draw conclusions concerning all the preceding density tests. From the data contained in table 9 and depicted in figure 42, it is evident that above the density of five, the average adult F_1 progeny per parental female decreases as the density of the parental parasites increases, becoming very low under conditions of extreme crowding, until it almost reaches zero at the 160-density. Obviously, extreme superparasitism results under high densities of *S. borinquensis* in relation to that of the host. It is interesting to see that a peak in progeny production per female is indicated at the density of five parasites per cell, with an average of 25.6 progeny. The progeny figure for one parental parasite per cell, being lower that that of either 5 or 10 per cell, perhaps shows the effect of what has been called "undercrowding" (Allee *et al.*, 1949). The isolated individual parasites probably lack stimulation because of the absence of random contacts with others, which otherwise would cause more continuous movement and oviposition.

Also from table 9 it is noteworthy that the percentage of dead scales from causes other that parasitism increases with crowding, probably due to the increasing host-feeding and ovipositional-related multilation taking place in relation to the density of the parasites. Such hosts appear dark and dessicated when dissected. Moreover, they show typical feeding "scars," or necrotic areas, whose number is in relation to the density of the parasites. Nevertheless, even at extremely high parasite densities there remains a low percentage of scales which escape attack (see fig. 43). The proportion of scales surviving decreases surprisingly little in relation to great increases in density of the parasites from five up.

These two facts, that (a) the number of hosts escaping attack decreases rapidly at first, although some escape even under maximum parasite density, and that (b) the number of hosts that die without yielding parasites increases as parasite density increases — were observed by Salt (1936) in his studies of superparasitism of *Trichogramma evanescens* and by various others.

These data show that considering all densities, a near maximal utilitization of hosts occurs at the relatively low parasite density of five and that overall parasite efficiency (progeny production and per cent parasitization) is about optimal at this density. Such information should be granted serious consideration in the face of proposals for mass-liberation of parasites to achieve control or even eradication. It is obvious from these data that merely releasing greater and greater numbers of parasites will not necessarily give better results in a periodic colonization program.

From dissections of scales exposed to different densities of parasites for three days (table 10), it is evident that little or no superparasitism occurs below a density of 20 parasites. Only at this density or higher were two or more eggs deposited in the same scale. It has often been observed that two well-developed adults can emerge from the same scale but rarely more; in other words, the presence of two eggs in the same scale is not always necessarily a sign of superparasitism. As discussed before, the behavior of the adult parasites under the 20-density condition shows a certain degree of interference which may account for the drop in F_1 progeny per female, but some superparasitism probably also occurs at this density. From the density of 40 upward, the average number of eggs found in a single scale increased markedly, an obvious sign of increasing superparasitism. At the high parental density of 160 females per cell, only 11 per cent of the hosts parasitized had less than three eggs per host, i.e., 89 per cent were superparasitized. Over half of the hosts parasitized had five to seven eggs deposited in each of them.

Similar results were obtained from the dissections of scales at the time when the larvae had just hatched and had started their activities inside their host. Again, in the 20-density cells, only one out of ten scales showed two larvae in a single host. These larvae were likely to reach the adult stage as pointed out above. From the 40-density onward, however, an increasing number of scales showed an increasing number of larvae inside each one. The more larvae present in a single scale, the faster the host was consumed and killed before the larvae were adequately fed. This accounts for the increasing number of dead scales, as well as for the decrease in progeny production at the higher parasite densities. The larvae found at high densities were mostly small, dark, and obviously dead. Their death may be the result of excretory substances accumulated in the host fluids, food shortage, or accidental damage to each other. It is unlikely to result from toxic substances given off by the larva that hatches first in order to eliminate its competitors, as happens in some other species of parasites. The fact that two adult parasites can normally develop in a single scale discounts this possibility as well as that of direct attack.

It is also apparent that once the pupa is formed, its further development is not affected by crowding as is the development of larvae. The danger of pupal mortality by stinging or feeding by the members of their own species as a result of crowding did not exist in these tests once the pupae were formed, since active crowding effects disappeared by that time.

VII. SUMMARY

The family name, Signiphoridae, is preferred to Thysanidae. The genus *Signiphora* includes species previously commonly referred to *Thysanus,* including probably all species that are primary parasites of diaspine scale insects. Morphological studies and host preference tests showed the species studied to be an undescribed *Signiphora,* herein described as *S. borinquensis* Quezada, DeBach and Rosen.

Signiphora borinquensis is thelytokous. It develops as a primary parasite of certain diaspine scale insects. Larval development is unusual with the first two instars being endoparasitic, the last two ectoparasitic. The life cycle at 80°F ± 2°F and 55 ± 5 per cent RH averages 25 days, the F_1 progeny production per female averages 26 and the adult longevity, 25 days. At 90°F, development is completed in 16 days, but average

progeny production is reduced to 14 per female. At temperatures lower than 80°F, development is gradually prolonged and progeny production gradually diminishes until at 50°F no development occurs. Details regarding behavior, development and morphology of all immature stages are given.

Adult females vary from 0.3 to 0.75 mm in length, with larger parasites producing larger and more progeny per female. The size of the host scale also influences the size of the resulting parasite, larger hosts giving rise to larger parasites.

Ethology of the adult female is treated extensively. Host-finding is indicated to be good. Host-feeding occurs nearly immediately after adult emergence and is described. It is generally a prerequisite to oviposition. Oviposition follows soon thereafter and generally within less than one hour after emergence. No preoviposition period occurs. The newly emerged females have a complement of about six eggs ready for oviposition. They deposit over 50 per cent of their lifetime total during the first three days and about 75 per cent during the first week. A constant supply of honey (carbohydrate) and hosts (protein) is necessary to insure optimum longevity and progeny production. Serious reductions in progeny production and longevity occur if either of these requisites is withheld even for short periods.

A fair degree of host specificity is indicated for *S. borinquensis* which is known to develop on *Aspidiotus destructor* in nature. The natural host was not available, and in the laboratory it could be cultured only on *Diaspis echinocacti* but would not develop on *Hemiberlesia lataniae, H. rapax, Aonidiella aurantii* or *Aspidiotus hederae.* Nonpreferred hosts such as *A. aurantii* appear to cause premature mortality of adult parasites confined with them.

Normal production of males is less than 1 per cent. Production of males can be increased by subjecting young female pupae to 90°F for 48 hours. The males are able to copulate and inseminate the females, but the sperm may not be utilized inasmuch as thelytokous reproduction is the general rule.

Ovisorption occurs when adult females are stressed by absence of preferred hosts, honey, or the presence of of unpreferred hosts. Ovisorption does not compensate to insure the equal replacement of ovisorbed eggs by newly developed ones, as has been previously postulated.

A series of seven adult parasite densities from one to 160 were tested, utilizing constant host densities of 190 scales to determine the effect of parasite density on progeny production, longevity, and superparasitism as well as on parasitization and survival of the hosts. Undercrowding was indicated at the parasite density of one, because progeny production per female and parasitization were considerably better at the density of five. Superparasitization increased and longevity as well as progeny per female decreased at higher densities. At the highest density, superparasitization was extreme, and total progeny production was greatly reduced. The combined percentage of hosts parasitized and dead from other causes increased little above the density of five, which caused over 90 per cent total mortality; but some survived even at extremely high parasite densities. These results indicate that certain practices involving mass-release of parasites in the field need reexamination.

VIII. ACKNOWLEDGMENTS

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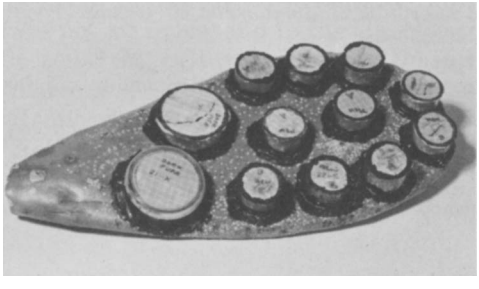


Fig. 1. Different types of plastic cells on cactus pad to confine parasites with the cactus scale hosts.

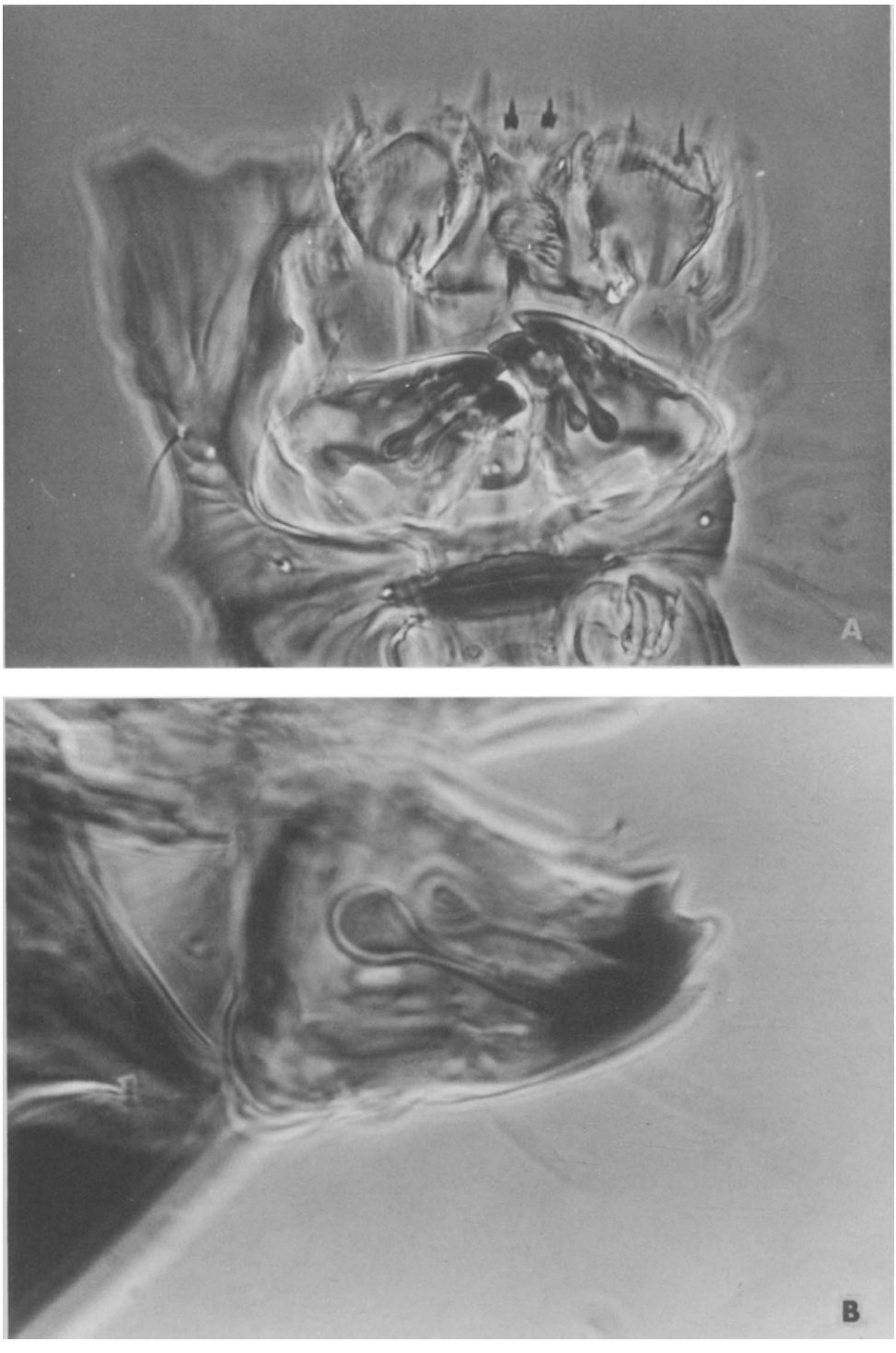
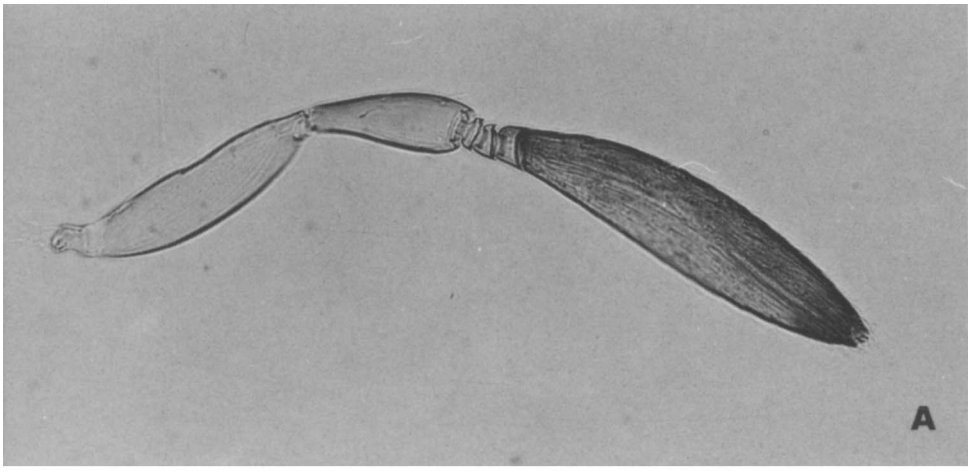


Fig. 2. (A) mandibles of *S. borinquensis* (bidentate); (B) mandibles of *Thysanus* sp. (tridentate).



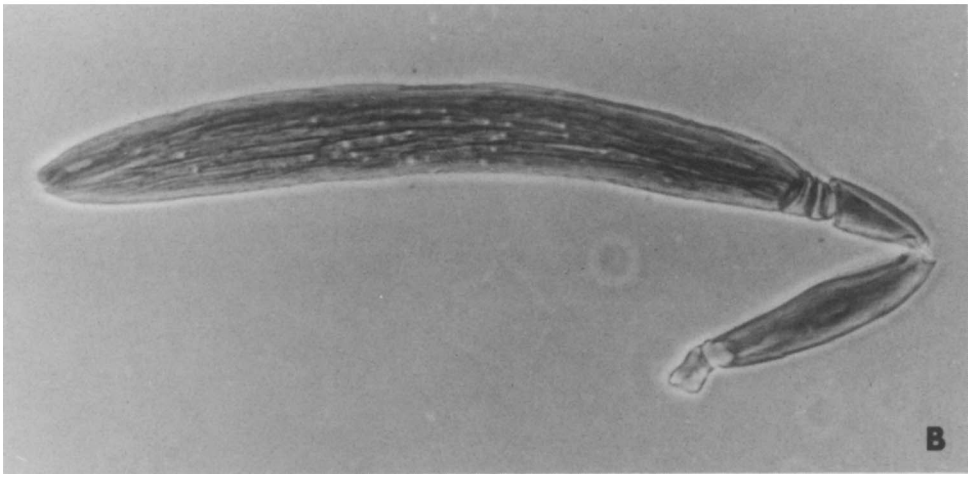


Fig. 3. (A) Antenna of *S. borinquensis;* (B) antenna of *Thysanus* sp. Shows different proportion between club and scape and different numbers of sensilla on antennal club. (Funicular segments not clearly visible; see fig. 4).

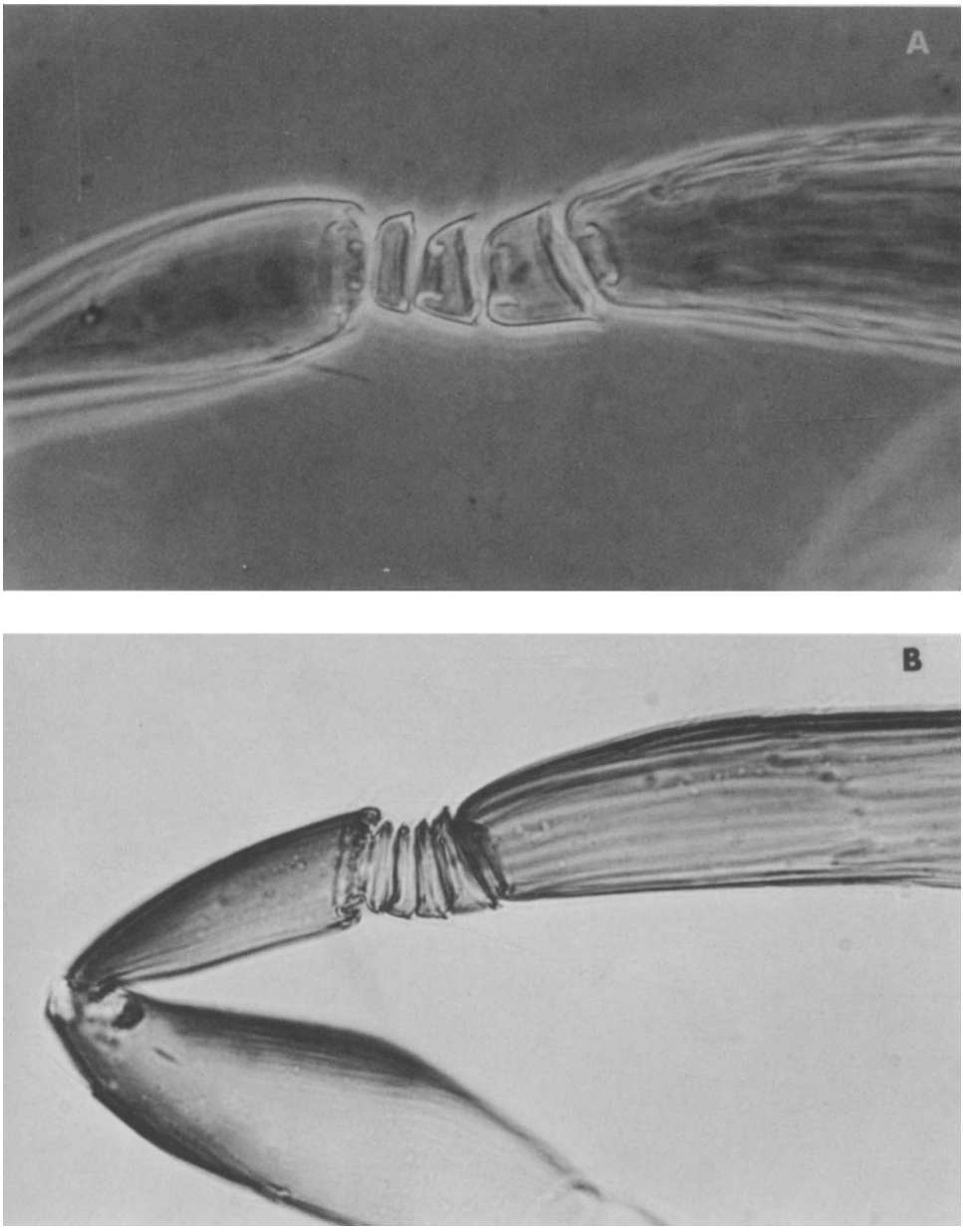


Fig. 4. (A) antennal funicle of *S. borinquensis* (tri-segmented) in contrast with (B) the four-segmented funicle of *Thysanus* sp.

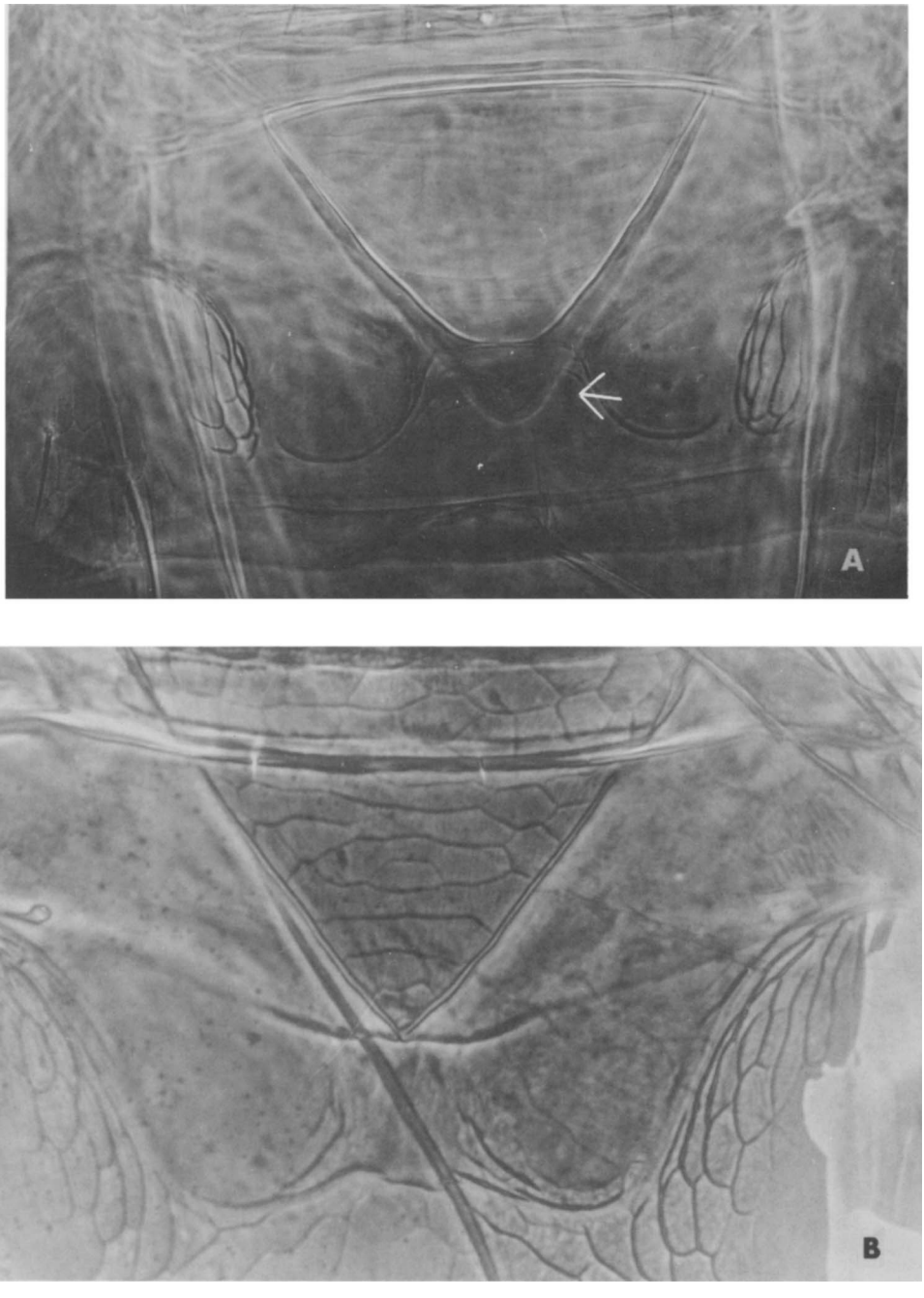


Fig. 5. (A) propodeal triangle of *S. borinquensis* showing a V-shaped apical process; (B) propodeal triangle of *Thysanus* sp. lacks such a process.

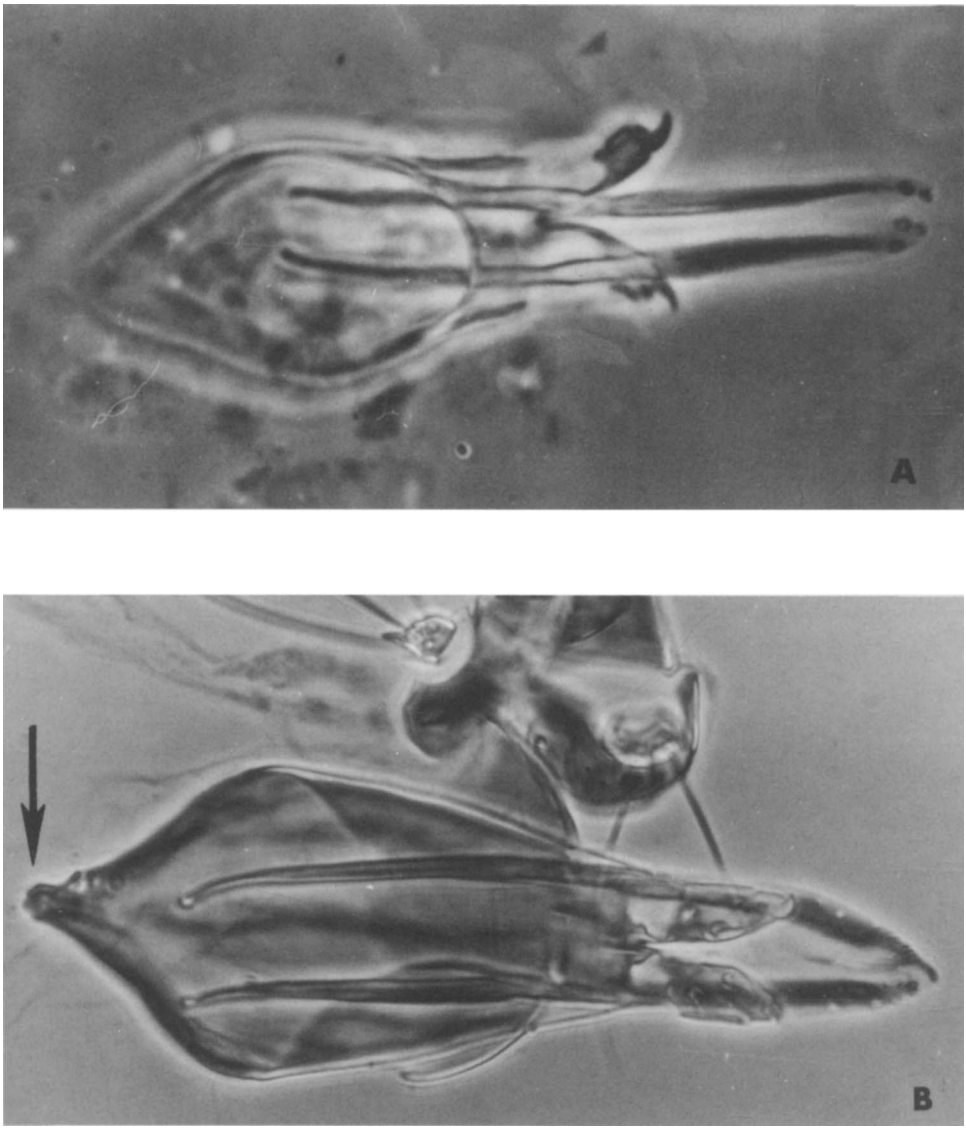


Fig. 6. (A) male genitalia of *S. borinquensis;* (B) male genitalia of *Thysanus* sp. with process on phallobase.

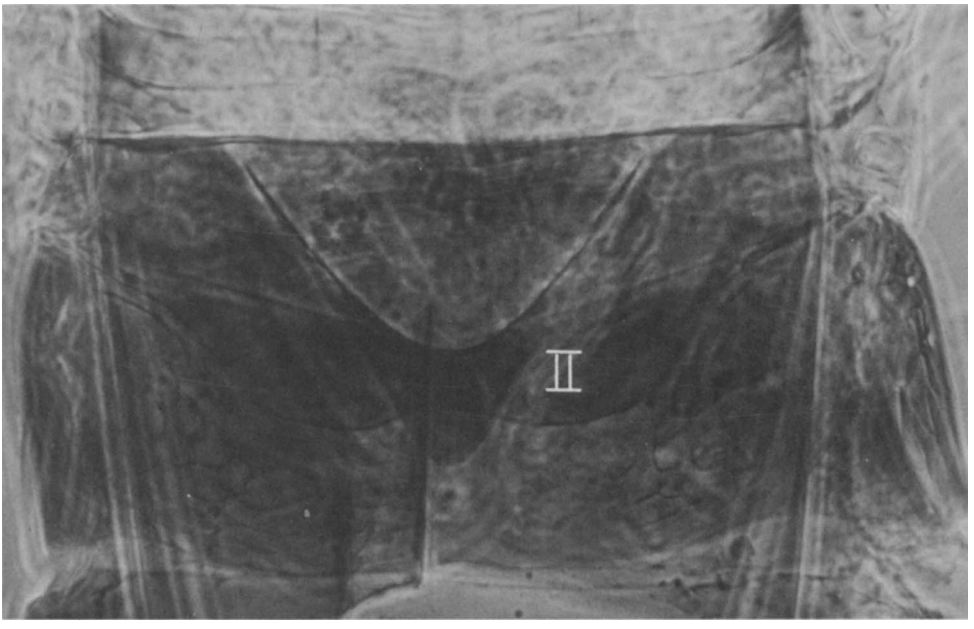


Fig. 7. *Signiphora rhizococci* Ashmead, type ♀, propodeum and basal abdominal tergites; second tergite (II) without pronounced lobes.

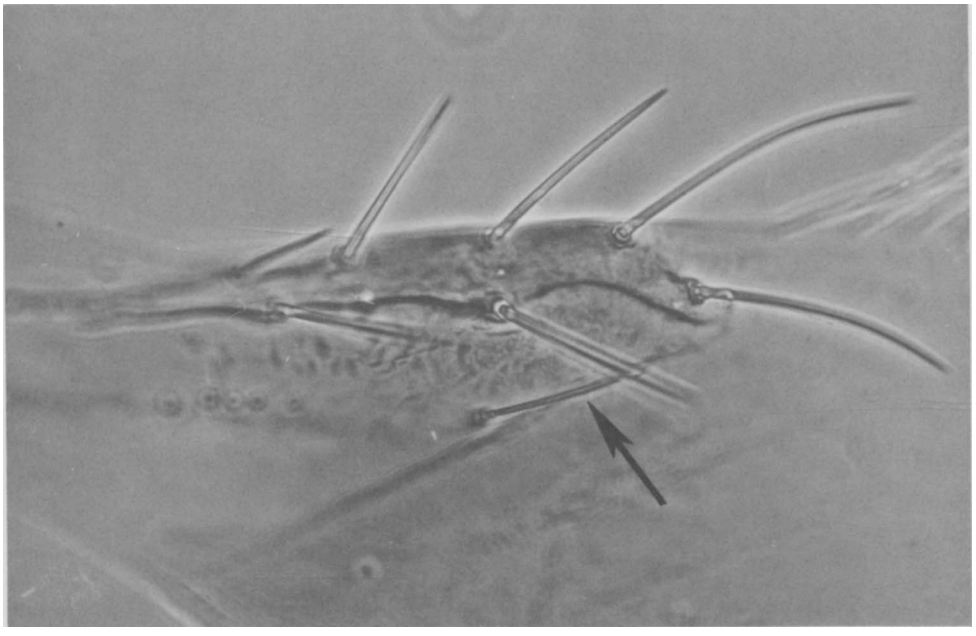


Fig. 8. *Signiphora flavopalliata* Ashmead, type ♀, forewing; arrow indicates discal bristle.

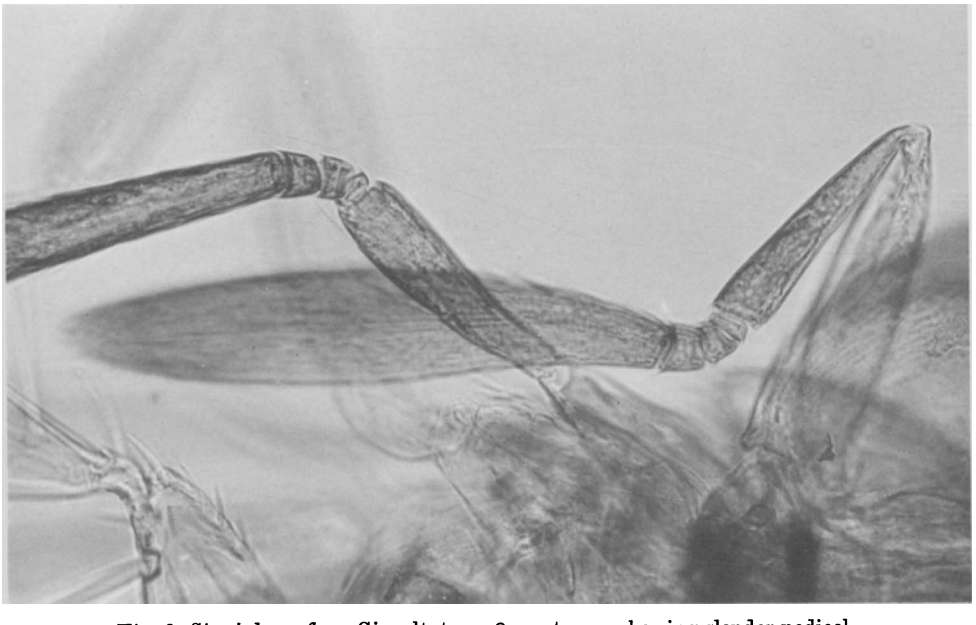


Fig. 9. *Signiphora flava* Girault, type ♀; antenna, showing slender pedicel.

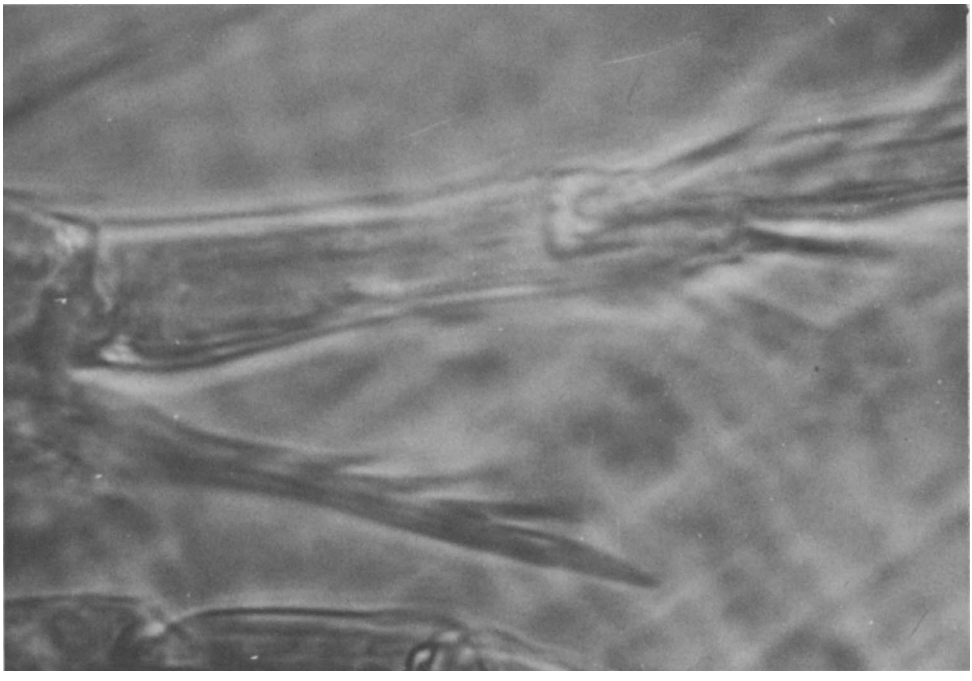


Fig. 10. *Signiphora basilica* Girault, type ♀, mid-tibial spur and basitarsus.

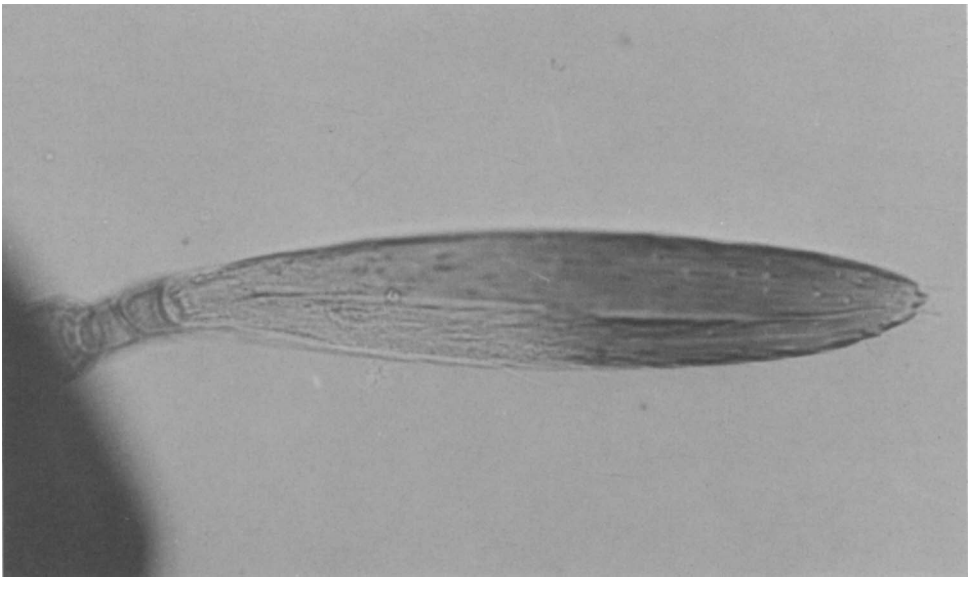


Fig. 11. *Signiphora aspidioti* Ashmead, type ♀; antenna, showing bicolored club.

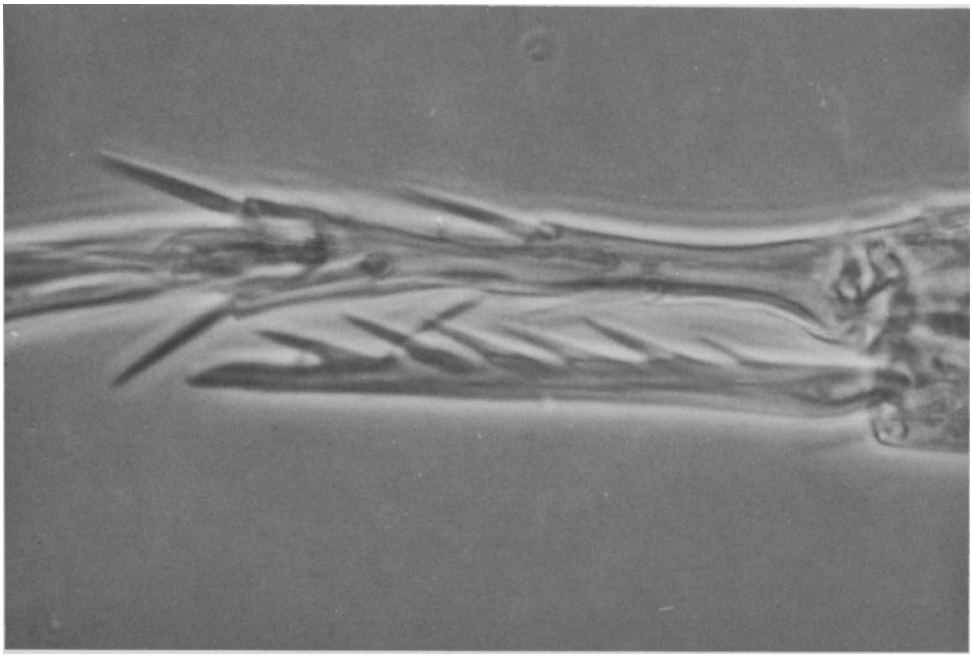


Fig. 12. *Signiphora lutea* Rust, type ♀ : mid-tibial spur and basitarsus.

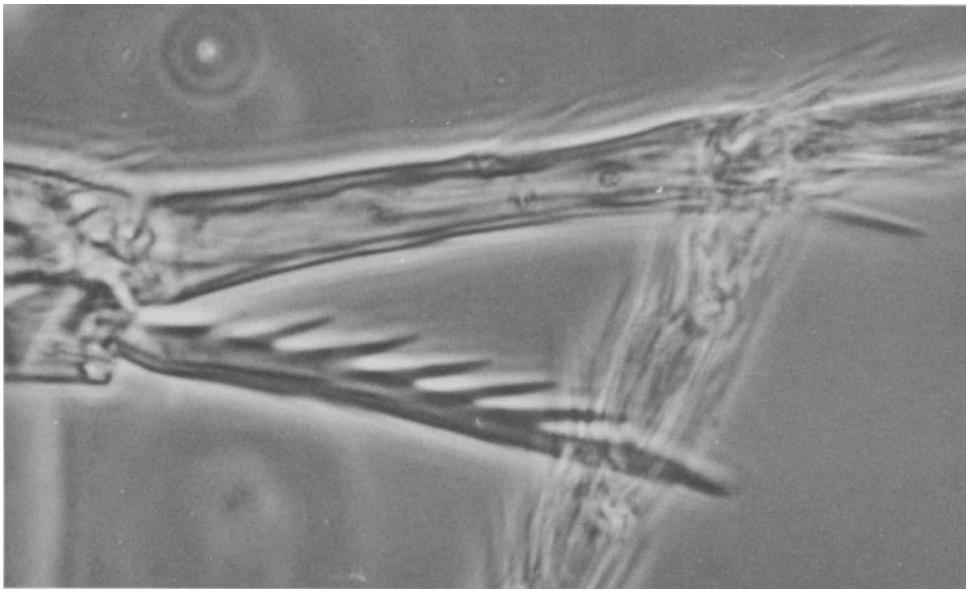


Fig. 13. *Signiphora aleyrodis* Ashmead, type ♀ : mid-tibial spur and basitarsus.

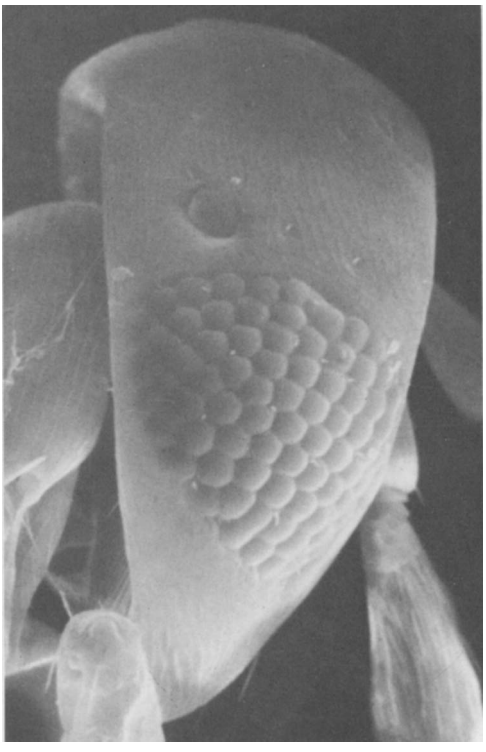


Fig. 14. *Signiphora borinquensis,* ♀ : head, lateral view. (SEM micrograph.)

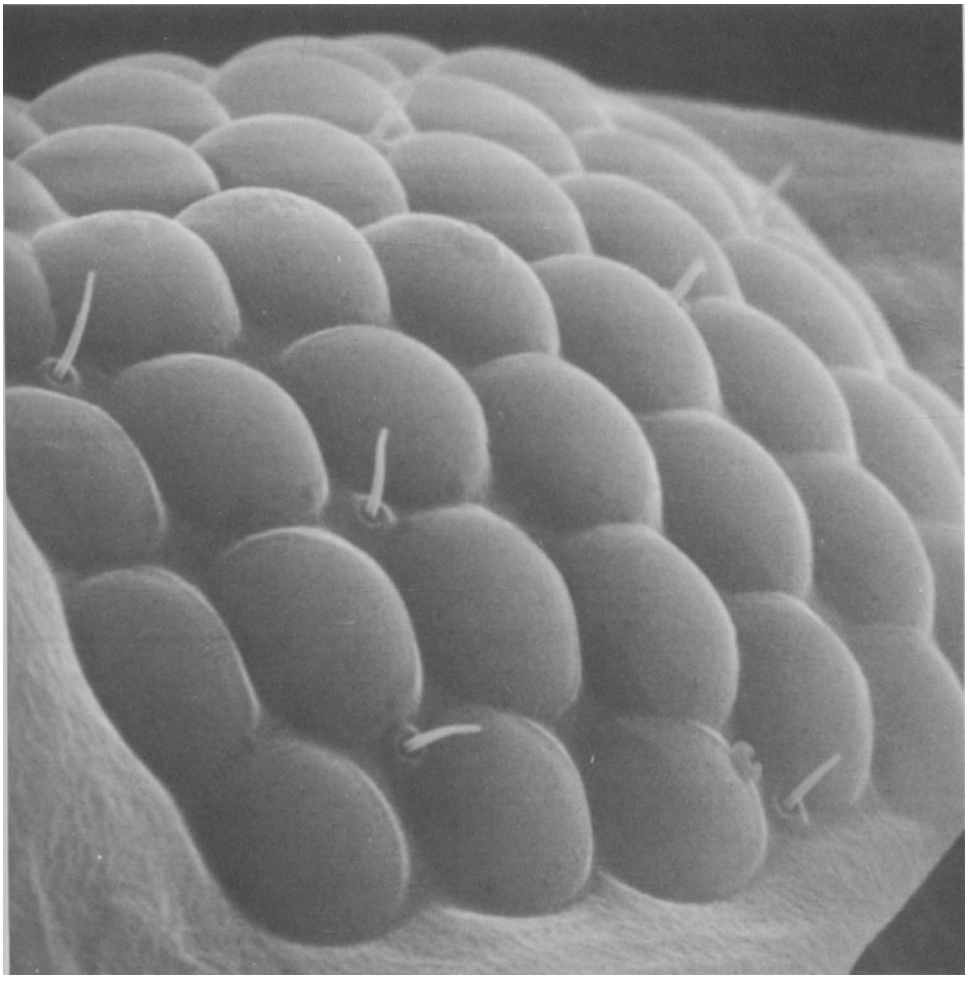


Fig. 15. *Signiphora borinquensis*, ♀ : compound eye. (SEM micrograph.)

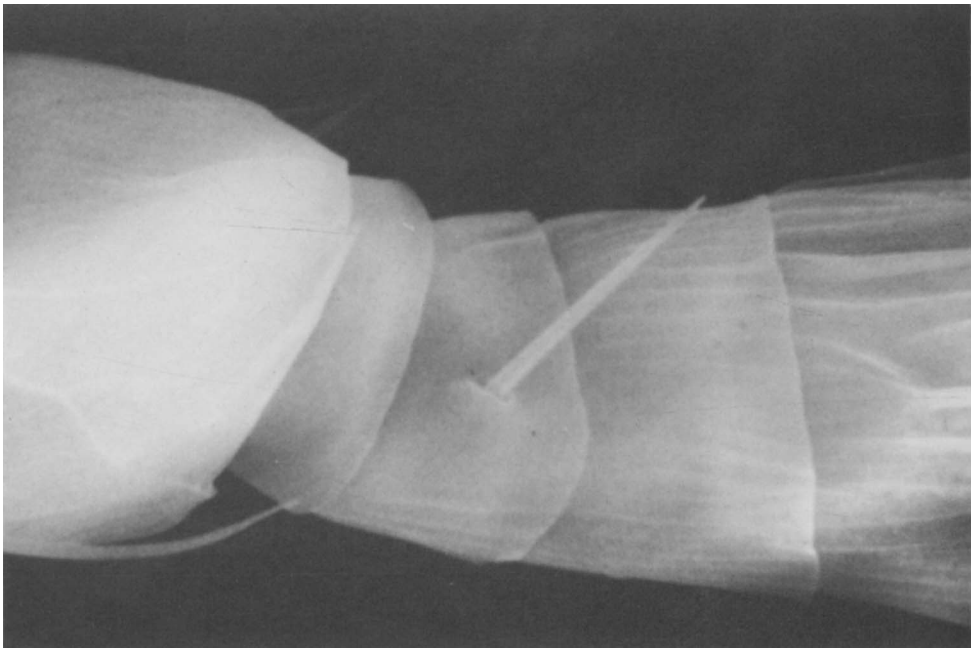


Fig. 16. *Signiphora borinquensis,* ♀ : antennal funicle. (SEM micrograph.)

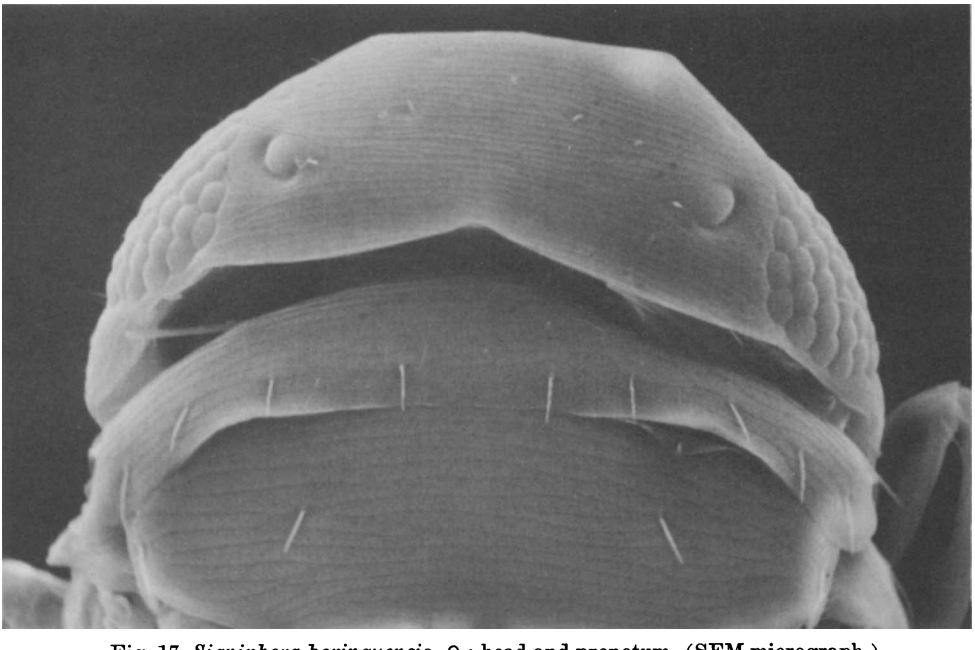


Fig. 17. *Signiphora borinquensis,* ♀ : head and pronotum. (SEM micrograph.)

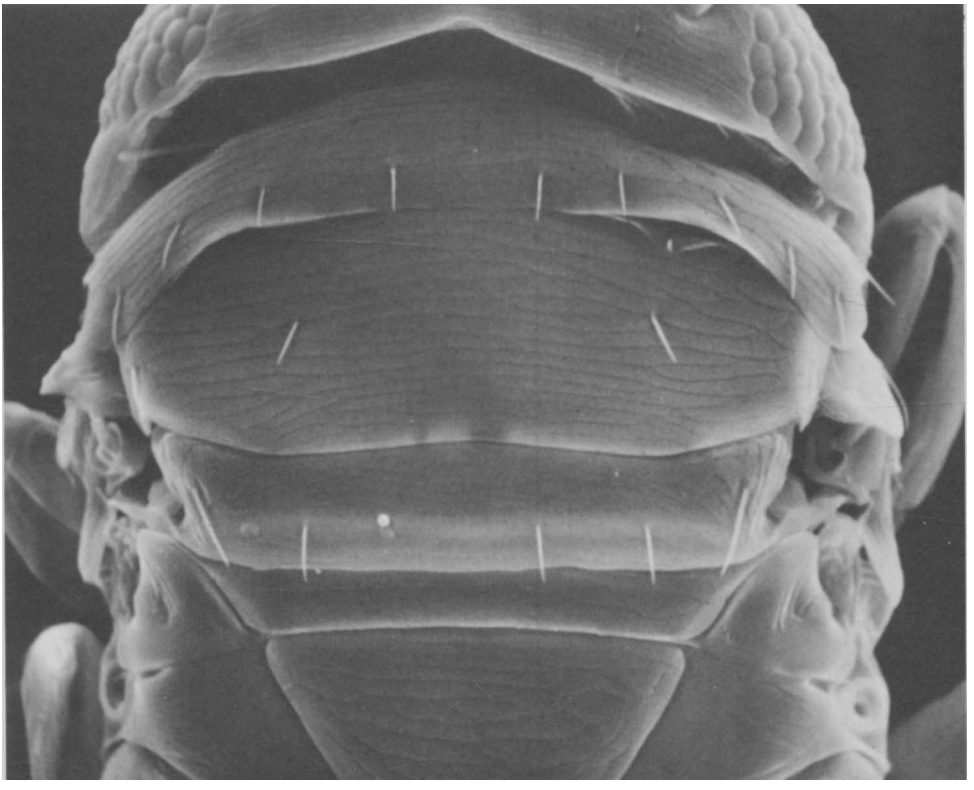


Fig. 18. *Signiphora borinquensis,* ♀ : thorax. (SEM micrograph.)

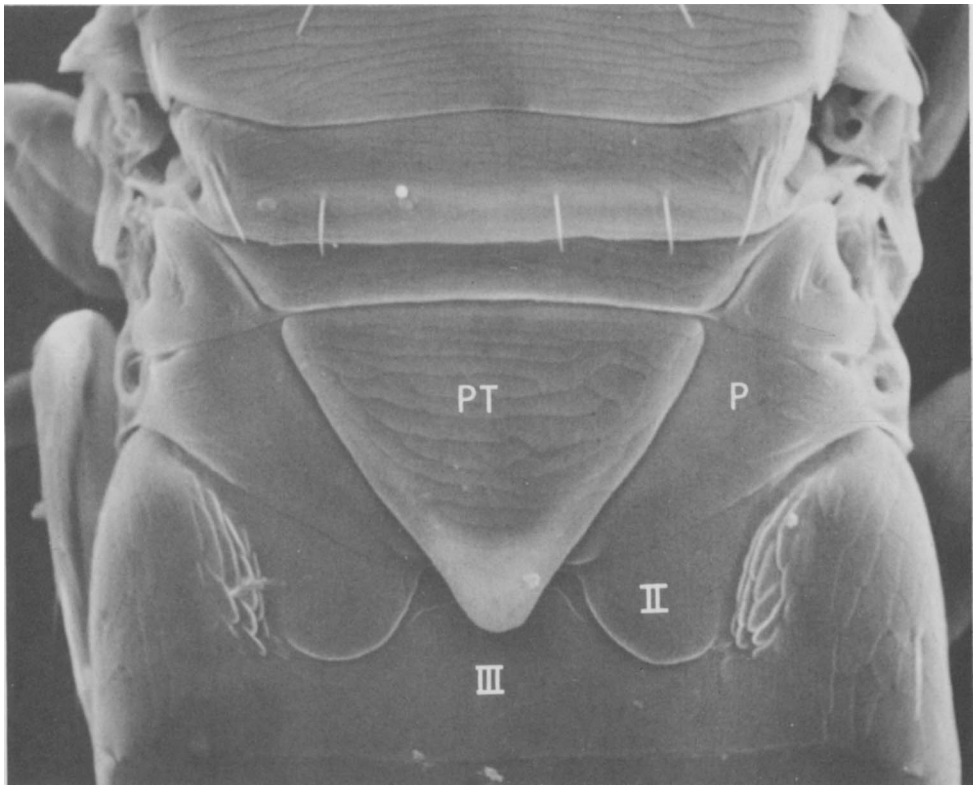


Fig. 19. *Signiphora borinquensis,* ♀ : scutellum, metanotum, propodeum (P) and triangle (PT), second (II) and third (III) abdominal tergites. (SEM micrograph.)

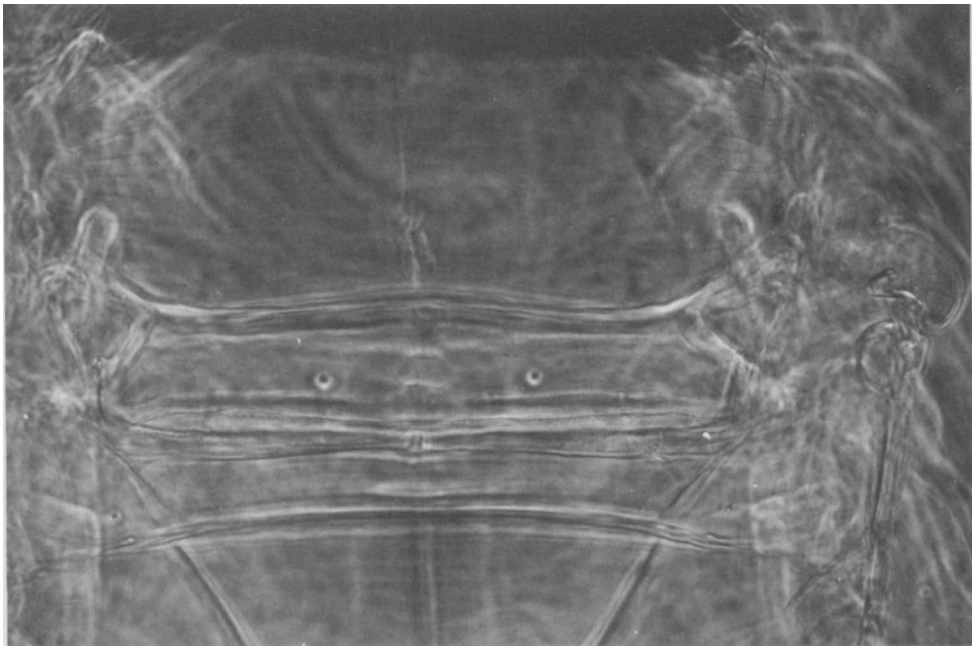


Fig. 20. *Signiphora borinquensis,* ♀ : thorax of cleared specimen, showing the internal scutello-axillar ridges.

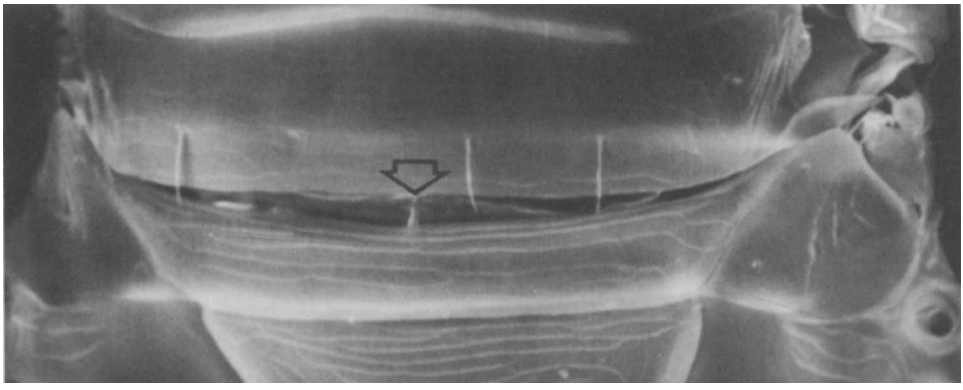


Fig. 21. *Signiphora borinquensis,* ♀ : metanotum; arrow indicates the anteromedian apodeme. (SEM micrograph.)

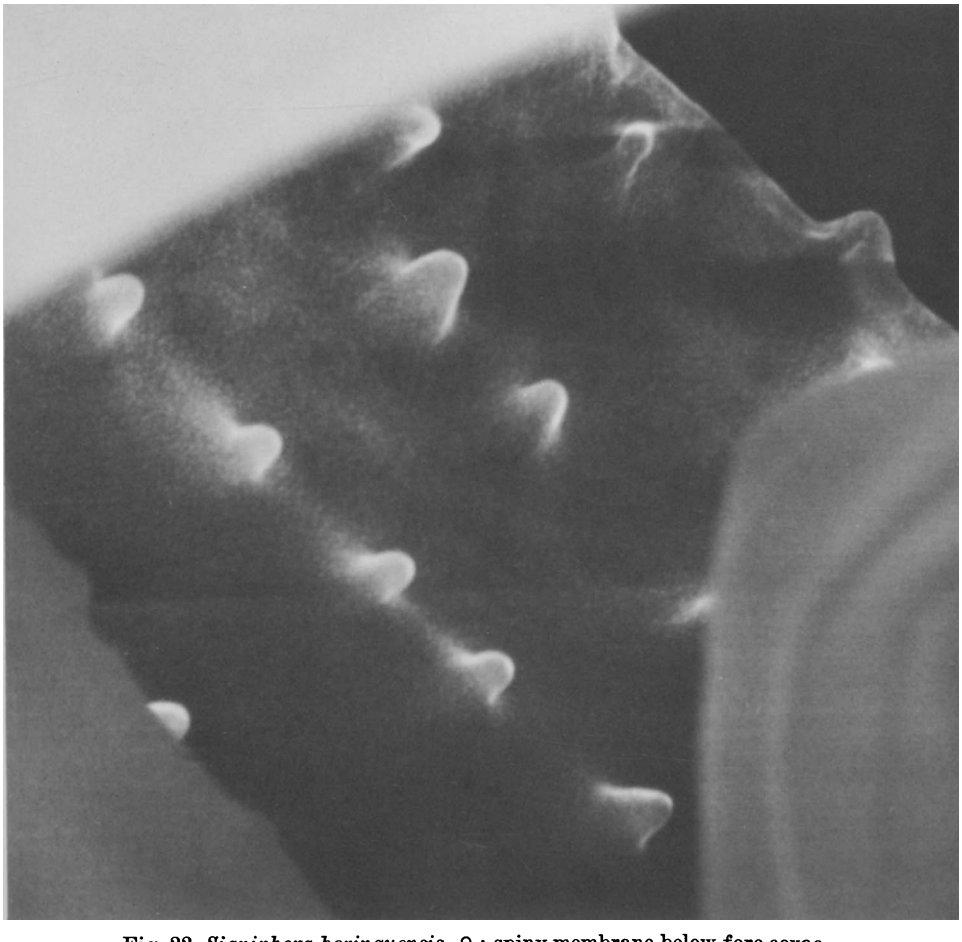


Fig. 22. *Signiphora borinquensis,* ♀ : spiny membrane below fore coxae.

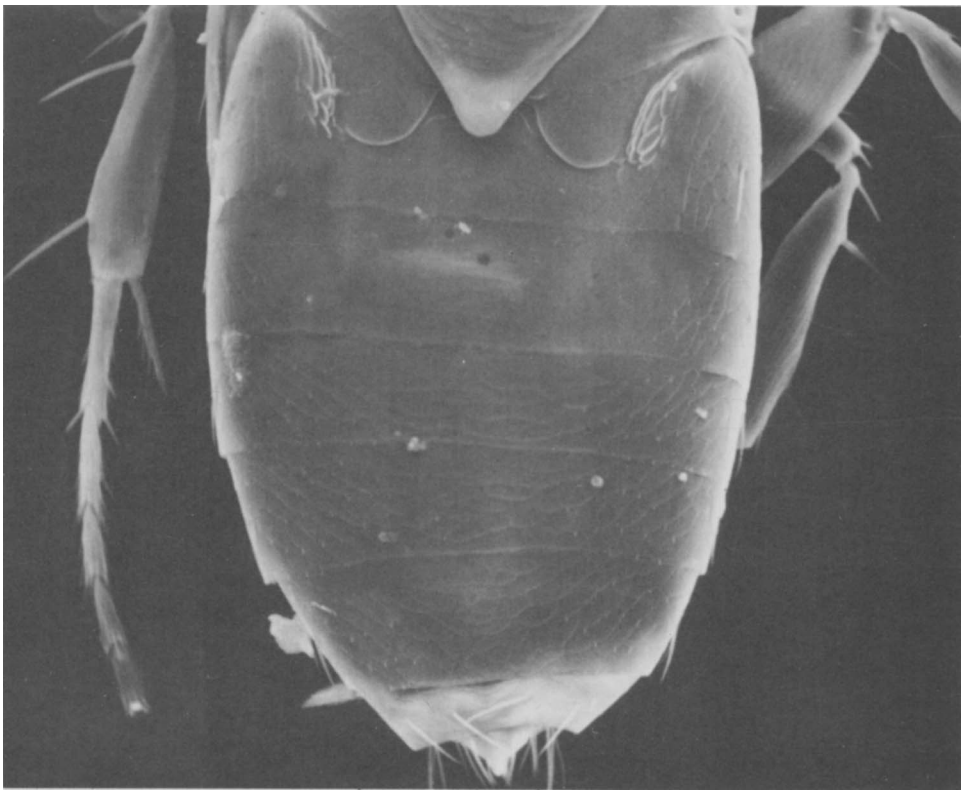


Fig. 23. *Signiphora borinquensis,* ♀ : gaster. The middle leg can also be seen. (SEM micrograph.)

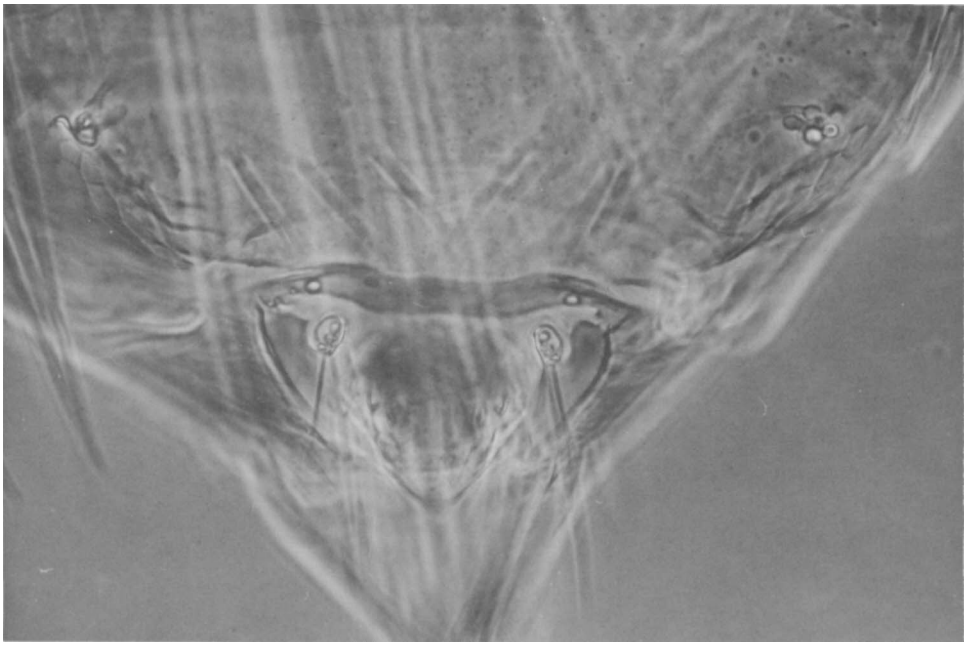


Fig. 24. *Signiphora borinquensis,* ♀ : ninth and tenth abdominal tergites. The spiracles on the eighth tergite can also be seen.

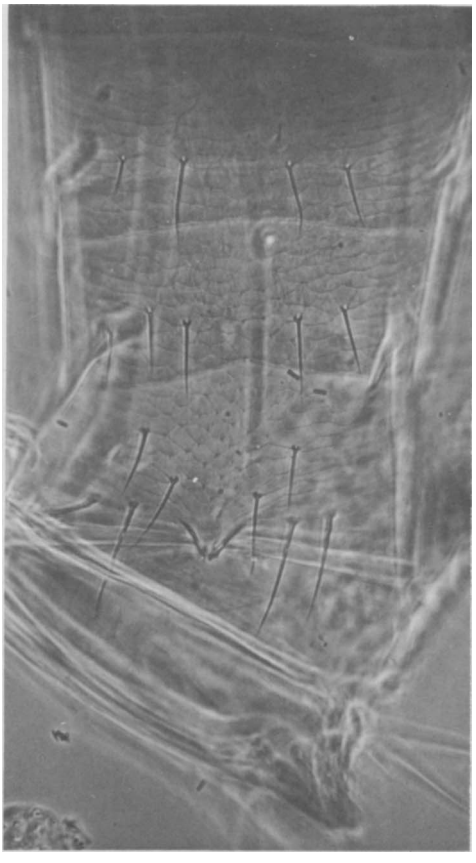


Fig. 25. *Signiphora borinquensis*, ♀ : abdominal sternites V to VII.

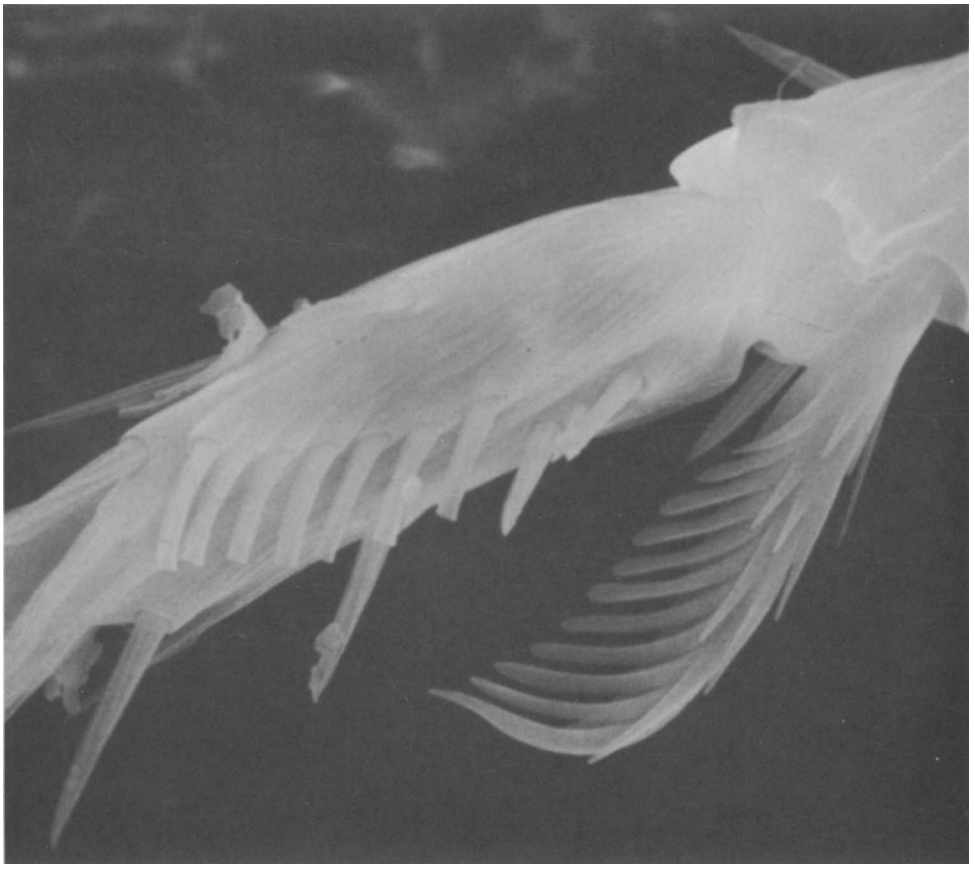


Fig. 26. *Signiphora borinquensis,* ♀ : strigil on fore leg. (SEM micrograph.)

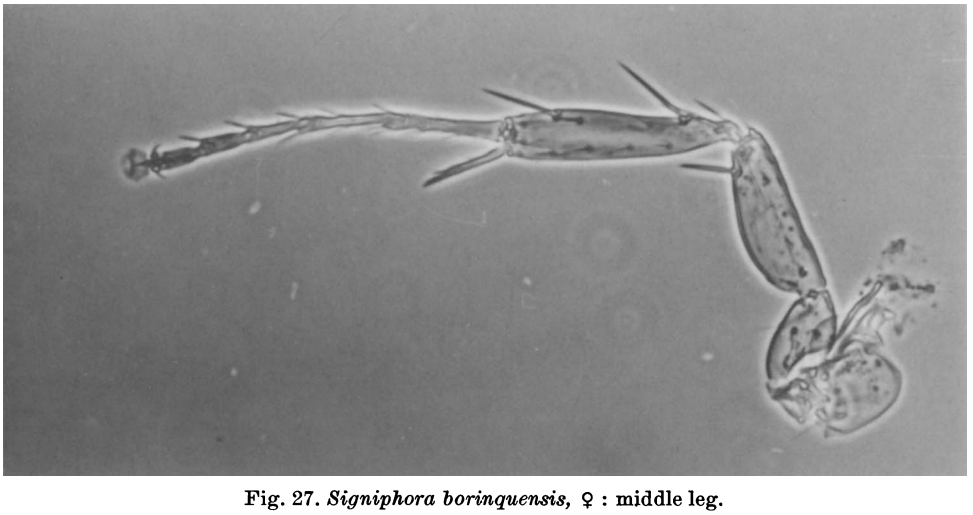


Fig. 27. *Signiphora borinquensis,* ♀ : middle leg.

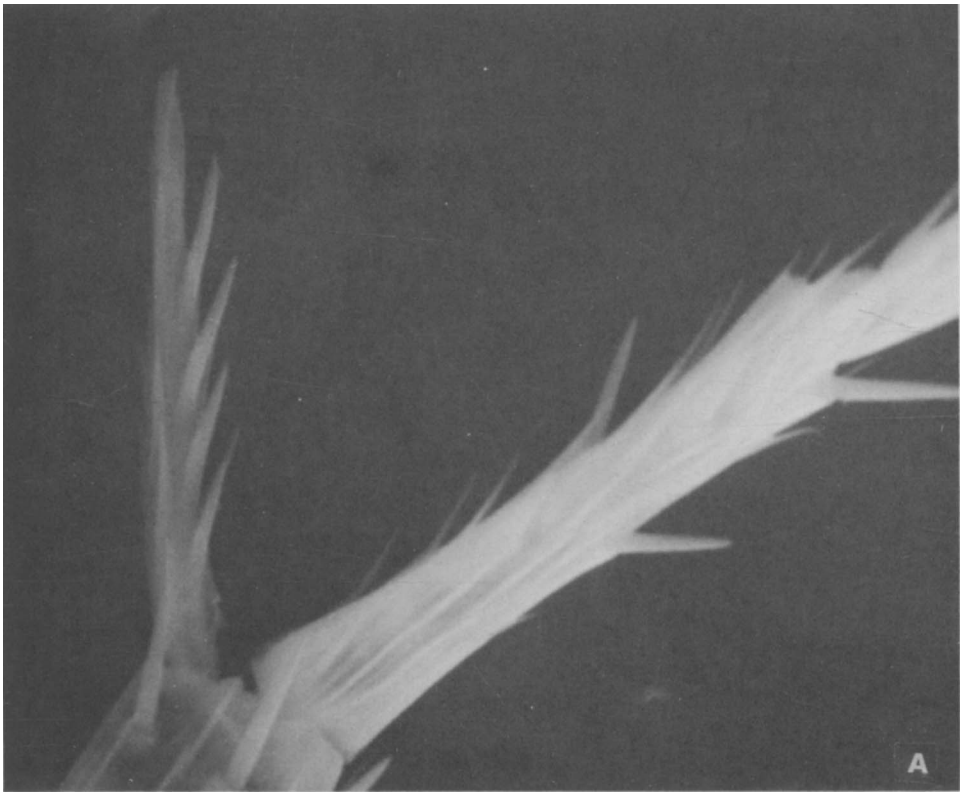


Fig. 28A: *Signiphora borinquensis*, ♀ : mid-tibial spur, lateral view, showing length relative to basitarsus. (SEM micrographs.)

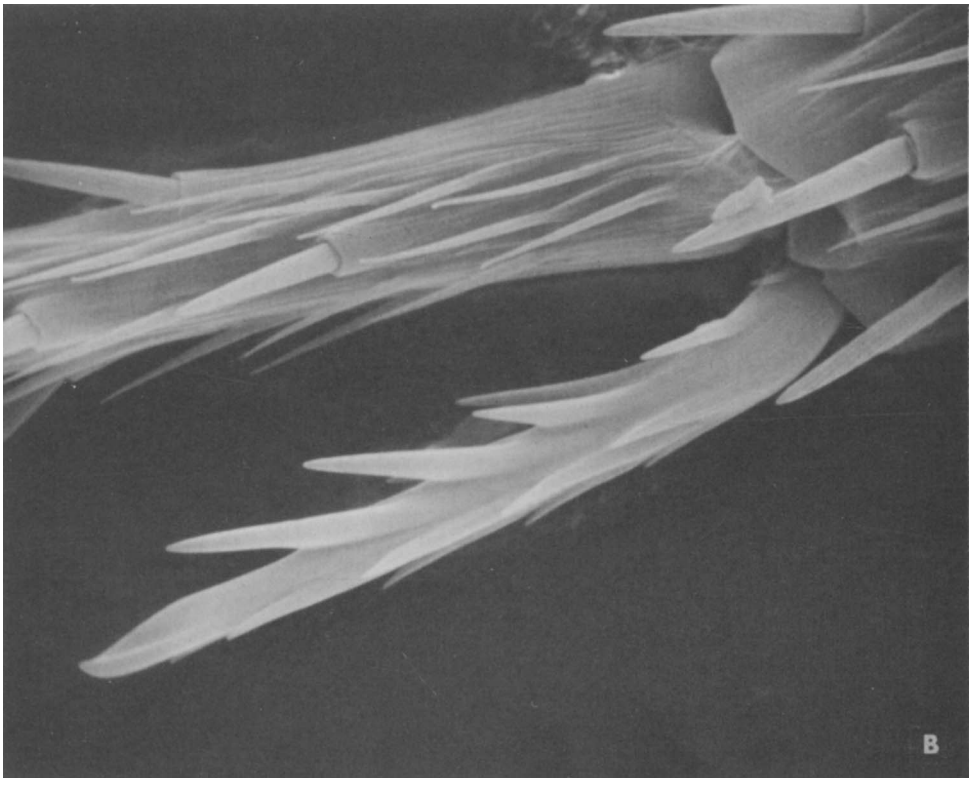


Fig. 28B: *Signiphora borinquensis,* ♀ : mid-tibial spur, inner (posterior) view at two different angles.

Fig. 28C: *Signiphora borinquensis,* ♀ : mid-tibial spur, inner (posterior) view at two different angles.

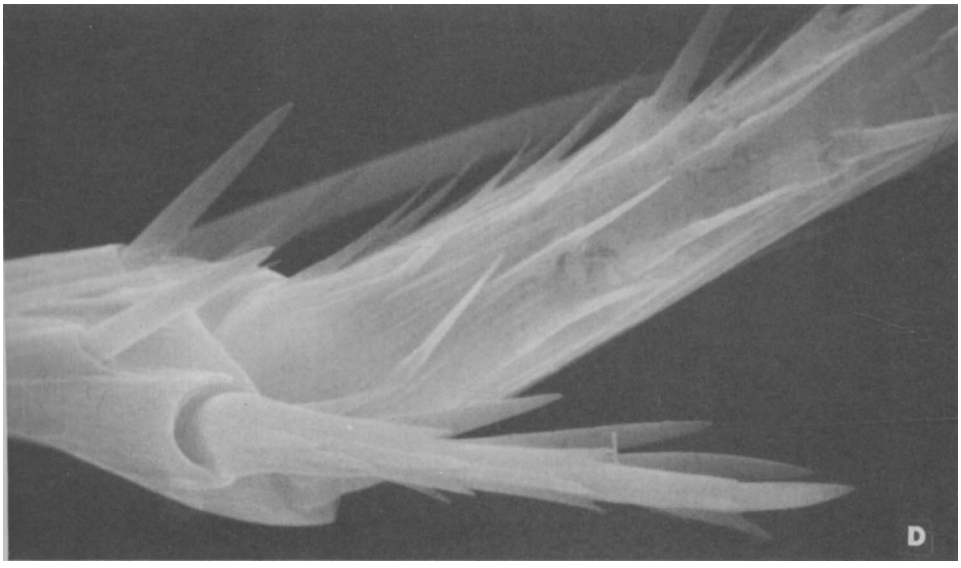


Fig. 28D: *Signiphora borinquensis,* ♀ : mid-tibial spur, outer (anterior) view. (SEM micrographs.)

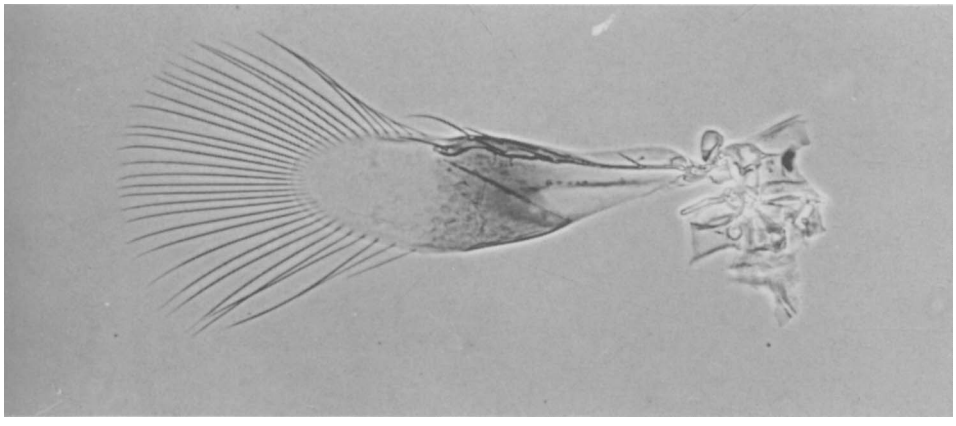


Fig. 29. *Signiphora borinquensis,* ♀ : forewing.

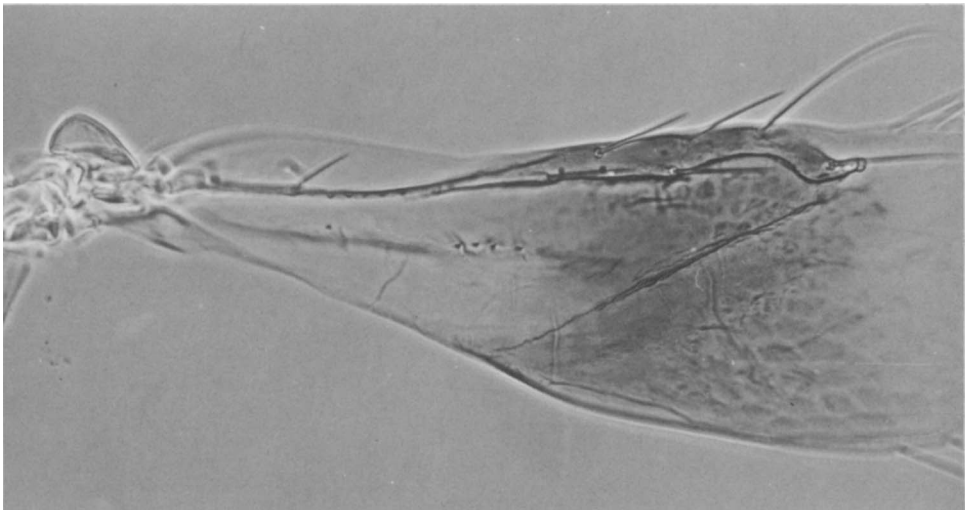


Fig. 30. *Signiphora borinquensis,* ♀ : forewing, showing the minute setae on ventral surface and details of venation.

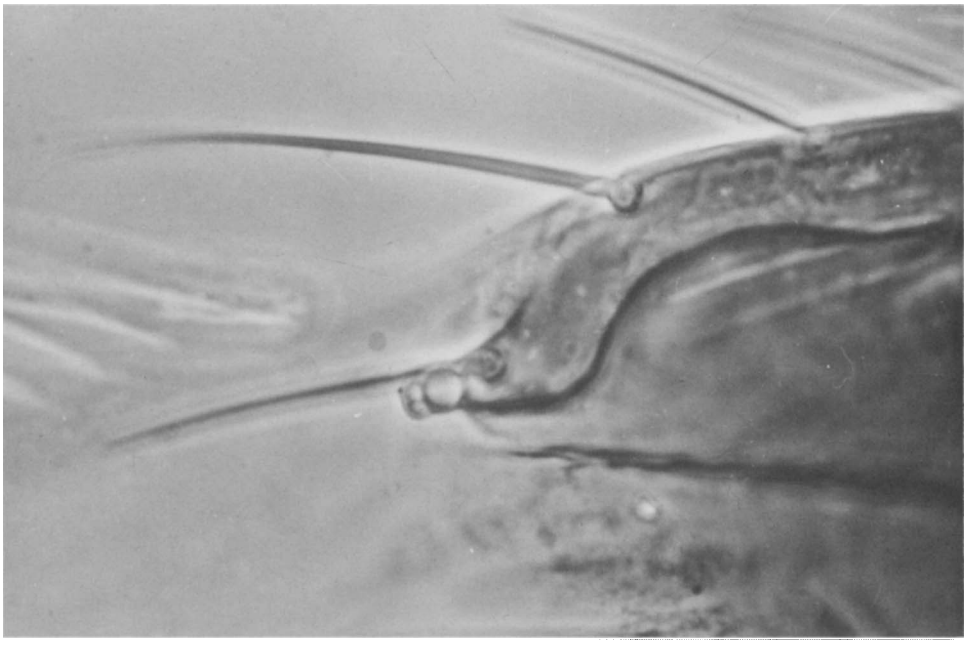


Fig. 31. *Signiphora borinquensis,* ♀ : stigmal vein of forewing.

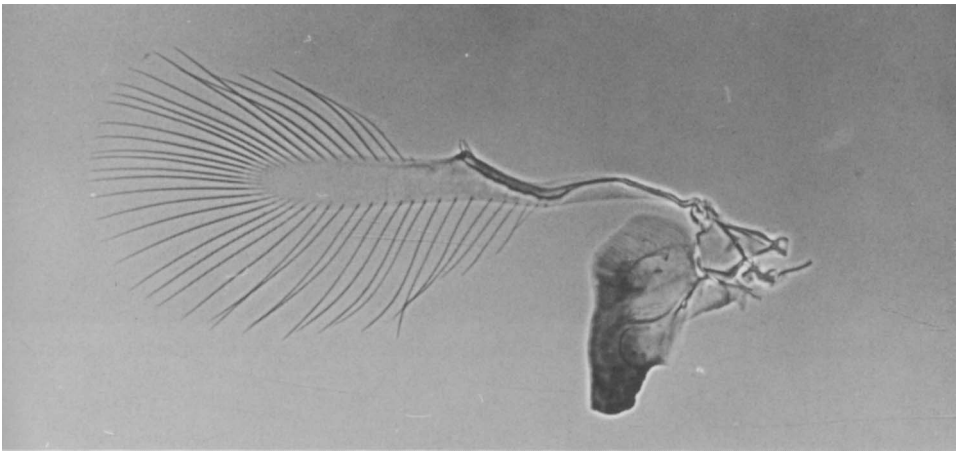


Fig. 32. *Signiphora borinquensis*, ♀ : hind wing.

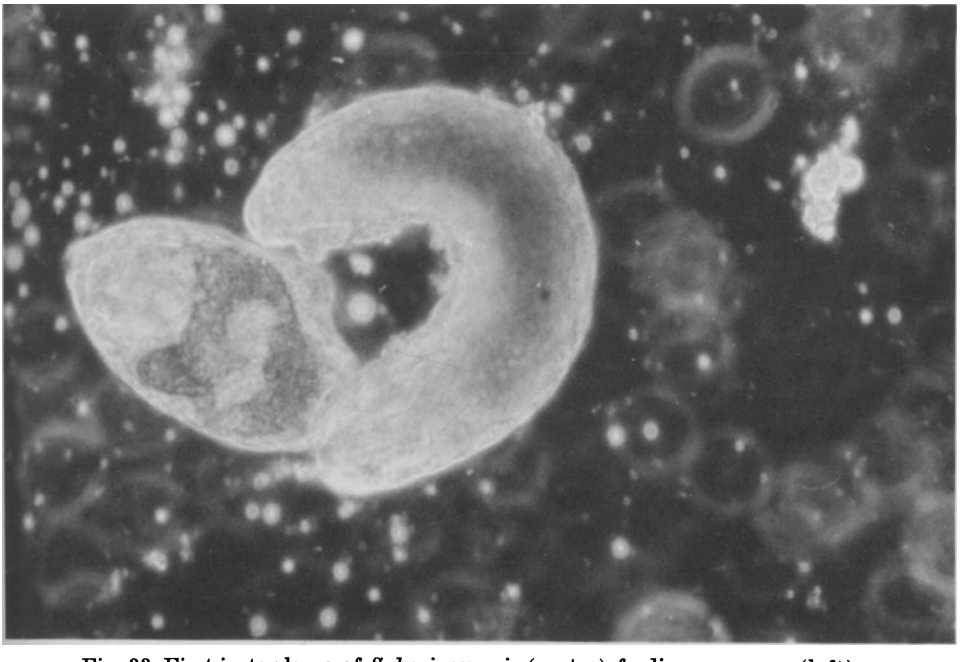


Fig. 33. First instar larva of *S. borinquensis* (center) feeding on an egg (left) of its host, cactus scale.

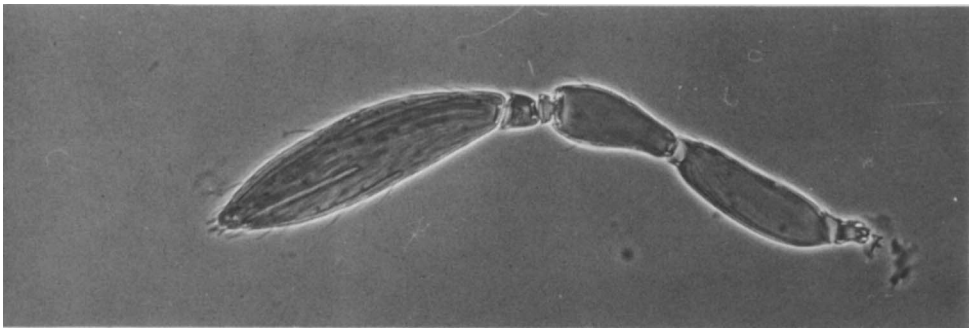


Fig. 34. *Signiphora borinquensis*, ♀ : abnormal antenna with only two funicular segments.

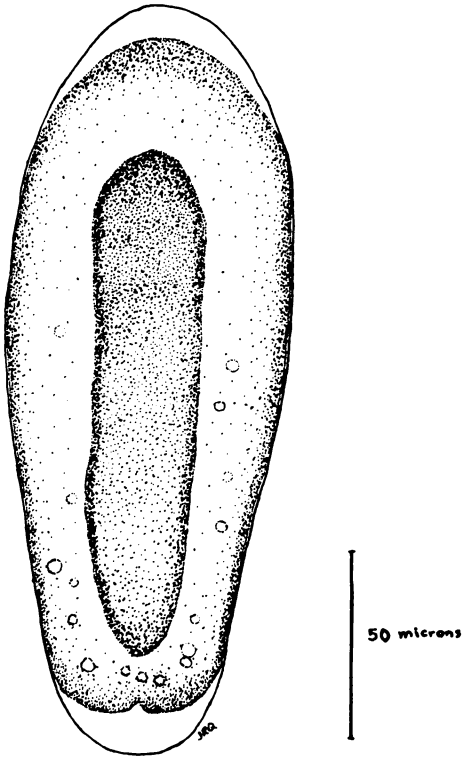


Fig. 35. Newly laid egg of *S. borinquensis*.

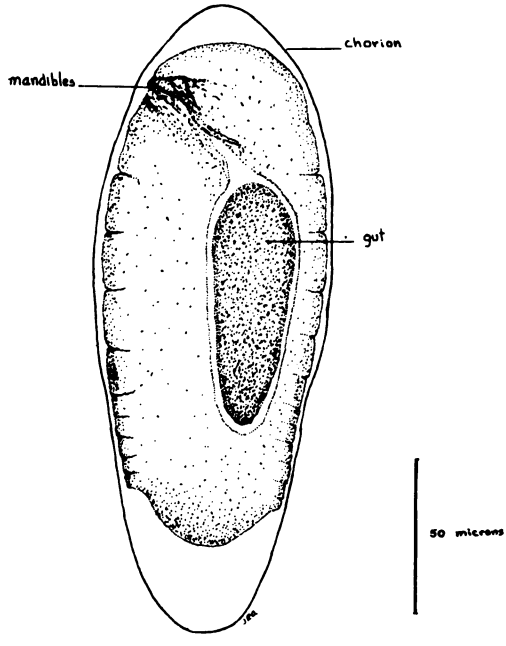


Fig. 36. Egg of *S. borinquensis* ready to hatch, 72 hours after being laid.

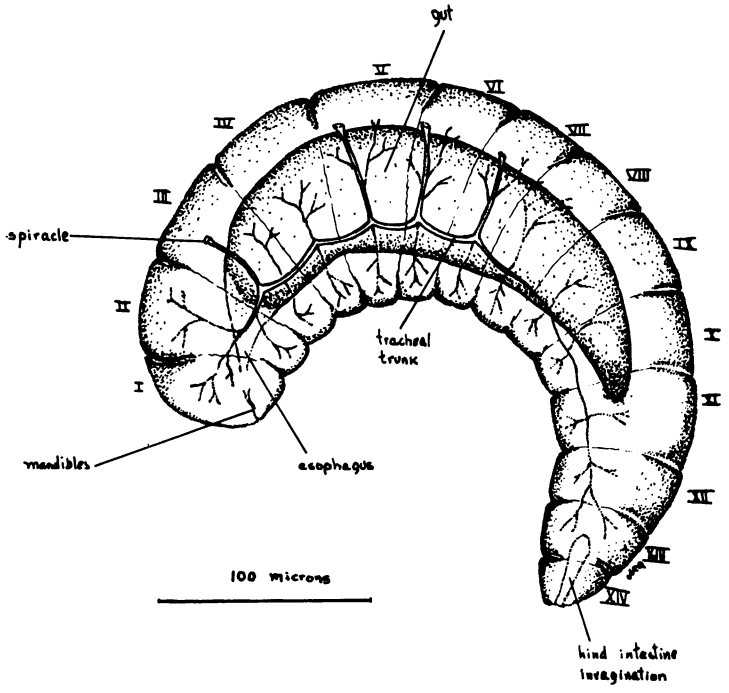


Fig. 37. First larval instar of *S. borinquensis.*

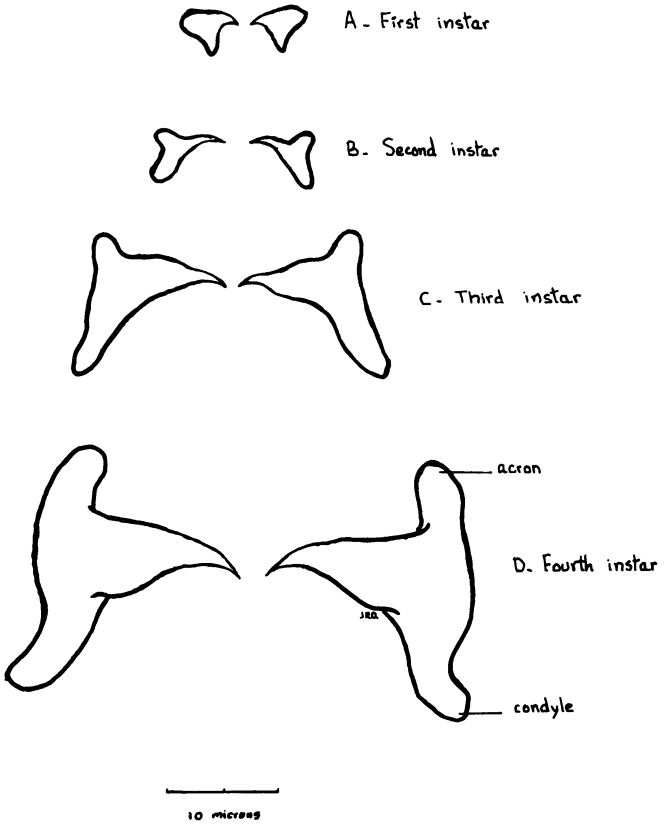


Fig. 38. Mandibles of different larval instars of *S. borinquensis.*

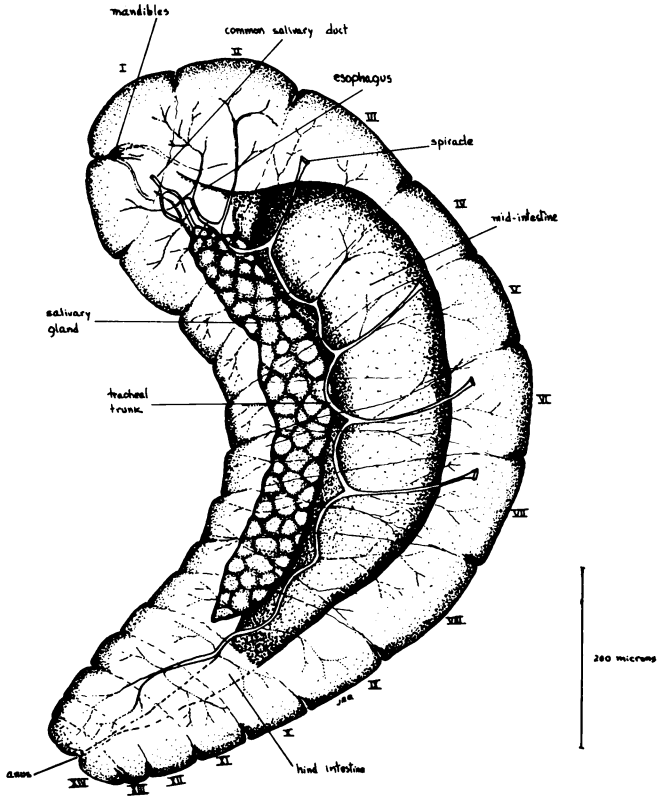


Fig. 39. Fullgrown (fourth instar) larva of *S. borinquensis.*

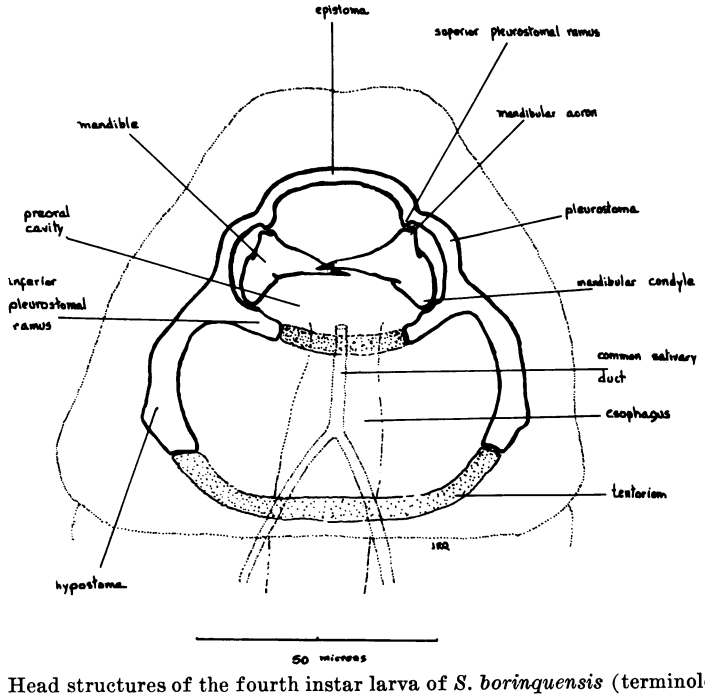
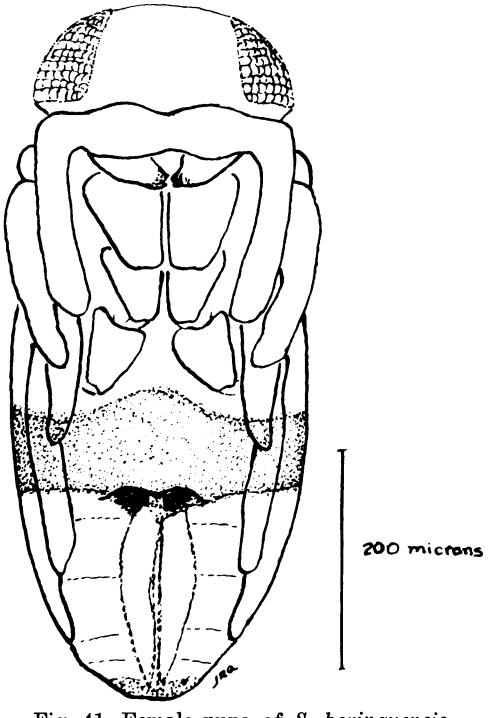


Fig. 40. Head structures of the fourth instar larva of *S. borinquensis* (terminology of Vance and Smith, 1933).



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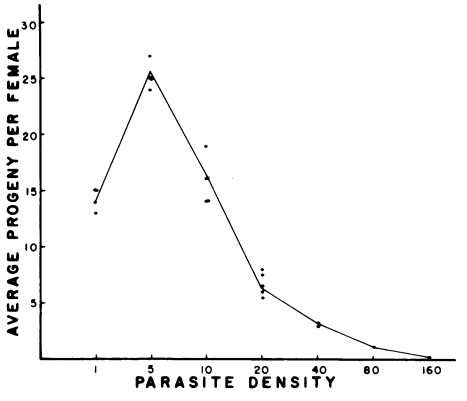

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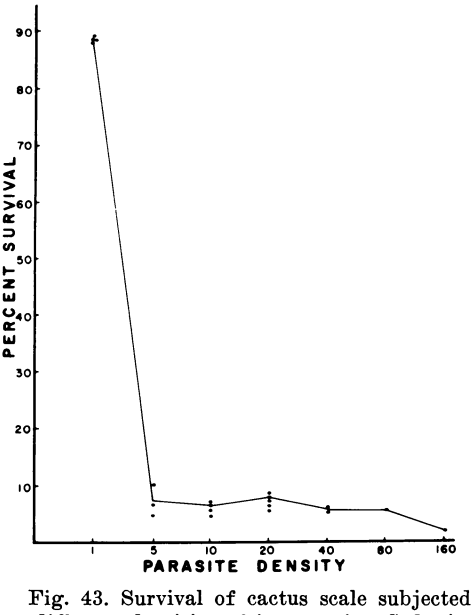

Fig. 43. Survival of cactus scale subjected to different densities of its parasite, *S. borinquensis.* Approximate constant density of host per test: 190.

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