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A preliminary report on the World species of *Bemisia* Quaintance and Baker and its congeners (Hemiptera: Aleyrodidae) with a comparative analysis of morphological variation and its role in the recognition of species

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A preliminary report on the World species of *Bemisia* Quaintance and Baker and its congeners (Hemiptera: Aleyrodidae), with a comparative analysis of morphological variation and its role in the recognition of species

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Abstract. Extreme economic effects globally of various populations of the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) led to an in depth study of the morphology of that species as well as that of numerous other species of whiteflies in the genus *Bemisia* Quaintance and Baker and other similar appearing species. The data collected are presented here as illustrations of the puparia (fourth instar nymphal stages) and discussions of morphology as it relates to species and generic separations within this closely knit group of insects. A brief history of the pest outbreaks of *B. tabaci* is given and an overview of the important morphological characteristics of aleyrodine whiteflies is provided. Each of the eighty illustrations is accompanied by a discussion of the more important aspects of morphology and how it relates to other populations or species with similar structure and characteristics.

Key words. Hemiptera, Aleyrodidae, whiteflies, *Bemisia tabaci*, puparia.

Introduction

This publication is meant to be a companion publication to Gill and Brown (2010), in which the problems with whitefly morphological variability are discussed as they relate to proposing a need for a well-supported phylogenetic classification, as well as a need for more accurate species identification, and a discussion of how molecular data may solve some of these grave issues. Included here are a brief history of the *Bemisia tabaci* problems worldwide, a brief overview of the basic morphology of whiteflies, primarily those used in species identification, comments and illustrations of various specimens of *Bemisia*, *Aleyrodes* Latreille and other morphologically similar genera with discussions of their variability and its effects on generic placement and general classification.

History

Bemisia tabaci was first described by Gennadius from Greece in 1889. It has occurred in the United States at least since 1900, when it was described as *Bemisia inconspicua* (Quaintance, 1900). Later, Louise Russell (1975) found collections in the U.S. National Museum from 1894. The species was for a time a pest of sweet potatoes (*Ipomea batatas* (L.) Lam., Convolvulaceae) in the Southeast, hence the commonly used name “sweetpotato whitefly.” In 1986, a whitefly then indistinguishable morphologically from *B. tabaci* began causing severe damage to greenhouse grown poinsettias (*Euphorbia pulcherrima* Willd. ex Klotsch, Euphorbiaceae) in Florida, and later to many other greenhouse plants in that state. Several years later, this whitefly began causing serious losses to field grown crops in Texas and Arizona. In 1991, the whitefly caused millions of dollars worth of losses in the Imperial and Palo Verde Valleys of California and in the Yuma Valley of Arizona (Gill 1992, Gonzalez et al. 1992). By that time, various researchers (Brown et al. 1992, 1994, 1995, 2004; Coats et al. 1994; Costa and Brown 1990; Costa and Brown 1991; Costa et al. 1993; Duffus, in Hsing-Yeh et al. 1992; Perring et al. 1992; Perring et al. 1993) had concluded that this whitefly was very

different from the *B. tabaci* that occurred throughout the U.S. previously. The differences involved chemical, behavioral, genetic and other criteria. Some very minor morphological differences were also found in the puparial stages. The taxonomic value of these differences was unclear, but it led to the question of how to classify or name these two forms, such as treating them as full species, or simply as a race, strains or biotypes. The new form was eventually described as *Bemisia argentifolii* Bellows and Perring, the silverleaf whitefly (Bellows et al. 1994). The scientific value of full species recognition for this form has been debated by numerous researchers, including Campbell et al. (1993) and Barnaga (1993), and the question may never be answered to the satisfaction of everyone. For example, De Barro et al. (2005) suggested that *B. argentifolii* should be synonymized with *B. tabaci*, but then later suggested that there are at least 24 separate species within the *tabaci* complex (Dinsdale et al. 2010; De Barro et al. 2011).

The *B. argentifolii* population was eventually called strain (or biotype) “B” while the original populations at least in California and Arizona before 1990 were to be called strain “A.” The first known record for *B. tabaci* in Hawaii was a collection made in 1982 (Lai 1985). While these specimens have not been located, a collection made in quarantine in California from Hawaii in 1984 is available for study, and these specimens agree morphologically with strain “B.” Further studies by Costa et al. (1993) showed the presence of the “B” strain in Hawaii but failed to show the presence of strain “A” on the Islands, and the 1982 collection was very likely also strain “B.” The 1982 collection appears to be the first known encounter with strain “B.” Work by Judy Brown and others (listed above) suggested that “B” was rapidly spreading in the New World and Old World alike. These studies on the *Bemisia* species had not positively proven the relationships between *B. tabaci* and *B. argentifolii*, nor had they proven the origin of *B. argentifolii*. A combined analysis of data gathered by many researchers suggests that a species complex is involved with *B. tabaci*, *B. argentifolii*, other morphologically inseparable populations of “*tabaci*”, and the very similar species *B. formosana* Takahashi and *B. graminus* David and Winstone. At that time, analysis also suggested a possible Old World origin for *B. argentifolii* (strain B) and possibly a New World origin for *B. tabaci* (strain A).

As research continued into the taxonomic issues of *B. tabaci*, it was discovered that there was a significant amount of molecular variation that occurred in otherwise morphologically identical forms (reviewed in Brown, 2010 and Gill and Brown, 2010). Also, as a result of conferences and action committee meetings convened to address the economic effects of *B. tabaci sensu lato*, a project was started that would attempt to clarify the morphological issues of the genus *Bemisia* in general, and *B. tabaci* specifically.

First, however, it is advisable to cover some pertinent points regarding whitefly morphology and taxonomy.

Taxonomy

Whiteflies are classified primarily by using morphological characters found in the puparium or 4th instar nymph (popularly referred to as the pupa). Adult whiteflies are unknown for most of the described whitefly species. Adults have some morphological characters that allow species separation, but in most cases adult morphology appears to be valuable at the generic level and above. The adult male typically has more useful morphology for species or generic separation than the female, especially on the genitalia. For an in depth review of the external morphology of whiteflies see Gill (1990).

Variable puparial morphology (polyphenism) is poorly understood and it has been shown repeatedly that it can be affected strongly by environment and particularly by the structure of the leaves of the host. Mechanisms for this are unknown but Neal and Bentz (1999) have shown that the phenomenon is triggered by environmental factors encountered by the first instar nymph. There are few morphological structures of taxonomic use in whiteflies, and their plasticity and other attributes result in a poor understanding of both generic limits and interspecific variation. Work by Campbell et al. (1994, 1995) on 18s rDNA has led to some phylogenetic insights, but many more generic groups need to be added before firmer conclusions can be drawn.

Following are some of the morphological characteristics that have been used in whitefly taxonomy:

Puparia

Body margin - The marginal line of most whitefly puparia is crenulated, toothed or bead-like. The depth, width and uniformity of the crenulations have been used for separation of species or species groups. The stigmatic furrows (also known as tracheal folds) are a lifting of the ventral derm that allows air access to the ventral spiracles, with an outlet at the margin on either side next to the thoracic legs, and one furrow at the posterior end leading to the pair of spiracles under and next to the vasiform orifice. At the point where these furrows intersect the margin, the marginal shape may be more strongly toothed or sclerotized than the rest of the margin, in which case they are called tracheal combs, or the margin may be undifferentiated. In others, there may be a deep, often sclerotized impression that is referred to as a tracheal pore.

Vasiform orifice - This organ system comprises several structures associated with the anal opening that are involved in the expulsion of honeydew droplets. The lingula is generally an elongated structure that is probably used solely in the removal of the honeydew. The operculum is a plate-like structure thought to act as a cover for the whole organ. The shape of the vasiform orifice, lingula and operculum are used in taxonomy. The presence of a rim around the posterior part of the orifice, in contrast to an open-ended orifice, is a generic or higher level characteristic.

Pores and porettes - There are numerous kinds of pores in whiteflies and these have been used to separate the two whitefly subfamilies. The compound or multi-loculed, flower-like pore is representative of the subfamily Aleurodicinae, which in some genera also have other distinctive, usually thick-rimmed pores. The subfamily Aleyrodinae has simple circular (discoidal) thin-rimmed pores only. Species of Aleyrodinae also may have porettes, which under the light microscope appear discoidal in type although smaller than the regular pores, but also in well-stained individuals will show as a broad clear halo surrounding the porette itself. Since they do not appear in scanning electron microscopy (SEM) pictures (personal communication and Rosell et al 1997) the porettes may be simply glandular, but they are plainly visible under the light microscope. The placement of pores and porettes is extremely important in specific and generic level identifications. Pore placement is thought not to be affected by environment. An interesting adaptation for the pores can be found in an undescribed genus and species from South America in the tribe Trialeurodini, in which all of the pores appear setiform.

Setation - Body setae are common to all whiteflies. There are several patterns of dorsal setal placement that have been used for specific and generic classification. However, most whitefly puparia have a few setal locations that are common throughout the family. These include in part the caudal pair, the dorsal body setae which include a pair each on the head, thoracic segments (most commonly the meso- and metathorax), the first abdominal segment, the eighth abdominal in association with the vasiform orifice, the anterior and posterior marginal setae, and a more or less complete complement of submarginal setae (15 or 16 pairs total). Setal size, and in some instances setal placement, is known to be environmentally variable, so these characteristics must be used with caution for specific and generic classifications. Setae are usually bristle-like, but may be lanceolate or otherwise swollen or fleshy. Ventral setae are few in number and usually are associated with the mouthparts, the legs and one pair located near the vasiform orifice. These setae are generally not of taxonomic value. The lingula may also have setation. In most species in the subfamily Aleurodicinae, the lingula has two pairs of setae, whereas the Aleyrodinae have one pair or none.

Papillae - These structures are generally restricted to the whitefly tribe Trialeurodini. They are conical structures occurring on the dorsum and may be protuberant (volcano-like) or flat and laid edge to edge (like a rack of machine gun bullets). A papilla contains a disk pore at the apex and usually also on the adjacent derm, both of which may be responsible for the production of a long, spine-like waxen rod. Both the presence and placement of the papillae can be environmentally influenced, although the associated pores apparently are not. Papillae should not be confused with generalized body tubercles, such as those commonly found in some species of *Bemisia*.

Molting sutures - There are two major sutures that rupture during adult eclosion, which allows the adult to exit the puparial shell. The transverse molting suture occurs along the line separating

the metathorax and the 1st abdominal segment. The longitudinal suture extends anteriorly along the midline from the junction with the transverse suture to near or all the way to the anterior margin. The lateral extension of the transverse suture and whether or not it reaches the lateral margin is used in specific classification. In some species, such as *Asterobemisia* spp., the transverse suture curls forward without reaching the margin and joins with the suture from the opposite side at a point immediately posterior to the anterior margin. In this case the longitudinal suture is weak or non-existent and does not reach the anterior margin. This arrangement of the molting suture forms a semi-circular plate that is pushed upward at eclosion, as compared to the more common type of suture in which two plates push open from the center to the margin, much like barn doors. In the genus *Bemisia*, a study of small, random lots of specimens indicates that the strength of this suture system may be mildly affected by environmental factors. The longitudinal suture in some specimens tends to fade anteriorly, and indications of a weak circular type of transverse suture may or may not be present at the same time. Because several *Bemisia*-like genera, including *Asterobemisia* Trehan and *Neobemisia* Visnya, are separated on the basis of the circular molting suture, actual generic lines are suspect.

Legs - Subfamilies can be separated based on leg morphology. Most of the subfamily Aleurodicinae have a single apical claw; the Aleyrodinae have a terminal fleshy pad.

Adults

Paronychium - This is an accessory structure associated with the tarsal claws. In the Aleurodicinae, it is spine-like; in the Aleyrodinae it is blade-like or semi-fleshy.

Metatibial combs - There are numerous setae on the legs of whiteflies. In the Aleyrodinae, there is a row of usually 10 or more setae in a long straight line along the distal, dorsal surface of the metatibia. Woolly whitefly, *Aleurothrixus floccosus* (Maskell), has a double comb in the adult female. Some species may have shortened combs of about 5 setae on the other tibiae.

Tibial brushes - These are groups of two to five setae that also occur on the tibiae. One set occurs on the metatibiae and two sets occur on the mesotibiae. The number of strictly adjacent setae in each brush can have tribal significance.

Male genitalia - Some whiteflies have species-specific structures on the aedeagus such as the ornate processes found in the aleurodicine genus *Paraleyrodes* Quaintance. In the Aleyrodinae, the claspers (harpagones, or parameres) often have generic or species specific morphology.

Compound eyes - In the Aleyrodinae, the eye is generally kidney-shaped or is totally divided into an upper and lower eye. The presence of a separation or the number of ommatidia connecting the upper and lower eye can be of generic or specific importance. According to Steve Nakahara, USDA SEL, Beltsville, Maryland, (pers.comm) the pigmented/non-pigmented pattern of the lower eye can be species or genus specific.

Antennae - Placement of the various sensoria on their associated segments can be important taxonomically, usually at the generic level or higher. There are many species that have unique antennal form or structures that can be very valuable at the specific and generic levels.

Materials

Type specimens of most of the following species were studied, although not all of those type specimens were illustrated. Deposition of studied specimens: **CSCA** – California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California USA; **NHM** - The Natural History Museum, London; **USNM** – United States National Museum (slide collections) Beltsville, Maryland USA; **NZAC** - New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand.

Bemisia: *B. bahiana* Bondar, CSCA; *B. centroamericana* Martin, NHM, CSCA; *B. caudasculptura* Quaintance and Baker, USNM, CSCA; *B. combreticula* Bink-Moenen, NHM; *B. confusa* Danzig, CSCA; *B. costalimai* Bondar, USNM; *B. emiliae* Corbett, CSCA; *B. eoa* Danzig, CSCA; *B. flocculosa* Gill and Holder, NZAC; *B. formosana* Takahashi, CSCA; *B. graminis* David and Winstone, CSCA; *B.*

hibisci Takahashi, CSCA; *B. inconspicua* Quaintance, USNM; *B. lauraceae* Martin, Aguiar and Pita, NHM; *B. mesasiatica* Danzig, CSCA; *B. minima* Danzig, CSCA; *B. miniscula* Danzig, CSCA; *B. poinsettiae* Hempel, CSCA; *B. rosae* Danzig, CSCA; *B. signata* Bondar, USNM; *B. silvatica* Danzig, CSCA; *B. subdecepiens* Martin, NHM; *B. tabaci* Gennadius, CSCA; *B. tuberculata* Bondar, USNM; *B. Bemisia* (*Asterobemisia*) *takahashii* Danzig, CSCA; *Bemisia* (*Neobemisia*) *atraxaxius* Danzig, CSCA; *Bemisia* (*Neobemisia*) *trifolii* Danzig, CSCA; *Bemisia* (*Bemisiella*) *artemisiae* Danzig, CSCA; *Bemisia* (*Bemisiella*) *lespedezae* Danzig, CSCA; *Bemisia* (*Lipaleyrodes*) *emiliae* Chen and Ko, CSCA. Other genera: *Rosanovia hulthemiae* Danzig, CSCA; *Aleyrodes philadelphi* Danzig, CSCA; *Aleyrodes zygia* Danzig, CSCA; *Aleyrodes borchsenii* Danzig, CSCA.

Unidentified Macronesian specimens, NHM, CSCA.

Methods

As many species as possible within the genus *Bemisia* or within genera that bear some resemblance in the puparial stages to *Bemisia* species were assembled for study. Whenever possible, paratype or type material labeled specimens were used. Specimens were studied at 400X magnification with a compound light microscope, and a camera lucida apparatus was used to illustrate pertinent morphological structures of each specimen. These initial illustrations were scanned into computer drawing software programs, and rendered into a digital image. Each complete image was then scaled to fit the 8.5 by 11 inch page format. Therefore the illustrations are not to scale. Pupal size is a variable that depends on nutrition, sex and environment, and therefore is not considered of much importance in this study.

The original generic names are used in this review even though many of the genera studied here have recently been synonymized under the genus *Bemisia*. It is hoped that using the original generic names with the specimen illustrations will help avoid some confusion and will specifically illustrate the morphologies that were originally used to separate genera. For instance, Bink-Moenen and Mound (1990) suggested that the *asterobemisia* group should be included within *Bemisia*. The genus *Neobemisia* has been synonymized with *Asterobemisia* by Mound and Halsey (1978), only to be further synonymized along with *Asterobemisia* under *Bemisia* by David and Dubey (2009). *Lipaleyrodes* Takahashi has also been synonymized under *Bemisia* by Dubey et al. (2009).

Species Morphology

The following is a generalized review on the morphology and taxonomy of the genus *Bemisia* and some of its possible relatives. Uncertainty of the specific limits of *B. tabaci* sensu stricto, or *B. tabaci* strain A, and *B. argentifolia*, or strain B, and the uncertainty of the native origin of both strains, were the major forces behind the initial attempt to understand the entire genus.

There are two major species assemblages (species complexes) within the genus *Bemisia* and those genera to which it appears most closely related: the **tabaci complex**, the **afer complex**, including the **afer group**, and the **asterobemisia group** (including the genera *Asterobemisia* and *Neobemisia*, now synonymized under the genus *Bemisia*). There are several other small groups of species either included in *Bemisia* or in apparently related genera, but their correct generic placement is open to question. Reference here to the **tabaci complex** is restricted to *Bemisia tabaci* Gennadius and its various populations, *Bemisia capitata* Regu and David and *Bemisia formosana* Takahashi. Other species or genera may actually belong in the complex, such as *Lipaleyrodes* Takahashi (now placed in *Bemisia* by David and Dubey 2009), but due to the type of dorsal wax production in the puparial stage, they are included here only at an intermediate group level. There is some morphological and molecular evidence to suggest that the **afer group** could be removed from *Bemisia* and elevated to generic rank, but, there are intermediates between the *tabaci* and *afer* complexes. This is true also with *Bemisia* in general and other genera that are similar morphologically. Only Sampson (Sampson 1943; Sampson and Drews 1956) has attempted to develop a key to the World genera, but it is mostly inadequate for separating genera. Nevertheless, the Sampson keys do utilize certain morphological characters that

have been important over the years in generic placement of many whitefly species, particularly characteristics of the vasiform orifice and associated structures. Characteristics that are currently shared by most *Bemisia* species involve the construction of the vasiform orifice, in which the shape is roughly triangular or chordate, often narrow and long. The operculum does not fill the entire orifice cavity, and nearly half of the length of the lingula extends beyond the posterior margin of the operculum. The vasiform orifice is shallow at the posterior end and appears to be “open” posteriorly and is usually filled with transverse ridges across the floor of the cavity. In morphologically similar genera, such as *Pealius* Quaintance and Baker, the vasiform orifice is closed posteriorly by a sclerotized ridge, and the lingula is short, spinose and generally covered in its entirety by the operculum, although the species *Pealius azaleae* (Baker and Moles) is an exception. The genus *Aleyrodes* Latreille is very similar in appearance to species in the **afer group**, except that the vasiform orifice tends to be broader and shorter, with a shorter lingula. *Aleyrodes spiraeoides* Quaintance, a species apparently native to western North America, normally has short dorsal seta, but specimens are known where these setae are enlarged and elongated, as they are in the tabaci and afer complexes. Adults of *A. spiraeoides* are also similar to adults in the afer group in those cases where the adults are known. Even though there is a great similarity in the morphology of *Aleyrodes* with some of the *Bemisia* groups, DNA analysis has shown that they probably are not closely related (Gill and Brown 2010), and their similarities may be due either to convergence or to the retention of ancient ancestral characters.

In order to understand the morphology of the *Bemisia* species, it is necessary to begin with the puparial morphology of *B. tabaci* populations of A and B, with inclusion of characteristics of the other groups for comparison. Economically, species within the tabaci complex and the afer complex have been of importance to agriculture and horticulture, and they have certain characters that separate them. This morphological overview does not necessarily include other species within *Bemisia*. The tabaci complex puparia are smaller than those in the afer complex, have a more tapered ovoid appearance, long caudal setae, certain setal placement patterns, and pore/porette combinations that are adjacent to each other and occur with no particular alignment to the margin. The afer complex puparia are larger, are more nearly circular rather than ovoid, have short caudal setae, different setal placement patterns and pore/porette combinations that are mostly nonadjacent and aligned with the porettes in each pair closer to the margin.

Figures 1-80, in conjunction with the text, will illustrate what appear to be species complexes and species groups within the genus *Bemisia*. It will also explain some of the morphological problems and how they bear on how the genus and its congeners are treated taxonomically. The first thirteen illustrations (Fig. 1-13) are of *Bemisia tabaci* sensu strictu and show morphological structures, variations in morphology, variations in placement and size of various dorsal setae, and the varying numbers of minute submarginal setae. Also, several specimens of *B. tabaci* are included that were formerly described as other species (Fig. 12-13).

In Fig. 1, the major body setae of the *B. tabaci* puparium are indicated. There are three pairs of setae that are typically found in most species of whiteflies. These are the caudal setae (CS), the anterior marginal setae (AMS), and the posterior marginal setae (PMS). There are six pairs of subdorsal setae (DS1-DS6). These setae may all be small and short, as in Fig. 2, 6 and 7, and are so primarily when the host leaf is smooth. If the host leaf has varying degrees of hairiness, these subdorsal pairs may become long and spine-like. Not all setal pairs enlarge in all cases; the anterior (cephalic pair) will often enlarge when none of the others do. The general distribution of enlarged setae is from anterior to posterior, although this order is variable. Enlargement patterns on any given puparium can vary amongst individuals within the same population. Usually both setae in a right/left pair enlarge simultaneously, but on rare occasions only one will enlarge. In the case of subdorsal seta on the metathorax (DS4), if the majority of the other subdorsal setae do not enlarge, DS4 cannot be found anywhere in the vicinity of its normal enlarged location. There are five pairs of submarginal setae (PSMS1-PSMS5) on the abdomen that are counted anteriorly from a position just anterior to seta PMS (e.g., Fig. 3). Setae PSMS1-PSMS4 are always roughly aligned in a shallow arc. Seta PSMS5, unlike the other submarginal setae, can become enlarged as in the subdorsal setae. If unenlarged, setae PSMS5 usually lines up in the shallow arc with the other PSMS setae. If PSMS5 becomes enlarged, its position will always be shifted medially into the shallow arc alignment occupied

by most of the subdorsal setae except DS5. There are three or four anterior submarginal setae (ASMS1-ASMS4). The ASMS setae do not seem to enlarge or shift position in the tabaci group. In the afer and asterobemisia groups, the submarginal and dorsal body setae rarely enlarge (but see Fig. 17, 23), and apparently the puparia typically respond to environment influences by producing different kinds of protuberances, varying from simple conical to star-shaped constructions. The afer and asterobemisia groups generally have more submarginal setae than in the tabaci group, particularly in the area between the second abdominal segment and the tracheal furrow.

All of the described species in *Bemisia* exhibit pore-porette combinations; in the illustrations the pore is represented by a dark rimmed circle and the porette is represented by a small dot surrounded by a much bigger, lighter circle. The pores are given group alignments in Figure 1 (SDP, SMep). In the tabaci complex, each pore and porette are immediately adjacent, with only rare exceptions. The alignment of the pore-porette pair is apparently random with respect to the margin of the puparium. In the afer and asterobemisia groups, however, the pore and porette pair is usually always separated by a distance considerably larger than the diameter of the pore, and the pore and porette pair are nearly always aligned with the porette closer to the body margin, particularly marginally.

The total number of pore-porette pairs is much greater in the afer and asterobemisia groups than in the tabaci complex. For instance, there is one pair of pore-porettes on the first abdominal segment between the subdorsal seta DS5 in the tabaci complex, but in the afer-asterobemisia groups there are usually two pairs in this position. There are, however, intermediate forms of uncertain generic placement that may have two pairs of pore-porettes on the first abdominal segment, but adjacent pores and porettes with random alignment to the margin, such as occurs in species formerly in the genus *Neobemisia*. There is also one population of afer complex specimens on *Hypericum reflexum* L.f. (Hypericaceae) from the Canary Islands (not illustrated) in which the pore/porette pairs are present on the first abdominal segment, but each individual may have 0–2 pairs on either side of the segment, a situation so far unseen in other afer complex populations, where the numbers are usually constant on each side of the segment. Also some specimens from the United States and Mexico may have three pairs of pore/porettes on the segment.

The tabaci complex

Fig. 1: Syntype specimen of *Bemisia tabaci* (part of the original material collected by Gennadius in 1889 in Greece). This illustration emphasizes the setal and pore-porette arrangements that are important morphological characteristics for the genus *Bemisia*. The dorsal setae on this specimen were broken off at their bases, and a their illustrated size and length is only speculation. Seta ASMS4 is present and well developed in all puparial specimens that were on the same slide with the illustrated specimen. The presence of this seta seems to be associated primarily with specimens of the tabaci complex that were collected in the New World prior to 1981. This seta or evidence of a setal base are normally absent (roughly 95% of the time or more) in specimens of *B. argentifolii* and from various races in the Old World. In the adults of both *B. tabaci* and *B. argentifolii*, the upper and lower eyes of the adults are separated by only one ommatidium, a condition that primarily is known only among whiteflies from the tabaci complex and some populations of males in the afer complex from the Macaronesian Islands.

Fig. 2: Typical long setal form of the tabaci complex collected in California in 1961. Seta ASMS4 is well developed and the specimen is assumed to be part of the original Type “A” New World populations. It was identified and labeled as an “extreme variant” by Louise Russell, as an indication of the long setae.

Fig. 3: Short setal specimen of *B. tabaci* collected from cotton at Tolima, Colombia in 1965. It has the ASMS4 seta and therefore is probably part of the Type “A” New World populations.

Fig. 4: Type specimen of *Bemisia poinsettiae* Hempel, described from Brazil in 1922. Because of the strong preference of *B. argentifolii* for poinsettias, this was a particularly important specimen to study. The seta ASMS4 is commonly present and well defined in all of the studied type material. It is typical of the New World tabaci complex and apparently not part of the strain “B” populations.

Fig. 5: Holotype of *B. argentifolii* (strain “B”), short-seta morph. Setal patterns and pore-porette placement are indicated. Note the absence of submarginal seta ASMS4.

Fig. 6: Paratype specimen of *Bemisia argentifolii*, long setal form. Locations of pore groups and setae are indicated. ASMS4 setae are absent.

Fig. 7: Specimen collected from citrus in the Coachella Valley of California. The specimen was part of the progeny of clouds of adults that had flown across the Salton Sea from Imperial Valley. They settled in large numbers on grapes, citrus and other hosts that were the first green plants available after crossing the sea. The population is known to be *B. argentifolii* exclusively and the seta ASMS4 is absent from all of the material.

Fig. 8: *Bemisia argentifolii* reared in culture at the University of Arizona, collected early in 1992. The seta ASMS4 is absent. It was observed in a number of these specimens from culture on poinsettia that the ventral thoracic stigmatic furrows were not visible.

Fig. 9: *Bemisia tabaci* complex collected in West Malaysia with supernumerary submarginal setae. The illustration shows the positions of these extra setae. (Figure reprinted by permission from Springer Science+Business Media B.V.).

Fig. 10: *Bemisia tabaci* complex collected in Hong Kong with supernumerary setae as well as setae ASMS4. The illustration shows the positions of the extra setae. An unemerged adult male in one puparium has a one ommatidium connection between the upper and compound lower eye.

Fig. 11: A paratype of *Bemisia minima* Danzig, described from the USSR in 1964, later synonymized with *B. tabaci* by Danzig. The seta ASMS4 is absent.

Fig. 12: A paratype specimen of *Bemisia miniscula* Danzig, later synonymized with *B. tabaci* by Danzig. There is a blemish in the derm on one side that could be seta ASMS4. An interesting feature of this particular specimen is the unusually wide vasiform orifice, a trait found also in several specimens collected in Southeast Asia. The significance of this is unknown.

Fig. 13: A specimen of *Bemisia formosana* Takahashi. *B. formosana* was described from grass from Taiwan in 1933, and *B. graminus* David and Winstone below is considered a synonym of it. Of all of the specimens of *Bemisia* that have been examined so far, this species seems to be the most closely related to *B. tabaci*. The species *Bemisia graminus* David and Winstone was synonymized under *B. tabaci* by David and David (2001), but has been further synonymized under *B. formosana* by Martin and Mound (2007). Cytochrome oxidase work by Brown (unpublished data) suggests that *B. formosana* is in a clade of populations of *B. tabaci* found in Pakistan, India and Nepal.

Fig. 14: A specimen from Pakistan of what is probably representative of *Bemisia graminis* David and Winstone. A paratype specimen of *B. graminus* from India was available for study, but the specimen was excessively bleached, which obscured the placement of many of the pores and setae. This specimen agrees with *B. graminus* in those details that could be seen in the paratype. It shows the same pore-porette arrangements as the *tabaci* complex, and the setal placement and setal enlargement patterns are identical. The seta ASMS4 is absent. The only character that differentiates it from *B. tabaci* sensu strictu is the elongate nature of the puparium, a character possibly a growth-form related to a graminous host. However, collections of both *B. tabaci* and *B. argentifolii* from grasses in the Imperial Valley of California fail to show this elongated character. It is also important that one of the specimens from this lot contains a fully formed adult female which has the upper and lower eye connected by one ommatidium, as in *B. tabaci* and *B. argentifolii*. The Takahashi species, *Bemisia formosana*, described from grass from Taiwan in 1933, may be the same species, and *B. graminus* would be a synonym of it.

Fig. 15: *Bemisia capitata* Regu and David, a species known from India and Australia. This species seems to be very close to *B. tabaci*, but with capitate dorsal setae, a very weak longitudinal molting suture and strongly developed protuberances.

The afer complex

Bemisia afer (Priesner and Hosny) was described from Egypt in 1934. The next 19 figures include species and individuals proposed as members of the afer complex. This complex includes two smaller groups, the afer group and those species previously included in the genera *Asterobemisia* and *Neobemisia*, which were separated from *Bemisia* because of the circular shape of the transverse molting suture that is directed anteriorly and meets the opposing suture near the front margin, forming a circular emergence opening for the adult. Type material of *B. afer* was not available for study and is not illustrated here, but it should be identical to the illustration of *Bemisia hancocki*

Corbett (Fig. 16). For a review of the morphological characteristics of *B. afer* and its puparial variability see Bink-Moenen (1983). Species level limits are unknown, but appear to be a diverse species complex. See Martin et al. (2000) for a detailed discussion of this issue and the possible synonymy of *B. hancocki* and *B. afer*. One of the most striking morphological characters of *B. afer* and *B. hancocki* is the abrupt change in the sclerotization of the marginal crenulations in the vicinity of the tracheal folds, although several species in Eurasia and elsewhere also have this character. However, this character is too variable and often not present to be of much use in comparison with other species in the complex, and it may be an environmentally induced character. Both *B. afer* and *B. hancocki* intergrade in many characteristics with *Bemisia tuberculata* Bondar in South America and with *Bemisia berbericola* (Cockerell) in western North America. There are numerous species described from Eurasia that also belong this species group. African *afer* complex species tend to have relatively short lingulae compared to some Asian forms, and especially with *B. berbericola* in the western United States, in which the lingula can be very long and narrow. Regu and David (1991) synonymized *B. afer* with *Bemisia leakii* (Peal) based on microspines at the bases of the antennae (these also occur on *B. tuberculata* specimens from South America) and ridges at the end of the vasiform orifice, but the variability of these characters and thus their reliability as taxonomic have not been assessed. The original illustration of *B. leakii* by Peal shows an elongated lingula, a characteristic of Asian members of this complex (e.g. *B. moringae* David and Subramaniam) and the new World (e.g. *B. berbericola*) rather than the shorter lingulae of Europe and Africa specimens of the *afer* complex. Specimens of *B. tuberculata* from South America tend to have lingulae of length that is intermediate between those of *afer* complex specimens from Africa and *B. berbericola* from North America. This also is a variable character and its usefulness as a taxonomic character is unknown. Populations in the *afer* complex exhibit extreme morphological variability in the length of dorsal setae and development of rugosities and protuberances.

There are some intriguing characters in some of the species of the *afer* complex from the Macaronesian Islands that are illustrated later. Specimens from one population have a different ommatidial arrangement in the adult compound eyes than those in other other populations, and also have a longer lingula. They also show molecular similarities with specimens from western North America, which have the same eye configuration (see discussion for Fig. 64).

Fig. 16: Labeled as *Bemisia hancocki* Corbett, but may be a synonym of *Bemisia afer* as there seems to be no morphological basis for treating them as separate. It is here considered to be in the *afer* complex of species. It is apparently African in origin. (Figure reprinted by permission from Springer Science+Business Media B.V.).

Fig. 17: *Bemisia guieriae* Bink-Moenen is a morphologically striking species because of the numerous long setae and the star-shaped protuberances. It is known from several widely separated localities in Africa, all on the same host species. It is obviously in the *afer* group, but whether it should have species level status is problematic. The double set of submedial and subdorsal pore-porette pairs could be host-induced variation. A similar morphological response can be seen in the specimens of *B. berbericola* from oak in Fig. 23, and particularly in some specimens from the Macaronesian Islands discussed below (see Fig. 66 and 70). (Figure reprinted by permission from Springer Science+Business Media B.V.).

Fig. 18: *Bemisia tuberculata* Bondar is the South American member of the *afer* group. This specimen, as determined by Louise Russell, deviates little from the form of *B. afer* except that it does not have the thickened crenulations at the ends of tracheal folds. Other South American specimens sometimes have microspines around the antennae and first thoracic legs and the cephalic setae are often elongated. Based on mtCO1 data, this species and *B. berbericola*, appear to be distinct from African *B. afer* (Gill and Brown, 2010, see fig. 1.3 and 1.4, ref. TUBBZ).

Fig. 19: A specimen of *Bemisia tuberculata*. This specimen shows variability from the above specimen and from *B. afer* by having a longer lingula and pore/porette combinations that are closer together.

Fig. 20: *Bemisia berbericola* (Cockerell) is the North American representative of the *afer* group. Like *B. tuberculata*, it does not show marginal crenulation thickenings at the ends of the tracheal folds. It is most commonly found on Oregon grape, *Berberis aquifolium* Pursh. (Berberidaceae) and California laurel, *Umbellularia californica* (Hook. and Arn.) (Lauraceae), both smooth-leaved species,

and so tuberculation is usually not pronounced (but see below). The species is under excellent biocontrol in the western U.S., and is thought to be native there. However, there are similar forms in eastern Asia and India. It tends to have a longer lingula than some specimens of *B. tuberculata* and most specimens of African-origin *afer* group specimens. The lingular shape is more closely comparable with Asian specimens such as *B. moringae* (David and Subramaniam). (Figure reprinted by permission from Springer Science+Business Media B.V.).

Fig. 21: Specimen from California near *B. berbericola* (see above). Occasional specimens are known which have an unusually elongated and narrow lingula. Whether this is a species level distinction or is environmentally induced is unknown.

Fig. 22: This specimen, probably also *B. berbericola*, shows some variation from the normal puparial characteristics. It is unusual compared to that species in that the pore/porette combinations are adjacent, although they are aligned with the porette closest to the margin, as they are in the *afer* groups. The specimen also has three pairs of pore/porette pairs on the first abdominal segment, and shows the development of some tuberculation on the anterior abdominal segment midlines and along the lateral edges of the dorsal disc. This specimen is from oak (*Quercus* sp.), which has a thick development of leaf hairs on the ventral surfaces.

Fig. 23: A specimen of *B. berbericola* that shows an atypical enlargement of some setae and the development of bead-like protuberances. The specimen is from Kings County, California on *Quercus* sp., many species of which have very hirsute lower leaf surfaces in that habitat. This specimen also has adjacent pore/porette combinations like the specimen in Fig. 22. The variation seen in these oak specimens are probably due to the morphology of the leaf surfaces. (Figure reprinted by permission from Springer Science+Business Media B.V.).

Fig. 24: An atypical specimen referable to *B. berbericola*. This specimen is different from other California specimens of *B. berbericola*. It is one of three specimens collected from two widely separated locations on *Adenostoma fasciculatum* Hook & Arn. (Rosaceae). The leaflets of this plant are tiny and cylindrical, 4-10 mm long and 1 mm wide. The puparium is elongate in shape instead of ovoid/circular as in *B. berbericola*, has an extremely long lingula, and the pore/porette combinations are sparse in the area between the submargin and the outer edges of the dorsal disc. There is a continuous row of pore/porettes along the submargin, and there are a few raised tuberculations. The variations here are apparently associated with the host leaf morphology. Whether this is a separate species from *B. berbericola* or adaptation to the leaf structure is not known.

Fig. 25: A type specimen of *Bemisia caudasculptura* Quaintance and Baker, from Mexico on *Fraxinus* sp. (Oleaceae). Recent collections from *Fraxinus* sp., from Mexico, were also available. This is a large species, with a long lingula and a small thickening of the crenulations at the thoracic stigmatic furrows. Otherwise it is typical of other species in the *afer* group, except that in the adults the wings have a dark banding pattern. Also unusual is the elongation of the 8th abdominal setae during the time prior to the emergence of the adults, as the empty puparia have the setae nearly as long as the body, and the stylets remain attached to the mouthparts and extend forward almost to the anterior body margin.

Fig. 26: A specimen identified as *Bemisia porteri* Corbett. This specimen is typical of the *afer* group. The specimen was parasitized, and enlarged dorsal setae have been broken off. It also shows thickened marginal crenulations at the thoracic tracheal furrows.

Fig. 27: *Bemisia confusa* Danzig, a Eurasian species in the *afer* group.

Fig. 28: *Bemisia eoa* Danzig, which is typical in all respects of *B. afer*.

Fig. 29: *Bemisia silvatica* Danzig, which probably belongs in the *asterobemisia* group. The molting suture is weak, but indicates a circular rather than "T"-shaped form. It has thickened crenulations at the tracheal fold ends.

Fig. 30: *Asterobemisia carpini* (Koch) is placed here as part of the *asterobemisia* group of the *afer* complex. The major morphological characteristic of this group is the circular transverse molting suture, which curves anteriorly to meet the suture from the opposite side, with the longitudinal suture not reaching the anterior margin of the puparium. David and Dubey (2009) synonymized this genus with *Bemisia*.

Fig. 31: *Asterobemisia shinanoensis* Kuwana, an Asian species. The circular molting sutures place it in the *asterobemisia* group.

Fig. 32: *Asterobemisia takahashii* Danzig, an Asian species that may be synonymous with *B. shinanoensis*.

Fig. 33: *Neobemisia trifolii* Danzig, a Eurasian species in the asterobemisia group. Unlike *Asterobemisia*, the pore-porette combinations are nearly always adjacent. It has an unusually large number of subdorsal pore-porette groups on the abdominal segments. Members of the genus *Neobemisia* were synonymized under *Asterobemisia* by Mound and Halsey (1978) only to be later synonymized under *Bemisia* by David and Dubey (2009).

Fig. 34: *Neobemisia atraphaxius* Danzig is similar to *N. trifolii* above, with mostly adjacent pore/porette combinations, but lacks the large number of abdominal pore/porette groups.

Intermediate and questionable forms

Fig. 35: Paratype *Bemisia rosae* Danzig is a problem in classification. This species is now synonymized under *Neopealius rubi* Takahashi (Evans, 2008), who placed it at that time in the genus *Bemisia*. Other authors including Bink-Moenen (1991) have since placed it back into *Neopealius*. The species *Aleyrodes rosae* Korobitsin is also considered a synonym by Huldén (1986). It resembles some *Aleyrodes* species, but the 7th abdominal segment is narrower than the other segments. It resembles *tabaci* in having one pair of pore/porette combinations on the 1st abdominal segment and long caudal setae, but differs in having a full complement of 14 well developed submarginal setae, a more rounded versus oval body shape, and a paucity of pore/porette groups in the area between the submargin and the edges of the dorsal disc. It does not show any *B. afer* characteristics. It may belong in the *tabaci* complex of species. Bink-Moenen (1991) discussed the morphological details of the species, and noted that the compound eyes have a two-ommatidium connection.

Fig. 36: *Bemisia mesasiatica* Danzig is a Eurasian species that appears to have affinities with two species in the genus *Aleyrodes*, *A. spiraeoides* Quaintance and *A. borchsenii* Danzig (see Fig. 58 and 61). The 7th abdominal segment is subequal in width to the other segments, a characteristic of *Aleyrodes*. In some specimens, all of the submarginal setae are elongate.

Fig. 37: *Bemisia giffardi* Kotinski is probably not in the *tabaci* group, and may not even be a *Bemisia*. Marginal pore/porettes are non-adjacent. The adult eye is connected by four or more ommatidia and the greatly elongated apical segment of the male antenna has an unusual appressed sensorium that extends the length of the segment. Molecular mtCO1 data varies a bit depending on which species are included in the phylogenetic trees, but see Gill and Brown (2010, figs. 1.3 and 1.4, ref. BGIF).

Fig. 38: *Bemisia centroamericana* Martin is an intermediate species between the *tabaci* and *afer* complexes. Similar to *B. afer*, it has two pairs of pore/porettes on the first abdominal segment and pore/porette combinations aligned with the porette closer to the body margin. Similar to *B. tabaci*, it has an ovoid body shape that tapers to a narrower posterior end, adjacent pore/porette pairs and setal arrangements similar to *B. tabaci*. The enlarged setae are supported by long tubercular bases that are much longer than those that sometimes occur in *B. tabaci*.

Fig. 39: *Bemisia centroamericana* Martin. This specimen is from a collection that was part of a mtCO1 analysis (Brown, 2010). It aligns in the trees with New World species in the *afer* complex. For molecular mtCO1 tree placements see Gill and Brown (2010, figs. 1.3 and 1.4, ref. BCENTRO and BCENTROAM).

Fig. 40: *Bemisia flocculosa* Gill and Holder has characteristics of *B. tabaci*, such as one pair of pore/porettes on the first abdominal segment, adjacent pore/porette combinations with the combinations not having any specific alignment with the body margin, and long caudal setae. The longitudinal molting suture does not reach the anterior margin, but the transverse suture does not appear to curve anteriorly. It does not appear to have any *afer* complex characteristics. Based on mtCO1 molecular data, it aligns between the *tabaci* and *afer* complexes. For molecular mtCO1 tree placement see Gill and Brown (2010, fig. 1.3, ref. NZEAL1 and NZEAL2). It has dorsal white wax secretions similar to species formerly placed in *Lipaleyrodes*, but the wax is produced along raised rugosities at the edges of the dorsal disc and along the median line, rather than along the submargin as in *Lipaleyrodes*. This species may be native to New Zealand, but molecular affinities to New World species raise some biogeographical questions about how it arrived in New Zealand.

Fig. 41: An apparently undescribed species of *Bemisia* from Gambiers Island in Eastern Samoa. It is similar to *B. tabaci* because of the adjacent pore-porette combinations and long caudal setae. However, it has two pairs of pore-porettes on the 1st abdominal segment, a weak longitudinal molting suture and the suggestion of a circular transverse suture. The raised, slightly sclerotized, pigmented dorsal protuberances are unlike anything seen in the *tabaci* group. It shows some resemblance to *B. porteri* Corbett (Fig. 26) but the pore/porette combinations are adjacent and the porettes are not aligned in any particular relation to the margin. It is known from this one specimen, but specimens from Fiji and Papua New Guinea on taro are similar and may be this species. There is also a possibility that this is *Bemisia leakii* (Peal), although the illustration of the vasiform orifice in the original description indicates otherwise. The specimen is bleached and marginally is partially covered with wax plates, and so the anterior submarginal setae are not discernible.

Fig. 42: *Lipaleyrodes emiliae* Chen and Ko is one of several species now synonymized under the genus *Bemisia*. This synonymy results in *Bemisia emiliae* Chen and Ko becoming a homonym of *Bemisia emiliae* Corbett, a current synonym of *Bemisia tabaci*. This grouping of species is characterized by bead-like structures around the body margin that are apparently responsible for the production of fluffy white wax. This species lacks the first abdominal setae, and the first abdominal pore/porette group may or may not be present. Based on molecular mtCO1 data, this species aligns between the *tabaci* and *afer* complexes. For molecular mtCO1 tree placement see Gill and Brown (2010, fig. 1.3, ref. LEP1 and LEP2).

Fig. 43: *Bemisia subdecepiens* Martin was described from Australia. It is similar to species in the *afer* complex, but differs by having only one pair of pore/porettes on the 1st abdominal segment, and the pore/porette combinations are adjacent and not aligned in any particular arrangement with regard to the body margin. It probably has been isolated as a species for so long that its affinities are only conjecture.

Fig. 44: *Bemisia combreticula* Bink-Moenen was described from Africa. It has a nearly full complement of submarginal setae that are bristle-like. It seems to have some resemblance to species of *Parabemisia* Takahashi (Fig. 46), but has non-adjacent pore-porette pairs.

Fig. 45: *Bemisia hirta* Bink-Moenen is a species known from several African locations, but is possibly an environmentally induced morph of *B. combreticula*. It shows some tuberculation, the setae are fleshy instead of bristle-like, and many of the setae show a medially directed migration, particularly PSMS5 (as in *B. tabaci*), and in the thoracic setae (the equivalents of DS3 and DS4).

Fig. 46: *Parabemisia myricae* (Kuwana) may be a *B. tabaci* relative. It has adjacent pore-porettes and an open-ended vasiform orifice with an elongated lingula. However, adult females have an unusual sensorium on the third antennal segment that is not known in *Bemisia*. The species is also apparently parthenogenetic.

Fig. 47: *Bemisia pongamiae* Takahashi is an Asian species that has an unusual pore/porette arrangement. Also, CO1 molecular data suggest that it is not particularly closely related to other *Bemisia* species.

Fig. 48: *Metabemisia filicis* Mound seems morphologically to be more closely related to *Parabemisia*.

Fig. 49: *Bemisiella lespedezae* Danzig is one of two species in this genus. The species are intermediate between the *tabaci* group, with adjacent pore-porettes, and the *asterobemisia* group, circular molting sutures and two pairs of pore-porette pairs on the first abdominal segment). This species was synonymized under *Bemisia* by David and Dubey (2009).

Fig. 50: *Bemisiella artemisiae* Danzig is morphologically similar to *Bemisiella lespedezae* (Fig. 49) above, and could be a hairy-leaf morph. This species was synonymized under *Bemisia* by David and Dubey (2009).

Fig. 51: This specimen is possibly an undescribed species. It was collected in Sudan on a grass. It is nearly identical to *B. tabaci* and *B. formosana* from smooth leaves, but with a more tapered lingula. The length of the puparium is intermediate between the two. A distinguishing character is the presence of rough C-shaped pores around the margin. These pores are similar to those in the genus *Bemisiella* Danzig. It is known only from two puparia.

Fig. 52: *Pealius azaleae* (Baker and Moles) has many of the characteristics of *B. tabaci*, and so has been included here. Based on the open-ended shape of the vasiform orifice and the setal pair, *P. azaleae* belongs in another genus, possibly *Bemisia*, but not in the genus *Pealius* (see fig. 53 below).

Fig. 53: *Pealius maskelli* (Bemis) is the type of the genus *Pealius*. It has a closed posterior rim of the vasiform orifice and a lingula with microspines instead of a pair of hair-like setae.

Fig. 54: *Rosanovia hulthemiae* Danzig possesses characteristics of *Bemisia*, such as reduced width of the 7th abdominal segment, a circular moulting suture with the longitudinal suture not reaching the anterior margin (as in the asterobemisia group), and adjacent pore/porette pairs with no particular alignment with the margins (as in species formerly placed in *Neobemisia*). Its current generic placement is questionable, but is probably conspecific with one of Danzig's *Asterobemisia* or *Neobemisia* species.

Fig. 55-56: Two unusual specimens from different locations in Panama that possibly are species of *Bemisia*.

Fig. 57: *Aleyrodes spiraeoides* Quaintance is a New World representative of several other North American and Palaearctic *Aleyrodes* species. Its superficial resemblance to *Bemisia afer* prompted a study of several *Aleyrodes* species morphologically, and a molecular analysis of *A. spiraeoides*. On molecular evidence, it is not a *Bemisia* (Campbell et al. 1994, 1995) and it differs from *B. afer* morphologically by having subequal abdominal segment widths on the middorsum in the puparium, and subequal 4th and 5th antennal segments in the adults. Similar to the case of *B. tabaci*, the separation of the puparia of the North American *A. spiraeoides* and the European *Aleyrodes proletella* (Linnaeus) is not possible. However, the male aedeagus of *A. spiraeoides* is slightly curved in lateral view, but the aedeagus of *A. proletella* is bent at an almost 90 degree angle at mid-length.

Fig. 58: A specimen of *Aleyrodes spiraeoides* that shows extreme elongation of submarginal setae as a result of environmental factors, indicating that this phenomenon is not restricted to *Bemisia* species.

Fig. 59: *Aleyrodes philadelphi* Danzig, a normal short-seta species typical of known *Aleyrodes* species.

Fig. 60: *Aleyrodes zygia* Danzig, also a short setal species.

Fig. 61: *Aleyrodes borchsenii* Danzig is a Eurasian species typical of other species in the genus, but with long setae. Other species of Eurasian *Aleyrodes*, such as *A. zygia* and *A. philadelphi* discussed above, are short seta forms, as is the European species *A. proletella*. These all may be morphs of the same species, since *Aleyrodes spiraeoides* shows both kinds of morphs, as indicated in Fig. 57 and 58 above.

The Macaronesian *afer* complex

Figures 62-80: A series of specimens in the *afer* group from the Canary and Madeira Islands, courtesy of Jon Martin at The Natural History Museum, London that show a remarkable amount of puparial variation. The specimens were collected from various hosts in different environments. Except for the first three specimens illustrated from the Canary Islands and Fig. 72 from Madeira, the remaining figures will not be discussed, but are included here to show the extreme puparial plasticity that seems to occur on what are thought to be mostly endemic populations on those islands. It should be noted that the lingulae of all of the specimens from these islands are rather short, except for the two specimens from *Euphorbia*, which are longer and rather narrow.

Fig. 62: A specimen from the Canary Islands from *Hypericum grandifolium* Choisy (Hypericaceae) that is typical of the morphology described in the type illustration of *Bemisia afer* Priesner and Hosny. Note the short lingula. In nine specimens studied from another population on *Hypericum reflexum* L.f. (not illustrated), the number of pore/porette pairs on the first abdominal segment varies from 0–2 on either side of each specimen, a character that otherwise seems very consistent at two pairs on both sides in most other known populations in the *afer* complex.

Fig. 63: A specimen from *Euphorbia* sp. Note a longer lingula than that found on the specimen in Fig. 62.

Fig. 64: A specimen also from *Euphorbia* sp. Note the longer lingula. This illustration is less detailed than in Fig. 62 and 63, but shows that the morphology is basically typical of *B. afer* and without setal enlargement or protuberances. However, the adult male and female eyes in this population are completely divided, while the adult eyes of all other adults collected on the islands have the female eyes divided but the male eyes connected by one ommatidium. The mtCO1 sequences of specimens from another population from *Euphorbia* sp. hosts suggested that these populations are more closely

related to New World populations than to the other “endemic” populations tested (Gill and Brown 2010, ref. fig. 1.4, represented as BAFEREuph23). In addition, afer complex adult specimens from other parts of the world also have different ommatidial numbers (Gill and Brown 2010).

Fig. 65-71: Additional specimens from the Canary Islands, showing puparial variability.

Fig. 72: *Bemisia lauracea* Martin, a species unique in the afer complex because it has raised protuberances around the dorsal disk margin that apparently are associated with the production of glass-like wax.

Fig. 73-80: Additional specimens from Madeira Island, showing puparial variability.

Discussion

Species groups within the genus *Bemisia* can exhibit dramatic variability in puparial morphology, some of which is environmentally induced. This variability is in the form of either very small or greatly enlarged, spine-like setal groups, and/or the development of various sizes and shapes of dorsal protuberances or rugosities. The range of variability of *B. tabaci* and “*B. argentifolii*” is now well understood, at least in North American populations, in which there is variation in setal size changes only, with apparently little protuberance development). Careful monitoring of populations from other parts of the World has resulted in the discovery of previously unknown variability in the tabaci complex (Fig. 9-10). But the sum total of this variability within the tabaci complex cannot account for non-morphological variability of these whiteflies in the areas of general biology, viability, host preferences, disease transmission and resistance to pesticides. Species in the afer complex occasionally display setal enlargements, especially the submarginal setae, which do not become enlarged in the tabaci complex of species. Species in the afer complex also differ from those in the tabaci complex species in the varied morphologies of the dorsal rugosities and/or protuberances, which is also apparently environmentally induced. However, variability within the afer complex is so great within and amongst populations that it is not yet possible to adequately delimit species. Also because of the tremendous amount of morphological variability, the synonymizing of species in the genera *Asterobemisia*, *Neobemisia*, *Lipaleyrodes* and *Bemisiella* cannot be fully justified. But the synonymy of *Asterobemisia* under *Bemisia* is not necessarily without merit. Except for the curving, circular molting suture they are otherwise identical in morphology with the afer complex as herein conceived. *Neobemisia* was synonymized first under *Asterobemisia* because it also has the circular molting suture found in that genus, then under *Bemisia*, partly because of its similarities to *B. afer*. There is however one major difference between these genera. *Asterobemisia* species have the pore/porette combinations non-adjacent to each other, with the porette closer to the margin in each case. *Neobemisia* species have the pore/porette combinations adjacent to each other with no particular alignment with the margin, as do the tabaci complex species. Otherwise, *Neobemisia* has the same morphological attributes of *B. afer* except that *B. afer* has non-adjacent pores. Unfortunately, species within the two genera *Asterobemisia* and *Neobemisia* have not been available for molecular analysis. It remains far from clear that these morphological differences justify treatment as distinct genera, or even distinct species. The genus *Aleyrodes* also appears to present the same problems, with not much variability between species and/or populations across the Northern Hemisphere.

The setal/protuberance variability patterns found in *Bemisia* seem, so far, unique to the genus. But puparial and setal variability occurs in many whitefly genera in the Aleyrodinae. The genus *Pealius* and its congeners show some variability in setal enlargement, but the pattern of setal enlargement is different than that in *Bemisia*, and they do not seem to develop the protuberances found in the afer group. In the tribe Trialeurodini [e.g. *Trialeurodes vaporariorum* (Westwood)], environment affects the puparial morphology area in a different way. Usually on more hairy leaf surfaces, papillae are produced in greater size and numbers. These papillae produce spine-like dorsal rays of wax that closely resemble the enlarged dorsal setae of *Bemisia*. Whiteflies in the genus *Aleyrodes* appear most similar to the *Bemisia* group of species (most specifically the afer group), although they do not exhibit the development of tubercles or other protuberances. They can be separated by the median width of the 7th abdominal segment anterior to the vasiform orifice subequal to the width of the other segments, and that in the adults the 4th antennal segment is subequal in

length to the 5th segment. In the *afer* group, the width of the 7th abdominal segment is much less than that of the other segments, and the adult antennal segment 4 is shorter than segment 5. Molecular data suggests that *Aleyrodes* and *Bemisia* are not closely related.

As suggested by Gill and Brown (2010), Dinsdale et al. (2010) and De Barro et al. (2011), the taxonomic status of *B. tabaci* is a complex problem, and is possibly a complex of as many as 24 sibling or cryptic species. Whatever the case, there is little morphological evidence to justify separating any of the forms within the *tabaci* complex, except for *B. capitata* (Fig. 15) and possibly the grass feeding form from Sudan (Fig. 51). If this is true, then there would appear to be a similar situation within the *afer* complex. The *afer* complex specimens show a much greater amount of morphological variability than does the *tabaci* complex, as illustrated here and by Gill and Brown (2010), and this morphology was at one time used to separate species and even genera. But after careful study of the morphological variability, it is apparent that the species and generic limits formerly used in this group of whiteflies are a problem even more complicated than it is in the *tabaci* complex. Due to the extreme variability in the *afer* complex, it is probably no longer feasible to try to maintain species or generic limits in this group and other intermediate forms based on morphology alone. The same is true for the *tabaci* complex, although the amount of morphological variation between populations of *B. tabaci* is not nearly as great.

The *afer* complex specimens show a highly variable morphology that is in part affected by host and possibly by other environmental factors. When this variability is studied on a worldwide scope, not only may species status be suspect, but also that of genera, as suggested by the synonymy of *Asterobemisia* and *Neobemisia*. Like the *tabaci* complex, there may be many cryptic species that are geographically isolated, or there may be fewer named species than there actually are. Unlike the *tabaci* complex, however, adults in the *afer* complex in some cases have morphological characteristics in the compound eye that suggest that more as yet unrecognized species may be involved as appears to be the case in *B. tabaci*. So far, there does not seem to be variability in the number of ommatidia that connect the upper and lower compound eyes in adults from the same population, although this needs to be studied further. Since the puparial morphology is so variable and seems to occur often in similar patterns in populations across the globe ommatidial number may therefore delimit some species.

Conclusion

The number of synonyms of *Bemisia tabaci* is due partly to the extreme plasticity of the puparial stages. Even though the mechanisms for the puparial variability are now largely understood, as are the limits of this variability within some generic groupings, we still cannot arrange this variability into well-limited species and genera. Early work by Mound (1963) and Russell (1957) showed that whitefly puparial morphology in the genera *Bemisia* and *Trialeurodes* Cockerell can be altered by environmental factors. Further studies have shown variable pupal morphology to be common in many other genera in the subfamily Aleyrodinae. Current molecular studies are beginning to shed some light on a few morphological structures that could be reliable generic and specific characters for some of the *Bemisia* species and related genera, by giving us a glimpse of evolutionary relationships that have not been visible to the classical taxonomist previously. Hopefully research will give us some indication of which morphological characters are useful in this way, and those characters that are not of importance. While there are no good morphological characters for separating the various races of *B. tabaci* (as currently understood), there are some interesting differences in biology, mating behavior, cross fertility and virus transmission that suggest that there are cryptic species involved, and molecular data are emerging suggestive of that possibility. Recent molecular work has provided insights into the relationships of many of the variants (biotypes, strains, races, haplotypes) of the *tabaci* complex. Several of the species that are close to *B. tabaci* morphologically include *B. capitata*, *B. formosana* and *B. graminus*, and are now included in a *tabaci* complex of species. However, the relationships of species in other genera that may in fact belong in the genus *Bemisia*, and may even be part of the *tabaci* complex, (e.g. *Bemisiella*, *Lipaleyrodes*, *Pealius azaleae* and *Parabemisia myricae*), are still unclear. In addition, the status of some species apparently related to *B. afer* are also open for question,

such as whether species of *Asterobemisia* and *Neobemisia* belong in the *afer* complex, or are possibly a single highly variable species. Based on these studies it is possible that the *afer* complex of species, including *B. tuberculata* in South America, *B. berbericola* in North America, *B. leakii* and *A. moringae* in India, may all be the same species that has been spread by humans, or more likely a collection of cryptic species like *B. tabaci* as has been suggested by the recent molecular work of Dinsdale et al (2010).

The whole premise here is based on an original suggestion that the A and B strains of *Bemisia tabaci* are separate species. Even though it was suggested at one time that *Bemisia argentifolii* should be synonymized under *B. tabaci* two papers now suggest that there are actually 24 species within the *B. tabaci* clades, which would include *B. argentifolii*. My contention is that, after the battle began over my original comment about strain A and B being separate species, and after a close study of *Bemisia* species, it is obvious that whitefly systematics is in veritable disarray. There can be no correct selection or alignment of species within genera, or an accurate selection of generic limits for that matter, until a very thorough study can be made of biologies, adults and other life studies in conjunction with intense molecular investigations. Most whitefly species in the Aleyrodinae have been arbitrarily placed in various genera over the years with no possible idea of their phylogenetic relationships. To determine which species belong in *Bemisia* will require an intensive molecular study of some of the other major genera outside of the ones that have been looked at so far. Species like *B. giffardi*, for example, probably do not belong in *Bemisia* based on some CO1 data and a very unusual last antennal segment structure in the adult, but we do not have enough molecular data now to determine even what the generic limits of *Bemisia* actually are.

As stated by Gill and Brown (2010), the answer to the question of what exactly is *Bemisia tabaci* cannot be supplied completely by the taxonomist or morphologist alone. Nor can answers be given for many other species and genera of whiteflies within the subfamily Aleyrodinae, and especially within the currently accepted parameters of the genus *Bemisia* itself. It will be necessary to carefully record as many morphological character states as possible of immatures and adults, plus biologies and other traits of living individuals, and to compare that with molecular information before any of these issues, whether they are species and generic placements, or phylogenies, can begin to be resolved.

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Literature Cited

- Anderson, P. K., J. H. Martin, P. Hernandez, and A. Lagnaoui. 2001. *Bemisia afer* sens. lat. (Homoptera: Aleyrodidae) outbreak in the Americas. *Florida Entomologist* 84: 316–317.
- Barinaga, M. 1993. Is devastating whitefly invader really a new species? *Science* 259: 30.
- Bellows, T. S., T. M. Perring, R. J. Gill, and D. H. Headrick. 1994. Description of a species of *Bemisia* (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America* 87: 195–206.
- Bink-Moenen, R. M. 1983. Revision of the African whiteflies (Aleyrodidae). *Monografieën van de Nederlandse Entomologische Vereniging, Amsterdam* 10: 1–211.
- Bink-Moenen, R. M. 1991. Comparisons between *Neopealius rubi* and *Bemisia tabaci* in Europe (Homoptera: Aleyrodidae). *Entomologische Berichten* 51: 29–37.
- Bink-Moenen, R. M. 1992. Whitefly from Mediterranean evergreen oaks (Homoptera: Aleyrodidae). *Systematic Entomology* 17: 21–40.
- Bink-Moenen, R. M., and L. A. Mound. 1990. Whiteflies: diversity, biosystematics and evolutionary patterns. p. 1–11. *In*: D. Gerling (ed.). *Whiteflies: their bionomics, pest status and management*. Intercept; Wimborne. 348 p.
- Brown, J. K. 2010. Phylogenetic Biology of the *Bemisia tabaci* Sibling Species Group. p. 31–67. *In*: P. A. Stansly and S. E. Naranjo (eds.). *Bemisia: bionomics and management of a global pest*. Springer; Dordrecht. 540 p.
- Brown, J. K., S. Coats, I. D. Bedford, P. G. Markham, and J. Bird. 1992. Biotypic characterization of *Bemisia tabaci* populations based on esterase profiles, DNA fingerprinting, virus transmission, and bioassay to key host plant species. *Phytopathology* 82: 1104.
- Brown, J. K., S. Coats, I. D. Bedford, P. G. Markham, and D. Frolich. 1994. Characterization and distribution of esterase electromorphs in the whitefly, *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae). *Biochemical Genetics* 33: 205–214.
- Brown, J. K., D. R. Frolich, and R. C. Rosell. 1995. The sweetpotato or silverleaf whiteflies: biotypes of *Bemisia tabaci* or a species complex? *Annual Review of Entomology* 40: 511–534.
- Brown, J. K., R. French, D. Rogan, R. Caballero, and J. Bird. 2004. Genetic variability and phylogeographical relationships of the *Bemisia tabaci* complex based on the mt cytochrome oxidase I gene. 2nd European Whitefly Symposium, October 5–9, 2004, Cavtat, Croatia.
- Caballero, R. and J. K. Brown. 2006. Positive evidence for interbreeding and differential gene flow between three well characterized biotypes of the *Bemisia tabaci* complex (Gennadius) (Homoptera: Aleyrodidae) excludes geographic and host barriers as isolating factors. Abstract and poster presentation, 4th International Bemisia Workshop, Duck Key, Florida, Dec. 3–6, 2006, Abst. Pg. 11.
- Campbell, B. C., J. E. Duffus, and P. Baumann. 1993. Technical comments: determining whitefly species. *Science* 261: 1333.
- Campbell, B. C., J. D. Steffen-Campbell, and R. J. Gill. 1994. Evolutionary origin of whiteflies (Homoptera: Sternorrhyncha: Aleyrodidae) inferred from 18S rDNA sequences. *Insect Molecular Biology* 3: 73–88.
- Campbell, B. C., J. D. Steffen-Campbell, and R. J. Gill. 1995. Origin and radiation of whiteflies: an initial molecular phylogenetic assessment. p. 29–51. *In*: D. Gerling and R. T. Mayer (eds). *Bemisia: 1995: taxonomy, biology, damage control and management*. Intercept; Andover, UK. 702 p.
- Coats, S. A., J. K. Brown, and D. L. Hendrix. 1994. Biochemical characterization of biotype-specific esterases in the whitefly *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae). *Insect Biochemistry and Molecular Biology* 24: 723–728.
- Costa, H. S., and J. K. Brown. 1990. Variability in biological characteristics, isozyme patterns and virus transmission among populations of *Bemisia tabaci* (Genn.) in Arizona. *Phytopathology* 80: 888.
- Costa, H. S., and J. K. Brown. 1991. Variation in biological characteristics and in esterase patterns among populations of *Bemisia tabaci* (Genn.) and the association of one population with silverleaf symptom development. *Entomologia Experimentalis et Applicata* 61: 211–219.
- Costa, H. S., M. W. Johnson, D. E. Ullman, A. D. Omer, and B. E. Tabashnik. 1993. Sweetpotato whitefly (Homoptera: Aleyrodidae): analysis of biotypes and distribution in Hawaii. *Environmental Entomology* 22: 16–20.

- David, B. V., and A. K. Dubey. 2009. New synonymies and combinations in *Bemisia* (Aleyrodidae: Hemiptera). *Oriental Insects* 43: 1–6.
- De Barro, P. J., J. W. H. Trueman, and D. R. Frolich. 2005. *Bemisia argentifolii* is a race of *B. tabaci* (Hemiptera: Aleyrodidae): the molecular differentiation of *B. tabaci* populations around the world. *Bulletin of Entomological Research* 95: 193–203.
- De Barro, P. J., S.-S. Liu, L. M. Boykin, and A. B. Dinsdale. 2011. *Bemisia tabaci*: a statement of species status. *Annual Review of Entomology* 56:1–19.
- Dinsdale, A., L. Cook, C. Riginos, Y. M. Buckley, and P. De Barro. 2010. Refined global analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. *Annals of the Entomological Society of America* 103: 196–208.
- Dubey, A. K., C.-C. Ko, and B. V. David. 2009. The genus *Lipaleyrodes* Takahashi, a junior synonym of *Bemisia* Quaintance and Baker (Hemiptera: Aleyrodidae) a revision based on morphology. *Zoological Studies* 48: 539–557.
- Gill, R. J. 1990. The morphology of whiteflies. p. 13-46 *In*: D. Gerling (ed.). *Whiteflies: their bionomics, pest status and management*. Intercept; Wimborne. 348 p.
- Gill, R. J. 1992. A review of the sweetpotato whitefly in southern California. *Pan-Pacific Entomologist* 68: 144–152.
- Gill, R. J., and J. Brown. 2010. Systematics of *Bemisia* and *Bemisia* relatives: can molecular techniques solve the *Bemisia tabaci* complex cunundrum – a taxonomist’s viewpoint. p. 1-29. *In*: P. A. Stansly and S. E. Naranjo (eds.). *Bemisia: bionomics and management of a global pest*. Springer; Dordrecht. 540 p.
- Gonzalez, R. A., J. I. Grieshop, G. E. Goldman, S. R. Sutter, E. T. Natwick, T. Funakoshi, H. R. Rosenburg, and S. Davila-Garcia. 1992. Whitefly invasion in Imperial County costs growers, workers millions in losses. *California Agriculture* 46 (6): 7–8.
- Hsing-Yeh, L., J. E. Duffus, and S. Cohen. 1992. Work group on *Bemisia tabaci* Newsletter No. 6. November, Tropical Whitefly IPM Project. Submitted on-line at: www.tropicalwhiteflyipmproject.cgiar.org/bemisianewsletter06.jsp. Last accessed May 2011.
- Huldén, L. 1986. The whiteflies (Homoptera: Aleyrodidae) and their parasites in Finland. *Notulae Entomologicae* 66:1-40.
- Lai, P. Y. 1985. *Bemisia tabaci* Gennadius. Notes and Exhibitions. *Proceedings of the Hawaiian Entomological Society* 25: 18.
- Martin, J. H., and L. A. Mound. 2007. An annotated check list of the world’s whiteflies (Insecta: Hemiptera: Aleyrodidae). *Zootaxa* 1492: 1–84.
- Martin, J. H., D. Mifsud, and C. Rapisarda. 2000. The whiteflies (Hemiptera: Aleyrodidae) of Europe and the Mediterranean Basin. *Bulletin of Entomological Research* 90: 407–448.
- Mohanty, A. K., and A. N. Basu. 1986. Effects of host plants and seasonal factors on intraspecific variations in pupal morphology of the whitefly vector *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae). *Journal of Entomological Research* 10: 19–26.
- Mound, L. A. 1963. Host correlated variation in *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Proceedings of the Royal Entomological Society of London* A38: 171–180.
- Mound, L. A., and S. H. Halsey. 1978. *Whitefly of the world*. British Museum (Natural History). John Wiley and Sons; Chichester. 340p.
- Neil, J. W., and J. Bentz. 1999. Evidence for the stage inducing phenotypic plasticity in pupae of the polyphagous whiteflies *Trialeurodes vaporariorum* and *Bemisia argentifolii* (Homoptera: Aleyrodidae) and the raison d’être. *Annals of the Entomological Society of America* 92: 774–787.
- Perring, T. M., A. Cooper, and D. J. Kazmer. 1992. Identification of the poinsettia strain of *Bemisia tabaci* (Homoptera: Aleyrodidae) on broccoli by electrophoresis. *Journal of Economic Entomology* 85: 1278–1284.
- Perring, T. M., A. Cooper, R. J. Rodriguez, C. A. Farrar, and T. S. Bellows, Jr. 1993. Identification of whitefly species by genomic and behavioral studies. *Science* 259: 74–77.
- Priesner, H., and M. Hosny. 1934. Contributions to a knowledge of the whiteflies (Aleyrodidae) of Egypt (III). *Bulletin. Ministry of Agriculture, Egypt. Technical and Scientific Services* 145: 1–11.

- Quaintance, A. L. 1900.** Contribution towards a monograph of the American Aleurodidae. Technical Series, Bureau of Entomology, United States 8: 9-64.
- Regu, K., and B. V. David. 1991.** A new species of *Bemisia* (Homoptera: Aleyrodidae) from India with a key to Indian Species. Entomon 16: 77–81.
- Rosell, R. C., I. D. Bedford, D. R. Frolich, R. J. Gill, J. K. Brown, and P. G. Markham. 1997.** Analysis of morphological variation in distinct populations of *Bemisia tabaci* (Homoptera: Aleyrodidae). Annals of the Entomological Society of America 90: 575–589.
- Russell, L. M. 1957.** Synonyms of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). Bulletin of the Brooklyn Entomological Society 52: 122–123.
- Russell, L. M. 1957.** Collection records of *Bemisia tabaci* (Gennadius) in the United States (Homoptera: Aleyrodidae). United States Department of Agriculture Cooperative Economic Insect Report 25 (12): 229-230.
- Sampson, W. W. 1943.** A generic synopsis of the hemipterous superfamily Aleyrodoidea. Entomologica Americana 23: 173–223.
- Sampson, W. W., and E. A. Drews. 1956.** Keys to the genera of the Aleyrodinae and notes on certain genera. (Homoptera: Aleyrodinae). Annals and Magazine of Natural History 9: 689–697.

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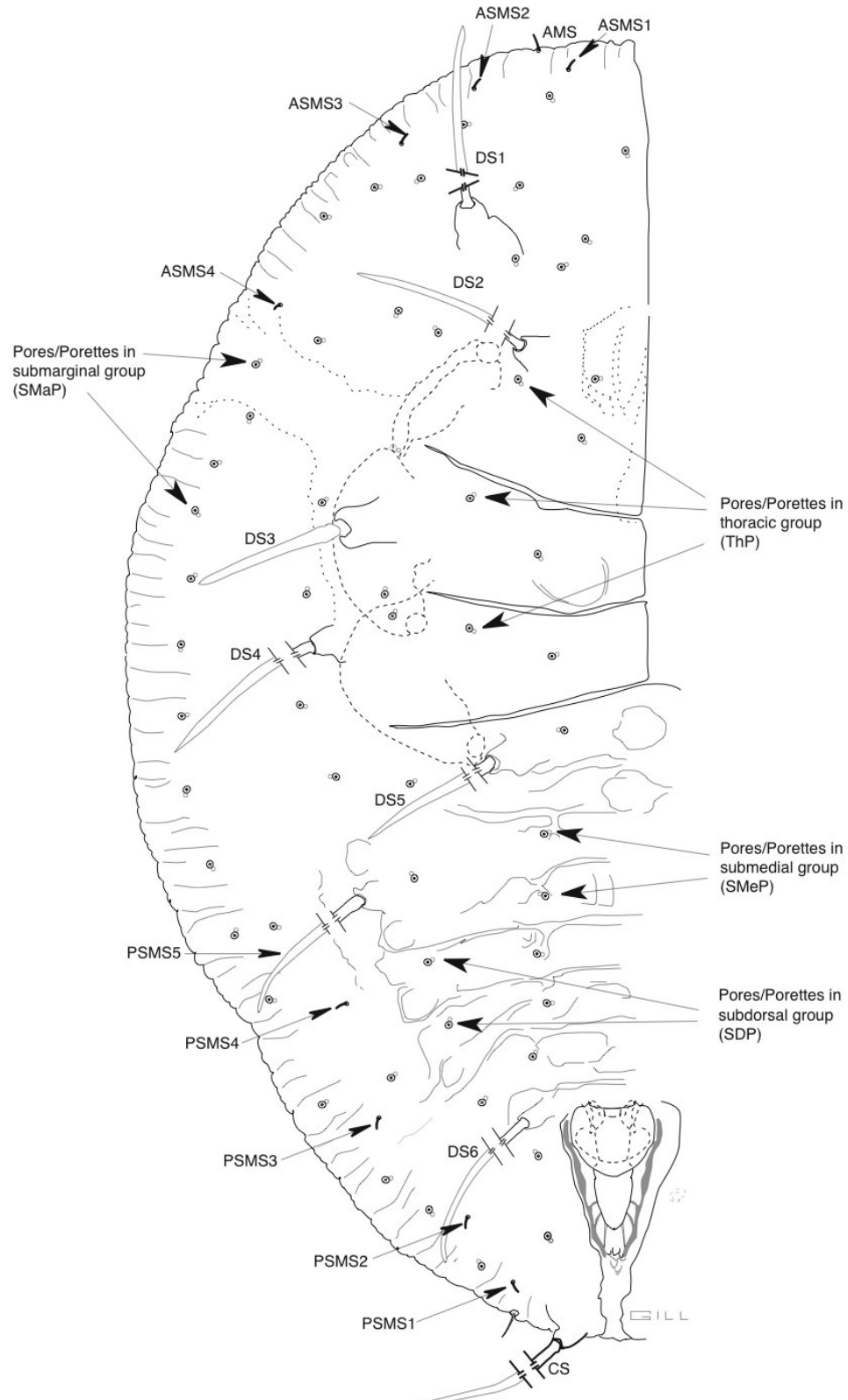


Figure 1. SYNTYPE, *Bemisia tabaci* (Gennadius) Slide #1, Specimen #4, Athens, Greece, June 10, 1889, P. Gennadius, coll., Q3120, Bur. Ent. #4449.

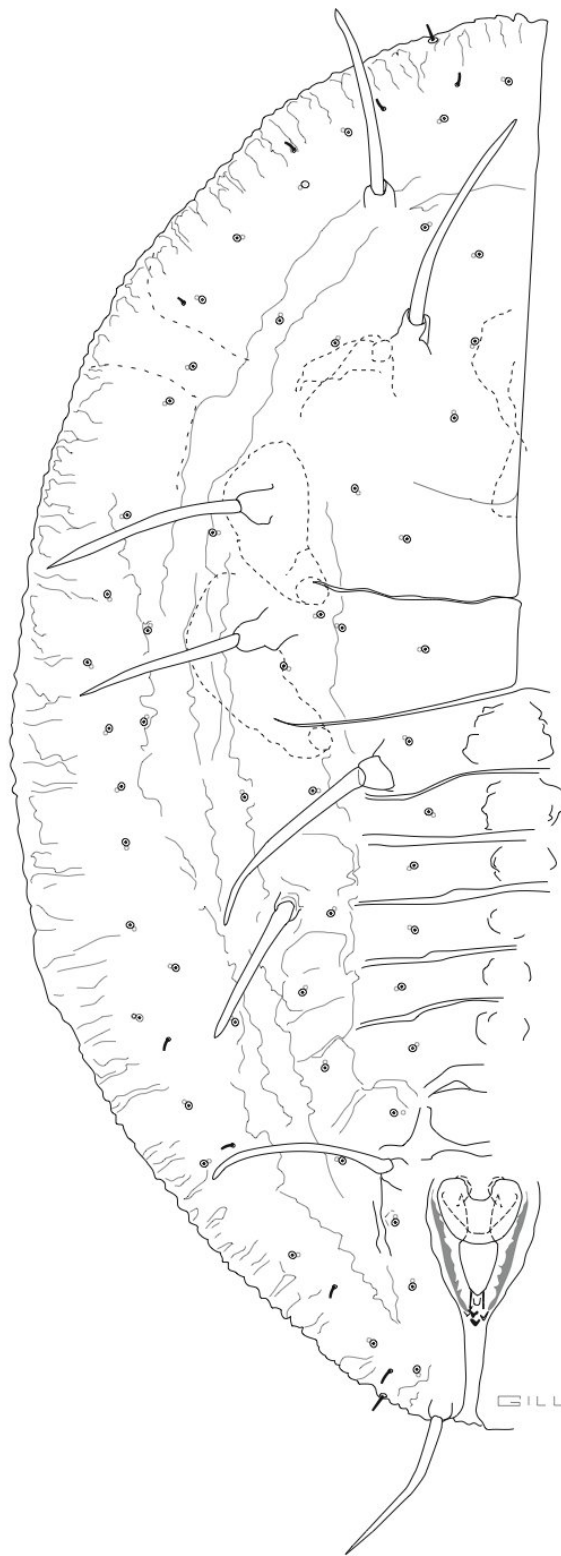


Figure 2. *Bemisia tabaci* (Gennadius), (labeled as “extreme variant” by Louise Russell), Yucca Valley, Calif., 8-XI-61, ex: Hibiscus.

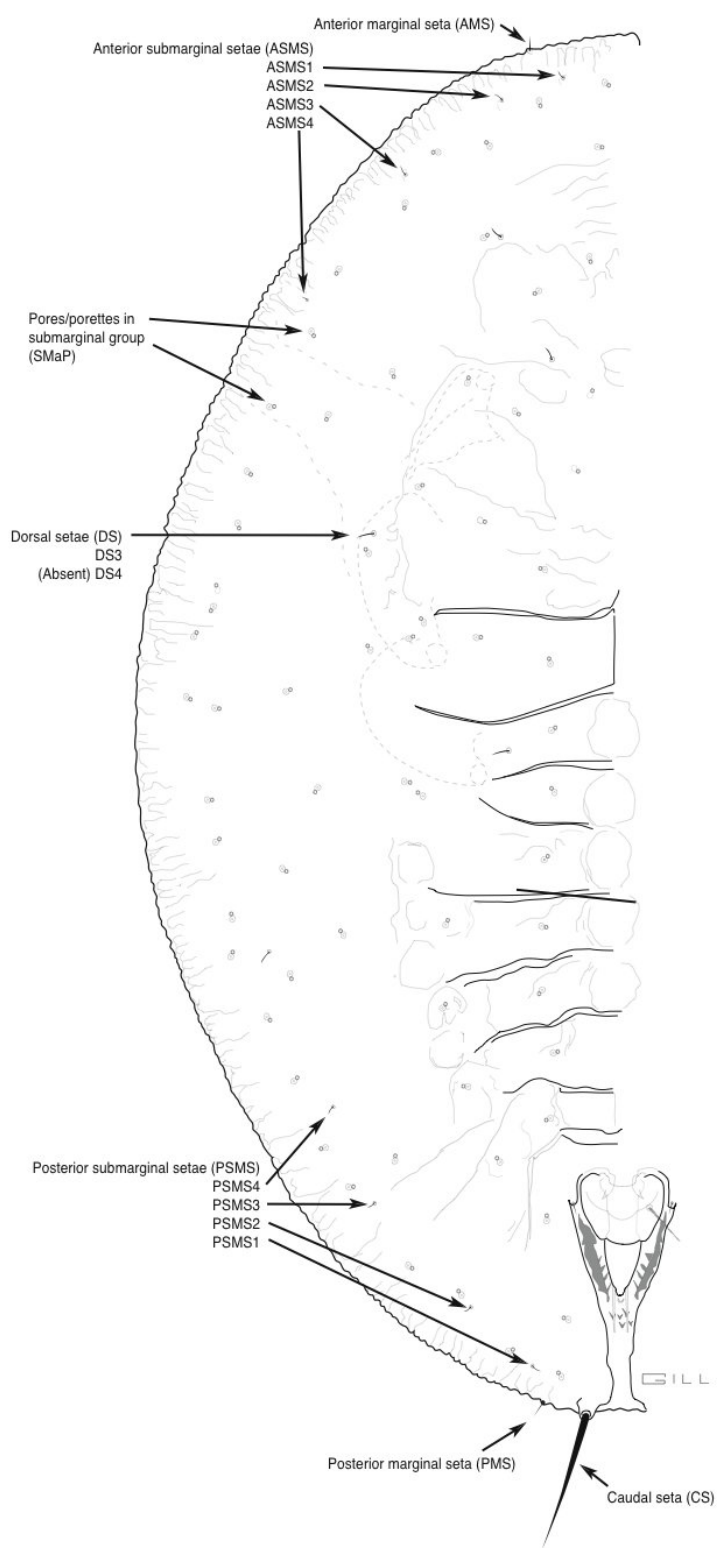


Figure 3. *Bemisia tabaci* (Gennadius) specimen 12A #1, Tolima, Colombia, ex: cotton.

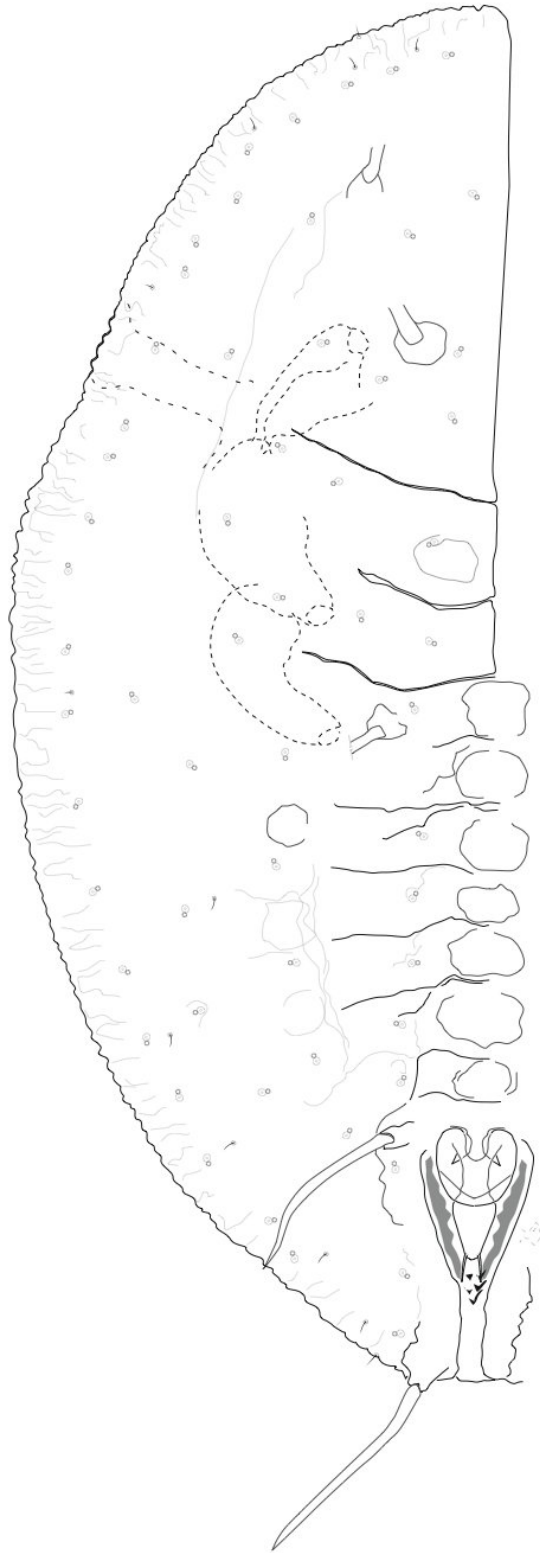


Figure 4. Type material, *Bemisia poinsettiae* Hempel, Belo Horizonte, Minas, Brazil, II-192, ex: Poinsettia.

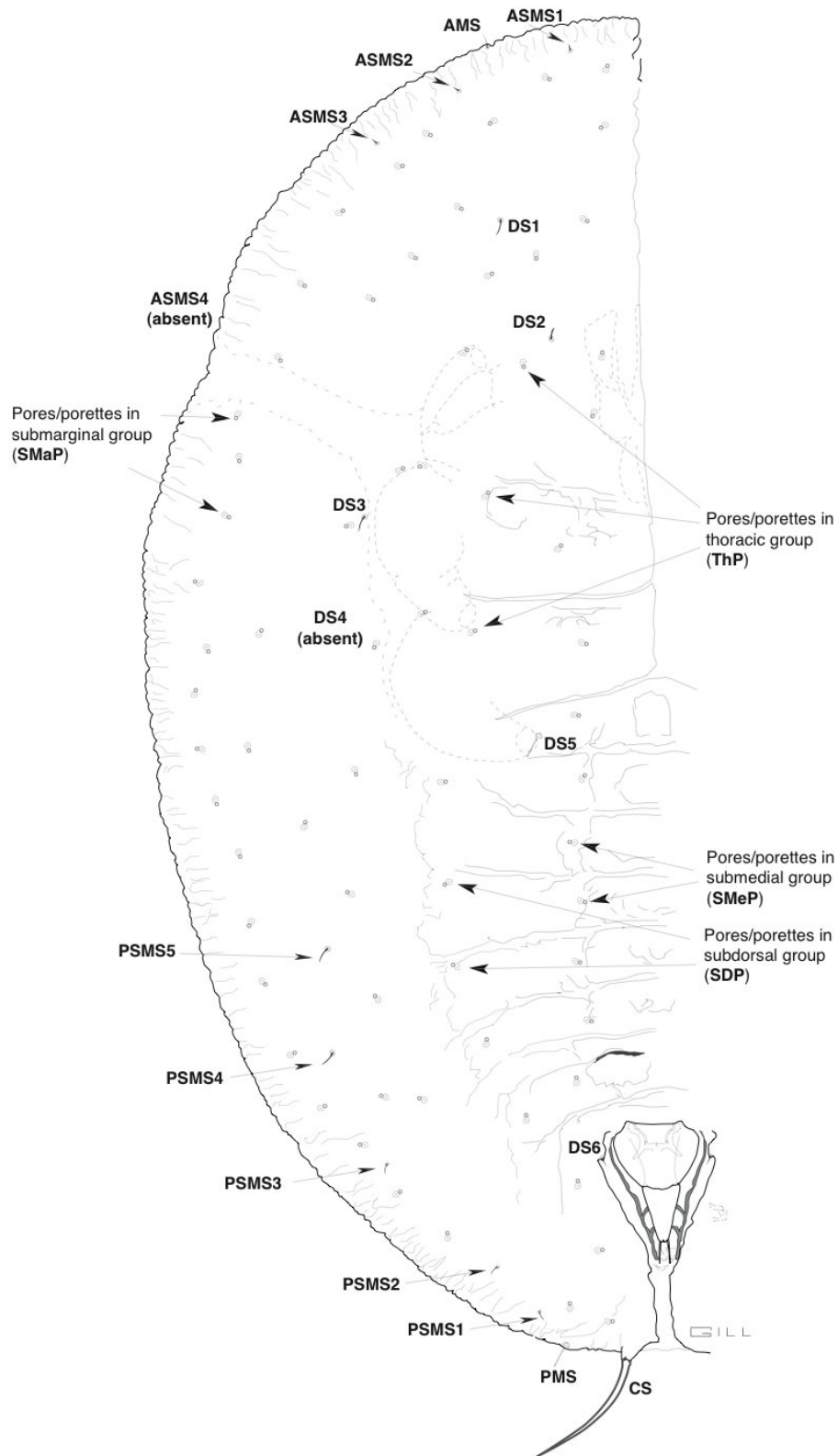


Figure 5. Holotype, *Bemisia argentifolii* Bellows and Perring, From Lab Culture, U.C. Riverside, Dec. 1992, ex: *Phaseolus limensis*.

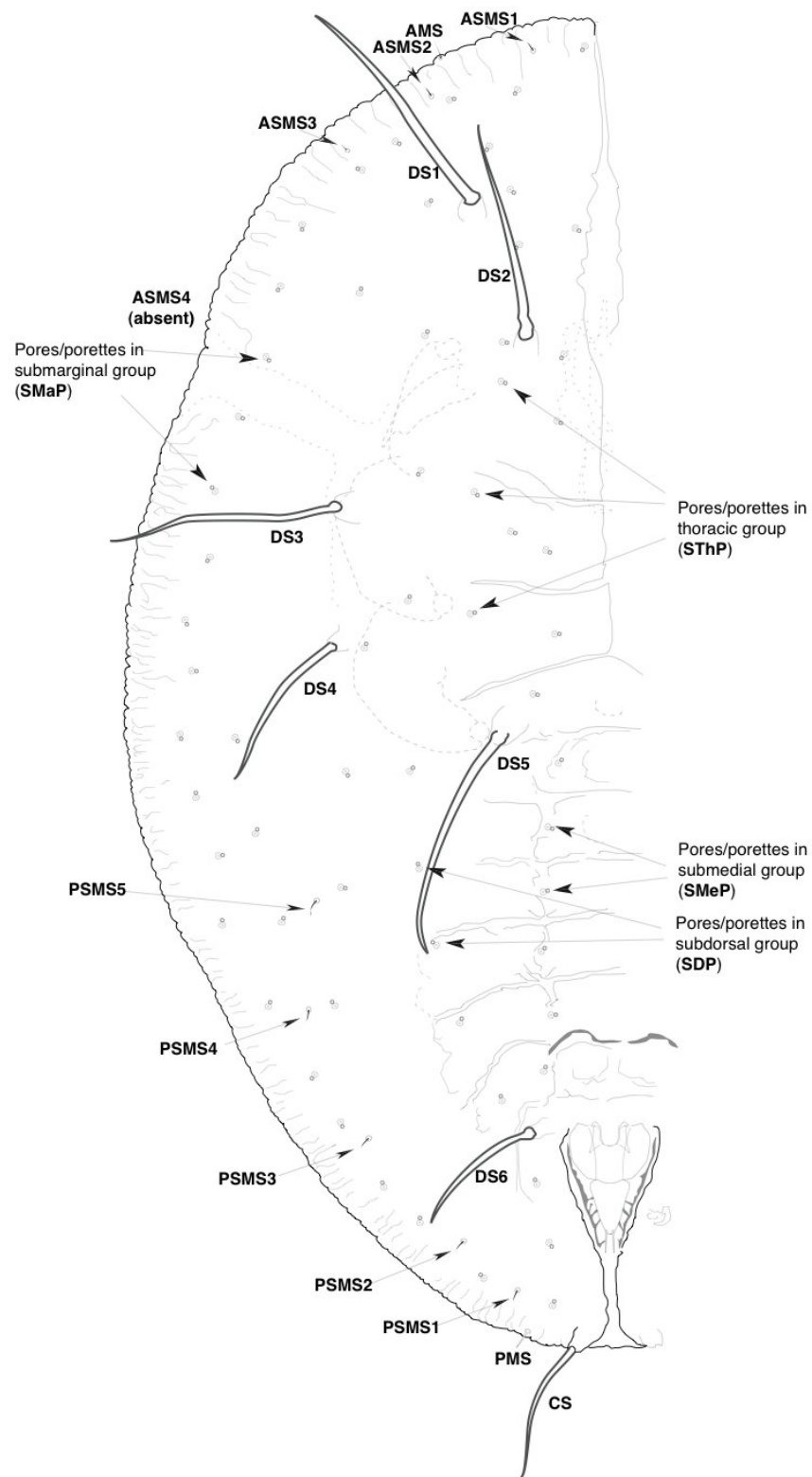


Figure 6. *Bemisia argentifolii* Bellows and Perring, Paratype, Stock Culture, U.C. Riverside, Dec. 1992, ex: *Phaseolus limensis*.

Specimen 108D #1
Mecca, CA IX-9-91
ex: Citrus

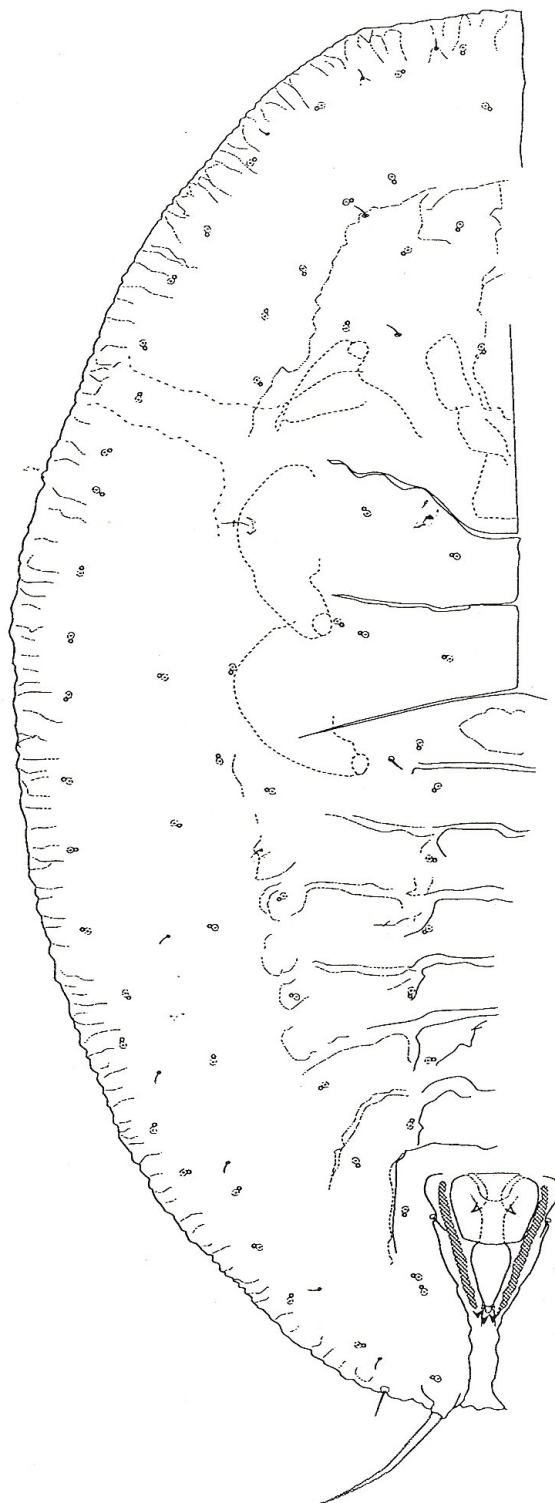


Figure 7. *Bemisia argentifolii* Bellows and Perring, specimen 108D, Mecca California, IX-9-91, ex. *Citrus*.

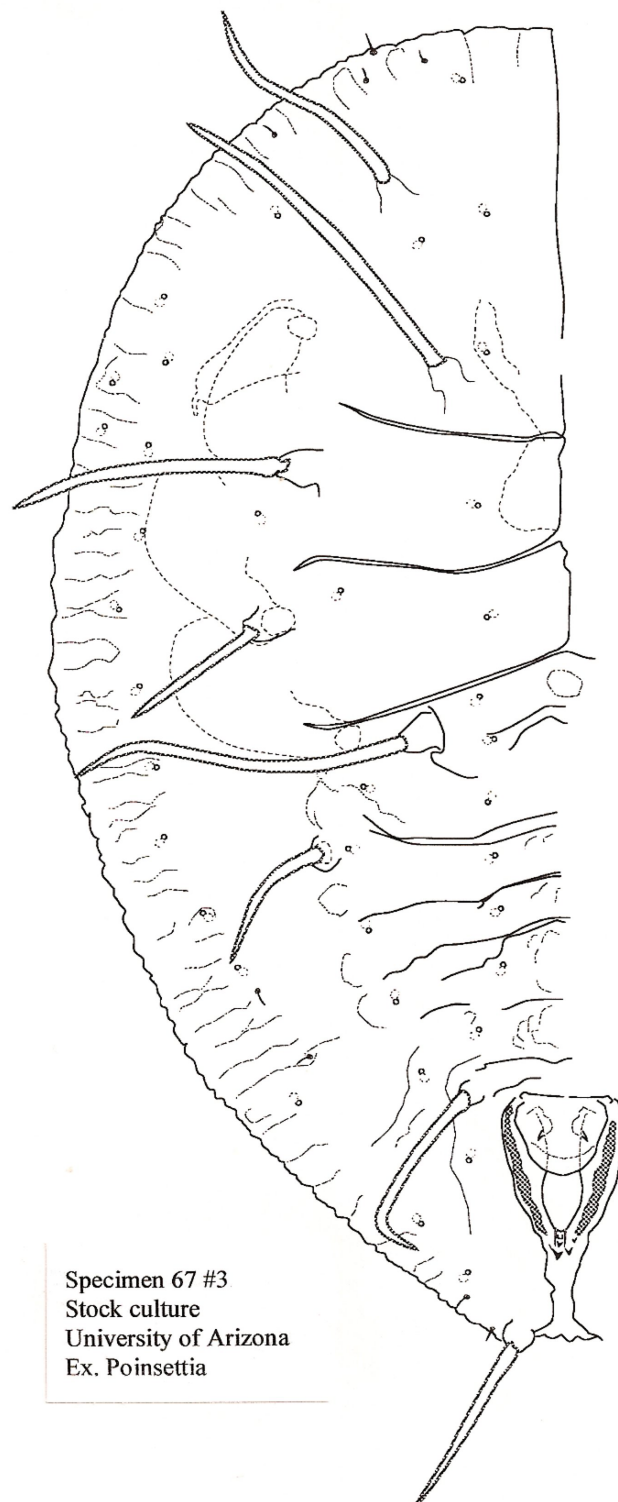


Figure 8. *Bemisia argentifolii* Bellows and Perring, specimen 68B #4, University of Arizona stock culture, Tucson, ex. cotton.

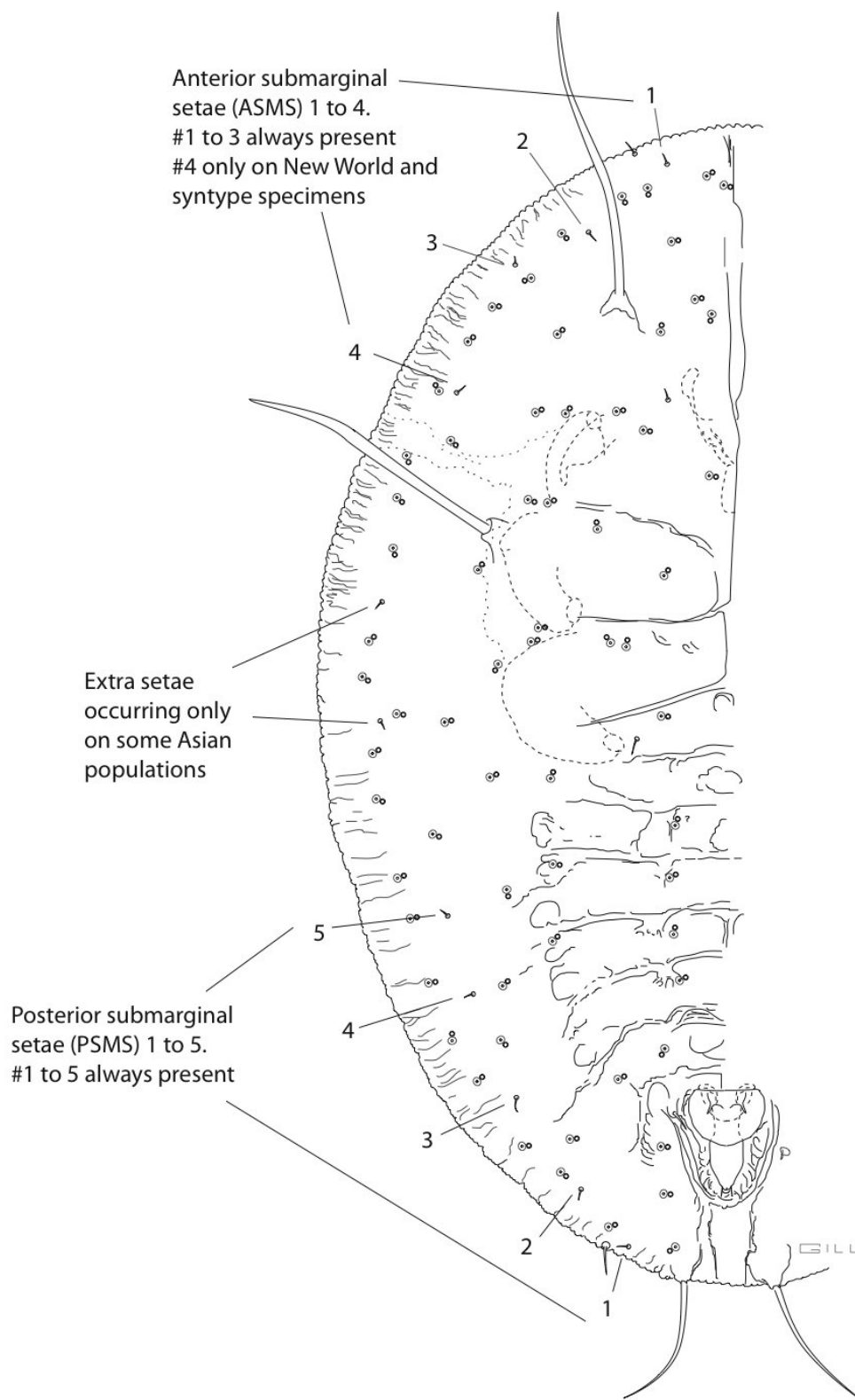


Figure 9. *Bemisia tabaci* complex, West Malaysia, Genting Highlands, 10/2/85, ex. Fern Fronds. (Reprinted by permission from Springer Science+Business Media B.V.).

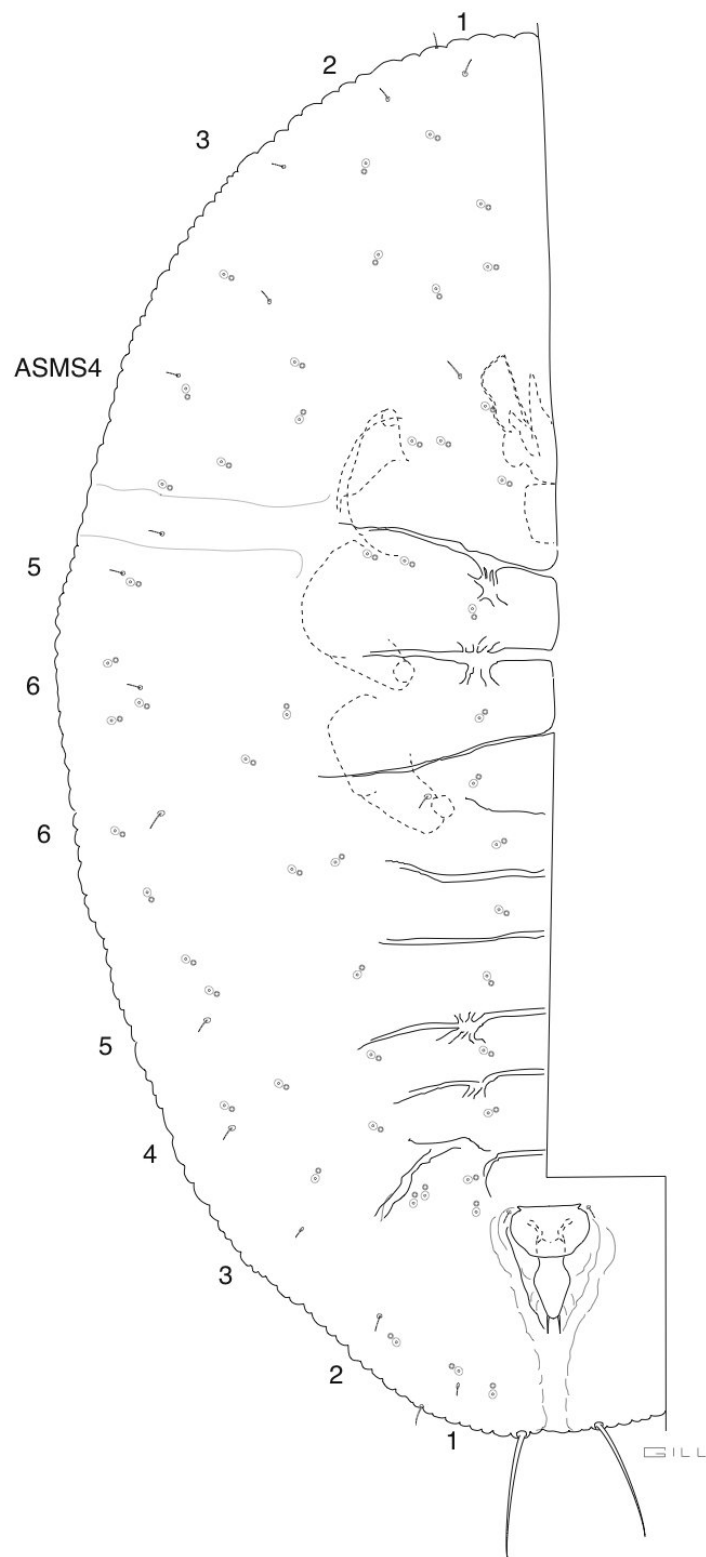


Figure 10. *Bemisia tabaci* complex, Hong Kong, Middle Gap Road, 01 Dec. 2003, S.K. Lau and J.H. Martin, coll., JHM #7881, ex. *Phyllanthus cochinchinensis*.



Figure 11. Paratype, *Bemisia minima* Danzig, Staraya Gagra, USSR, E. Danzig, coll., 26-IX-60, ex. *Helianthus cultus*. (Synonym of *B. tabaci*).

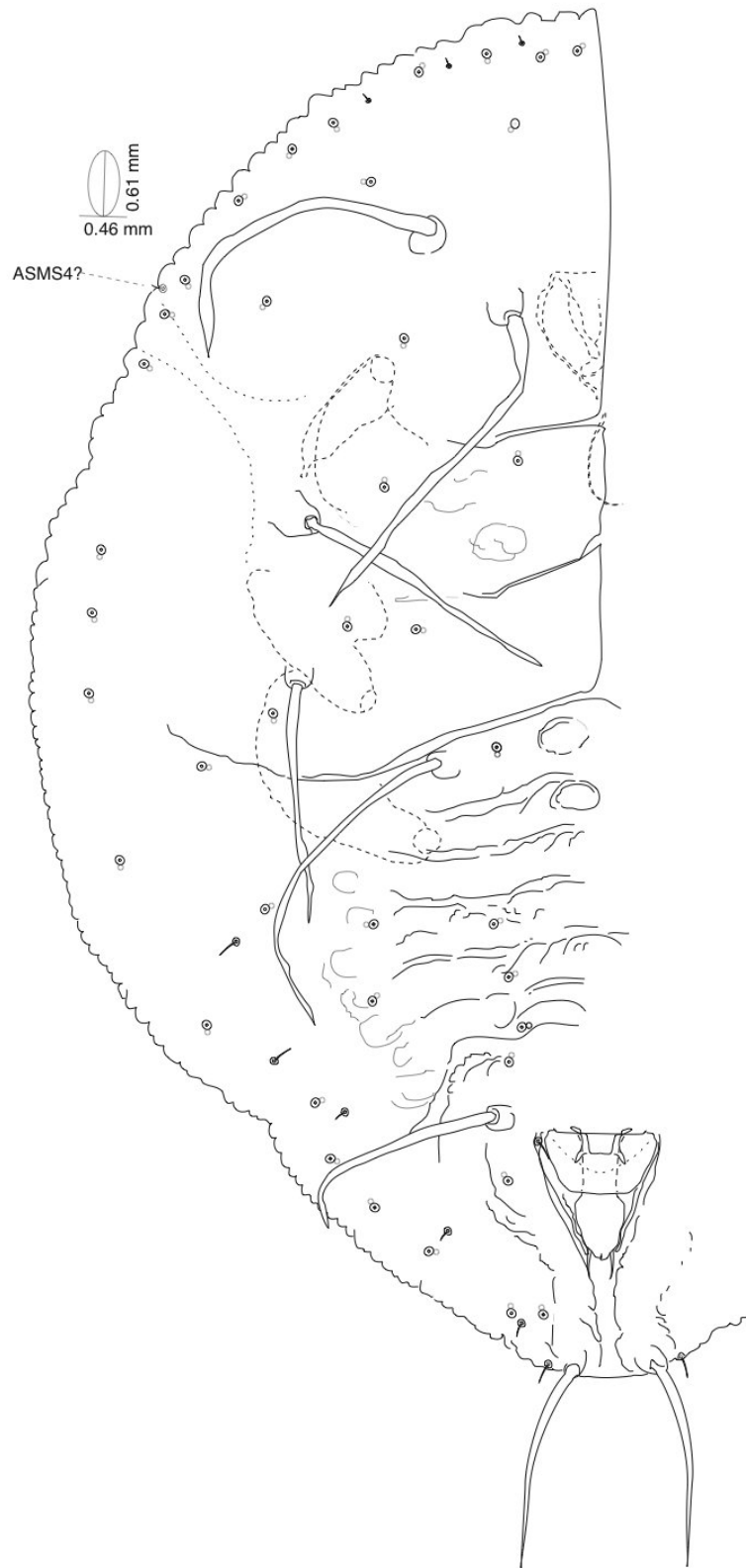


Figure 12. *Bemisia miniscula* Danzig, Adzharia, Keda, Caucasus, USSR, 3-IX-60, ex: *Cistus salvifolius*, E. Danzig, coll. (Synonym of *B. tabaci*).

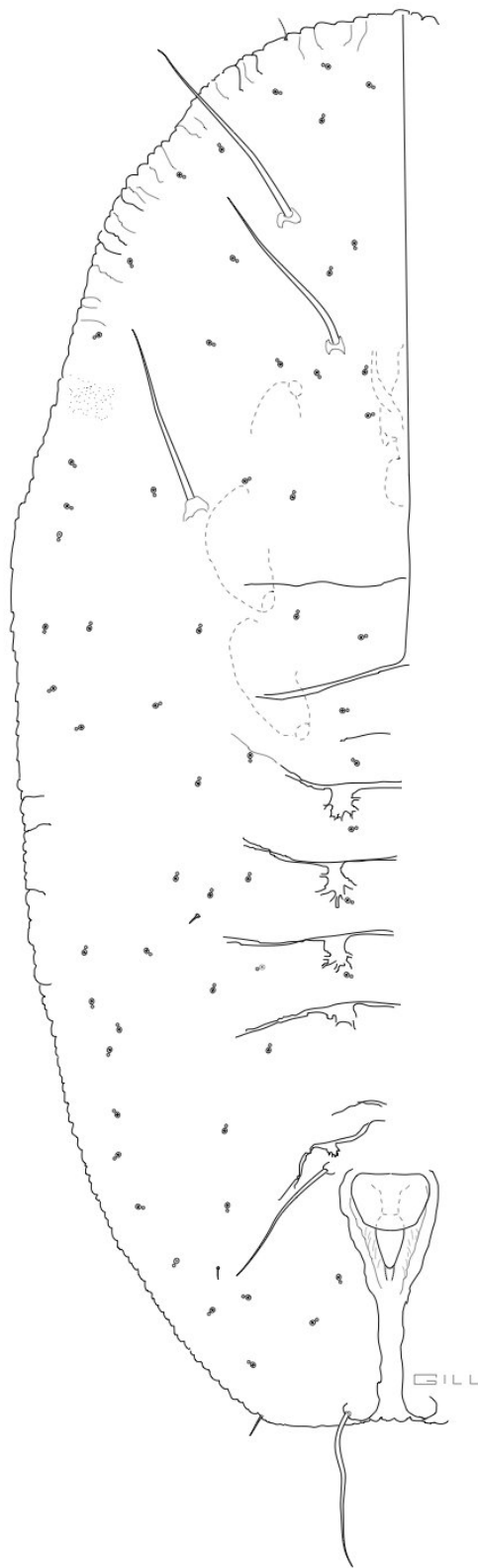


Figure 13. *Bemisia formosana* Takahashi, Chihpen-Wanchuan, Taiwan, 26-IX-1989 ex. *Setaria palmifolia*, I.C.Hsu, coll.

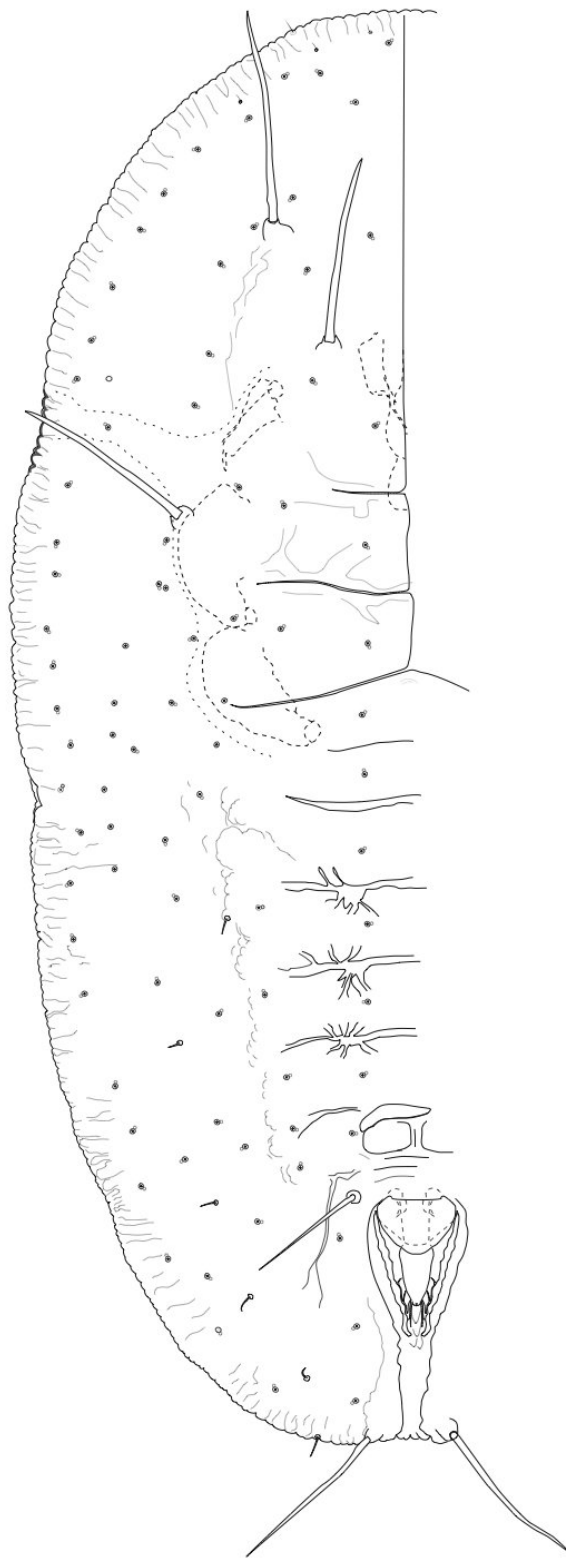


Figure 14. *Bemisia graminus* David and Winstone, Rawalpindi, Pakistan, 16.ix.1980, Ex. *Sorghum vulgare*, CEIA 12539, No. 2072.

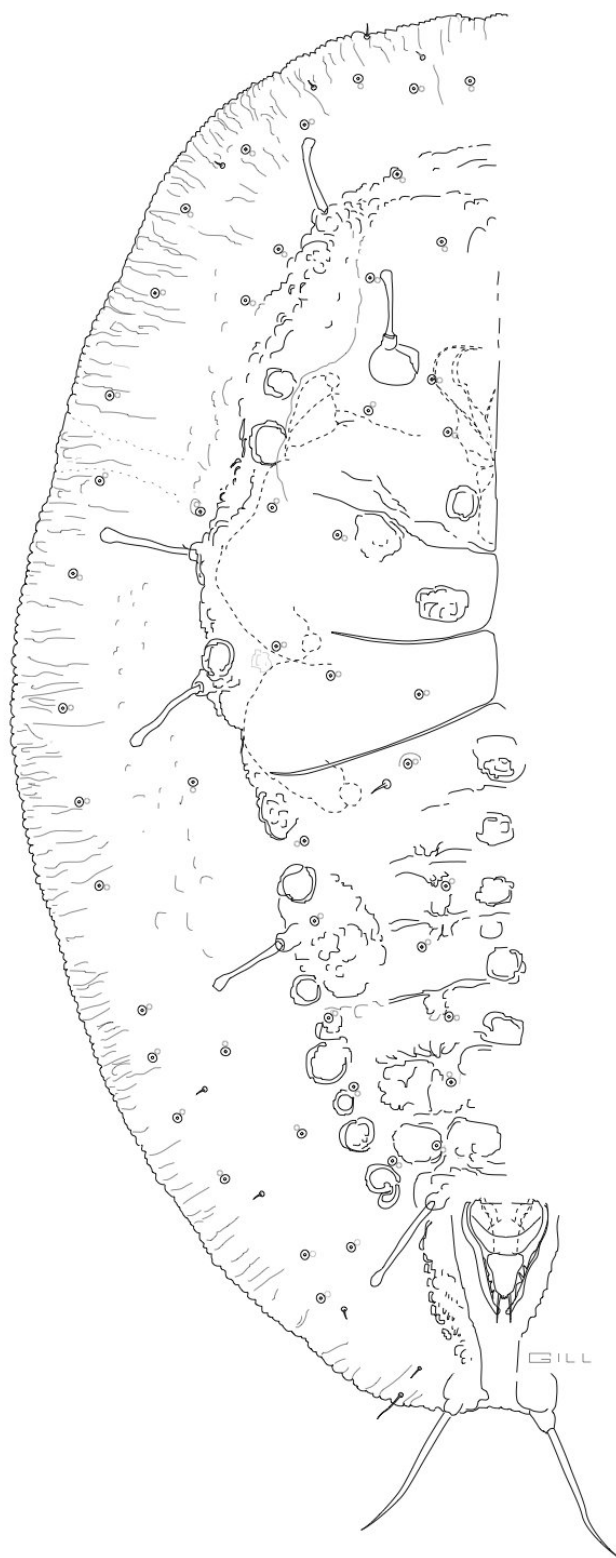


Figure 15. *Bemisia capitata* Regu and David, Padappi, Tamil Nadu, India, 2/3/93, ex: *Rivea hypocrateriformis*, Susan Coats, coll.

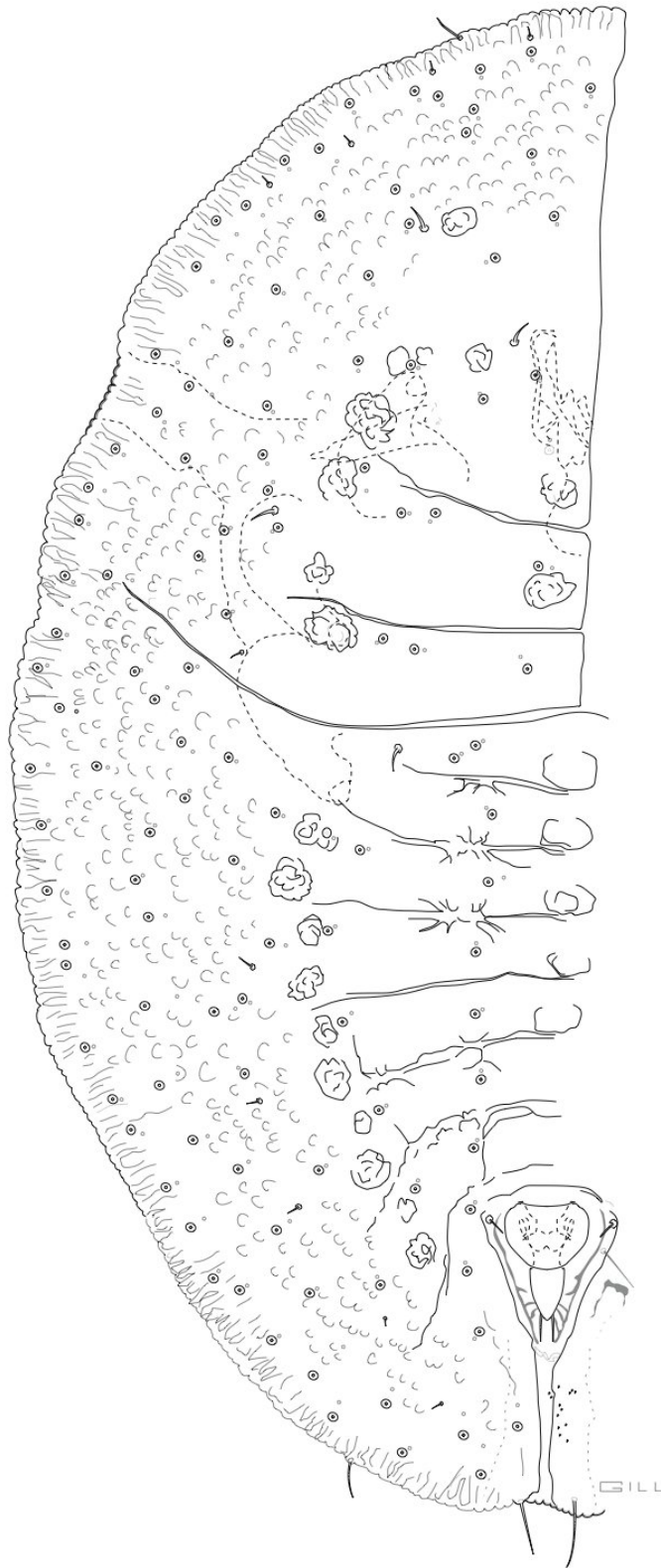


Figure 16. *Bemisia hancocki* Corbett, = *Bemisia afer*??, Uganda: Teso Prov., nr. Serere, ex. Cotton. (Reprinted by permission from Springer Science+Business Media B.V.).

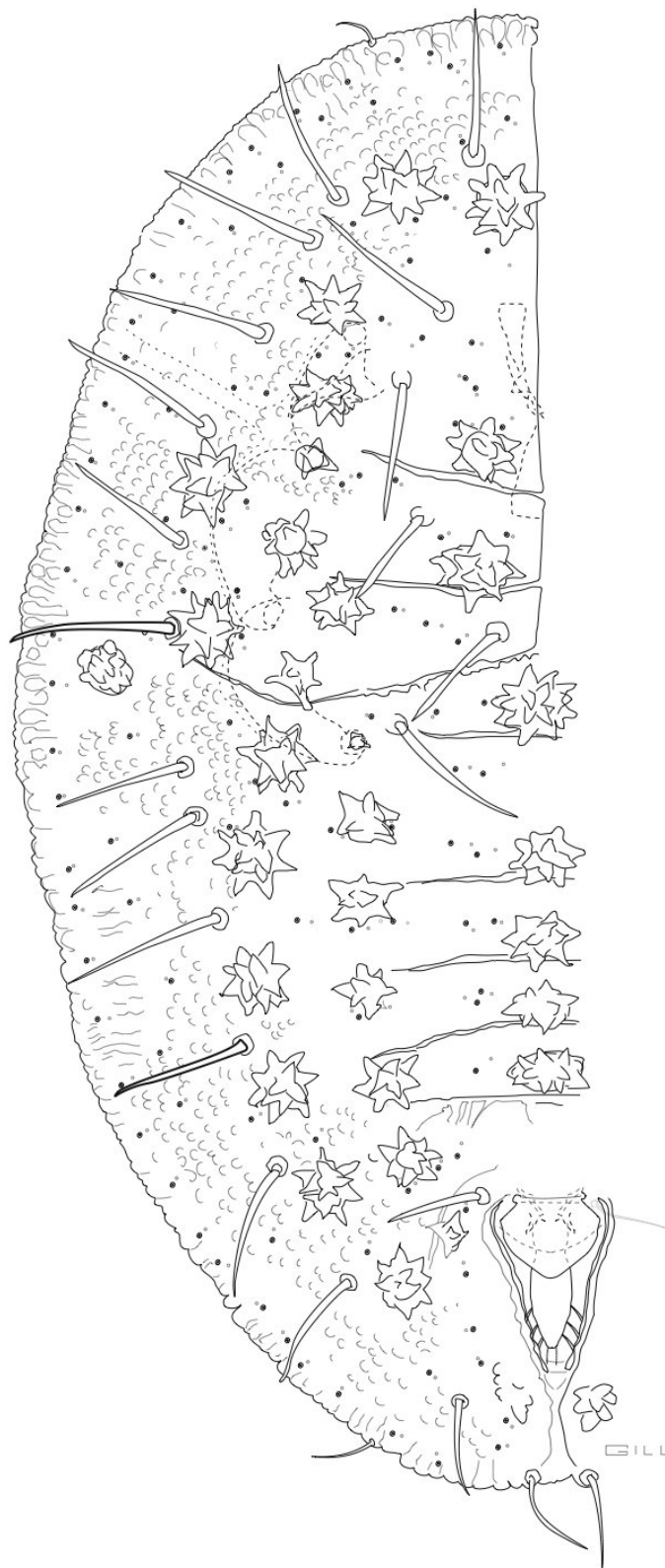


Figure 17. *Bemisia guieriae* Bink-Moenen, Sudan: Kordofan, 18-iv-81, ex: *Guiera senegalensis*, J. Martin coll. (Reprinted by permission from Springer Science+Business Media B.V.).

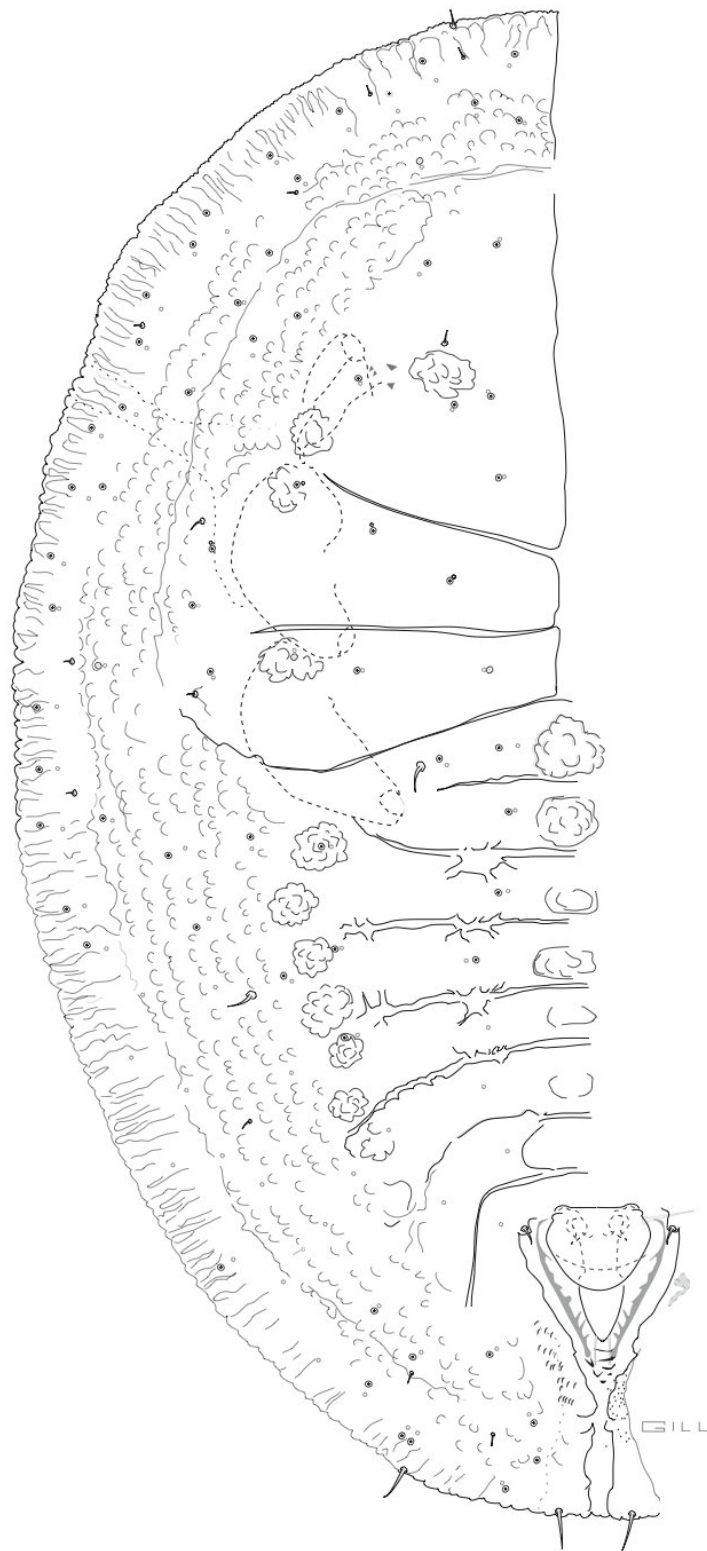


Figure 18. *Bemisia tuberculata* Bondar, Specimen TB2 #3, Araras P.C. Brasil, 6/69 ex. *Manihot ultissima*, A.S. Costa, Det. L.M. Russell.

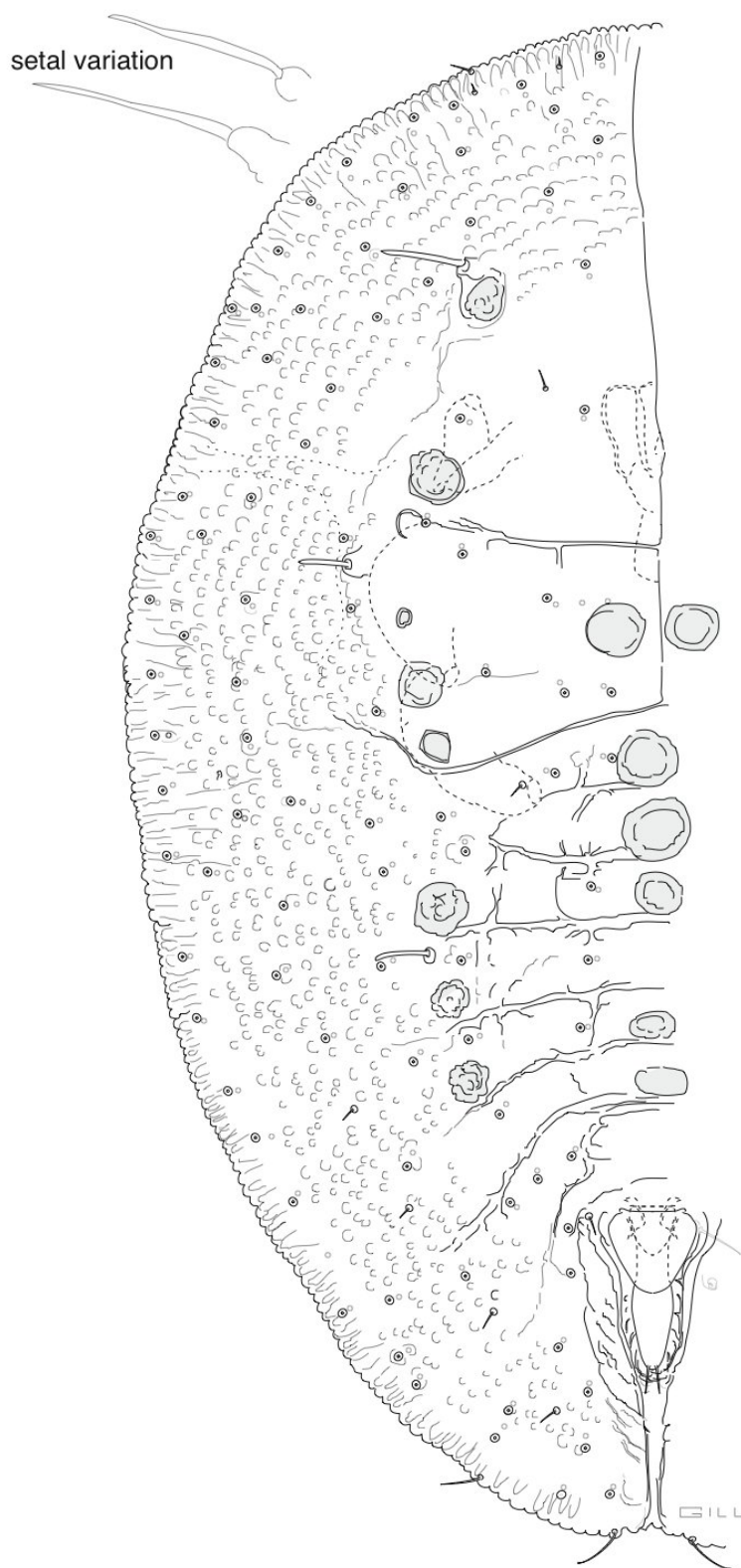


Figure 19. *Bemisia tuberculata* Bondar, PERU, Cañete SA, Dept. Cañete, 1/15/93, ex. cotton, D.E. Stevenson, coll.

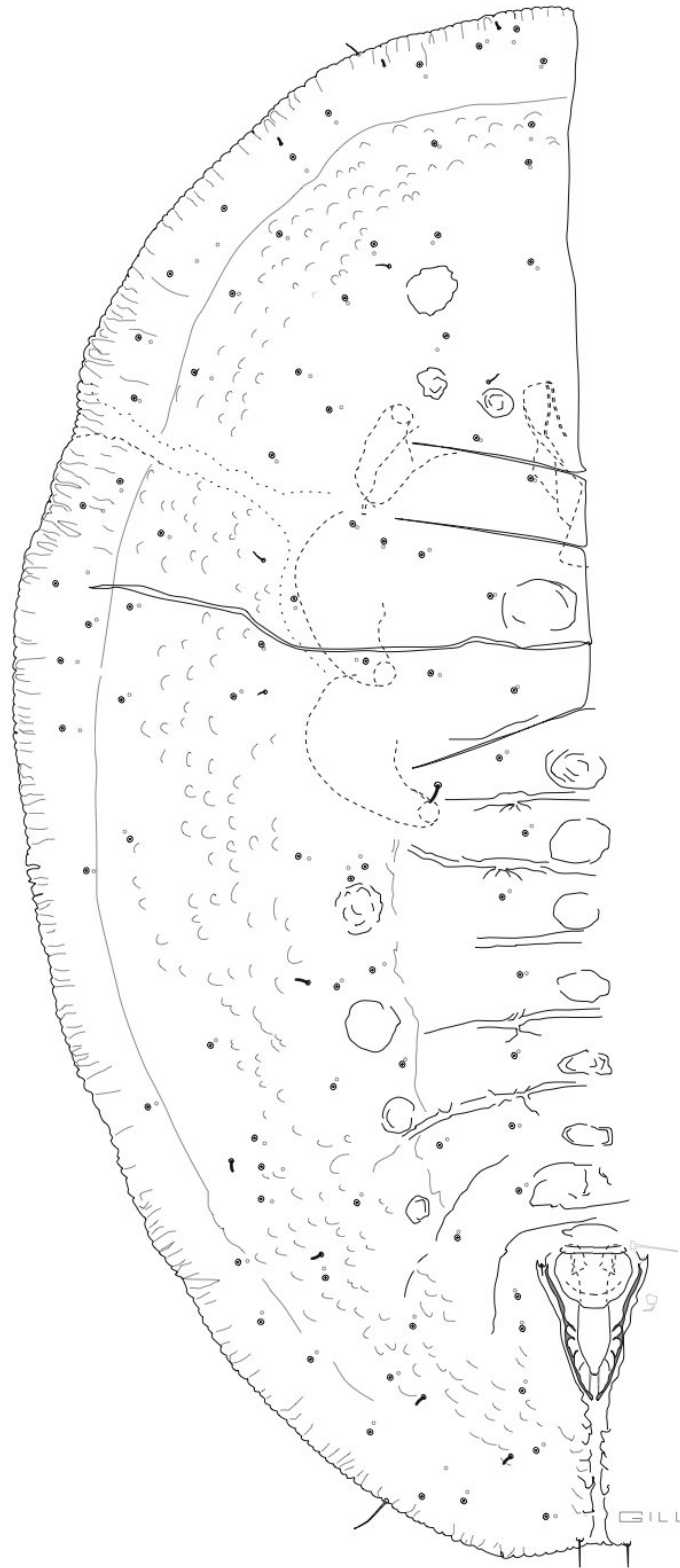


Figure 20. *Bemisia berbericola* (Cockerell), Specimen 92B #3, El Centro, California, 1/14/91, ex: rose, Weddle/Flock, colls. (Reprinted by permission from Springer Science+Business Media B.V.).

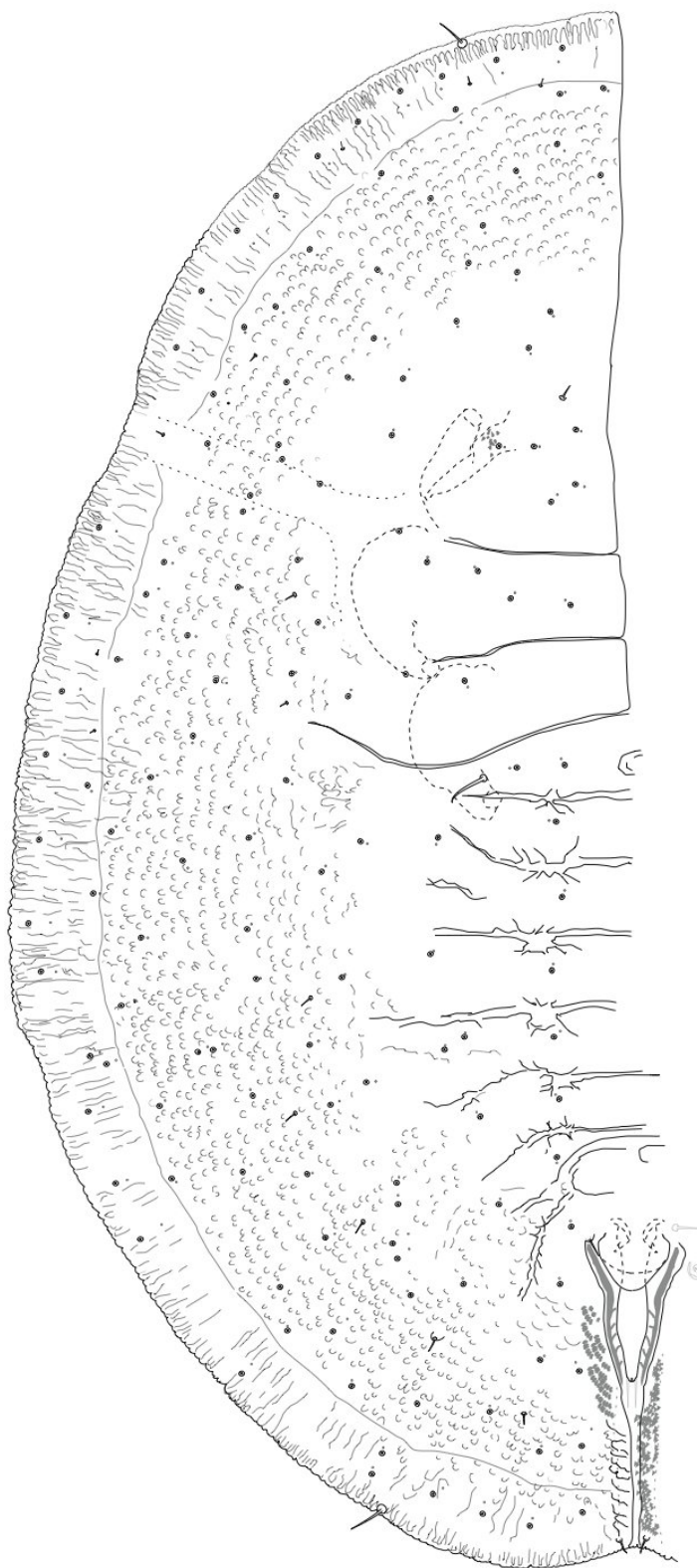


Figure 21. *Bemisia berbericola* (Cockerell), San Diego, San Diego Co. CA, II-1-67, ex Holly (*Ilex* sp.), B. Barnett, coll.

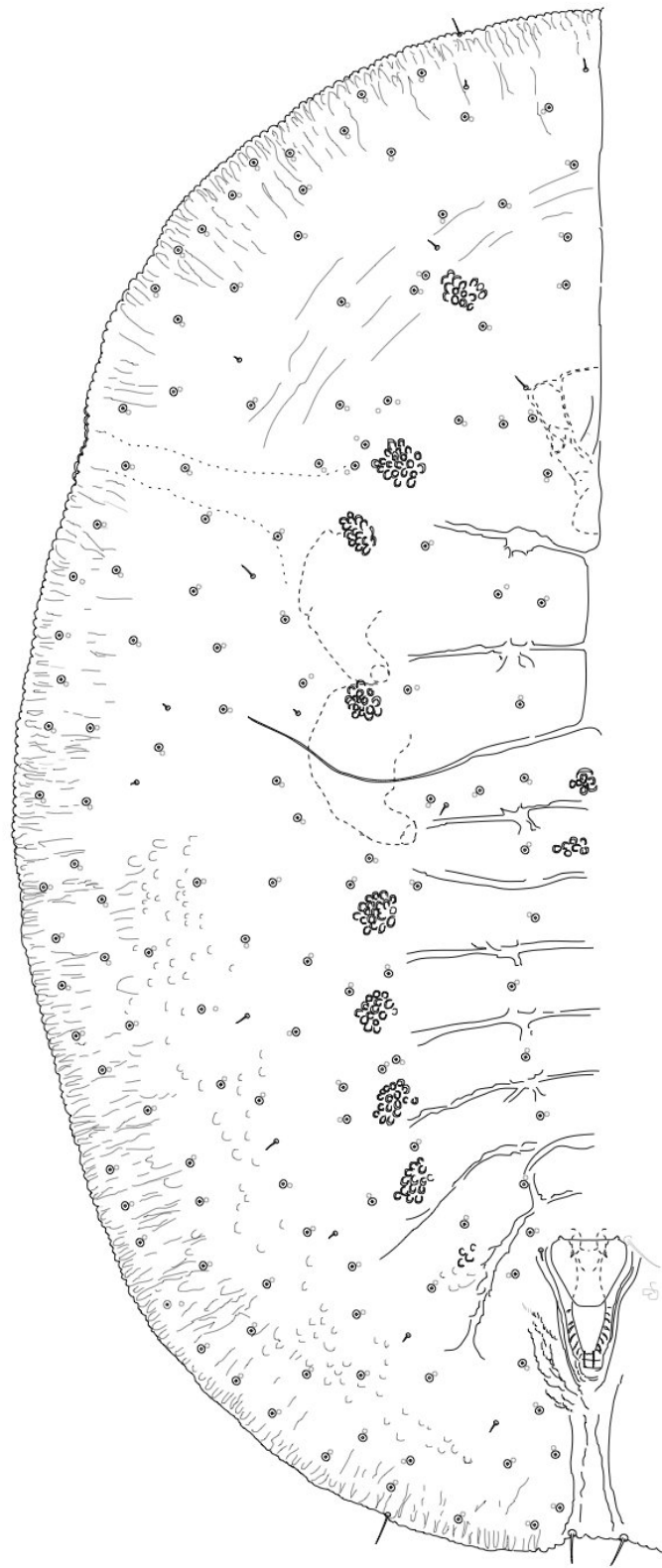


Figure 22. *Bemisia berbericola* (Cockerell), 10 mi. S/E Livermore, Alameda Co. CA (on, Mine Road), 3/29/95, ex. *Quercus agrifolia*, R. Gill/B. Campbell, colls.

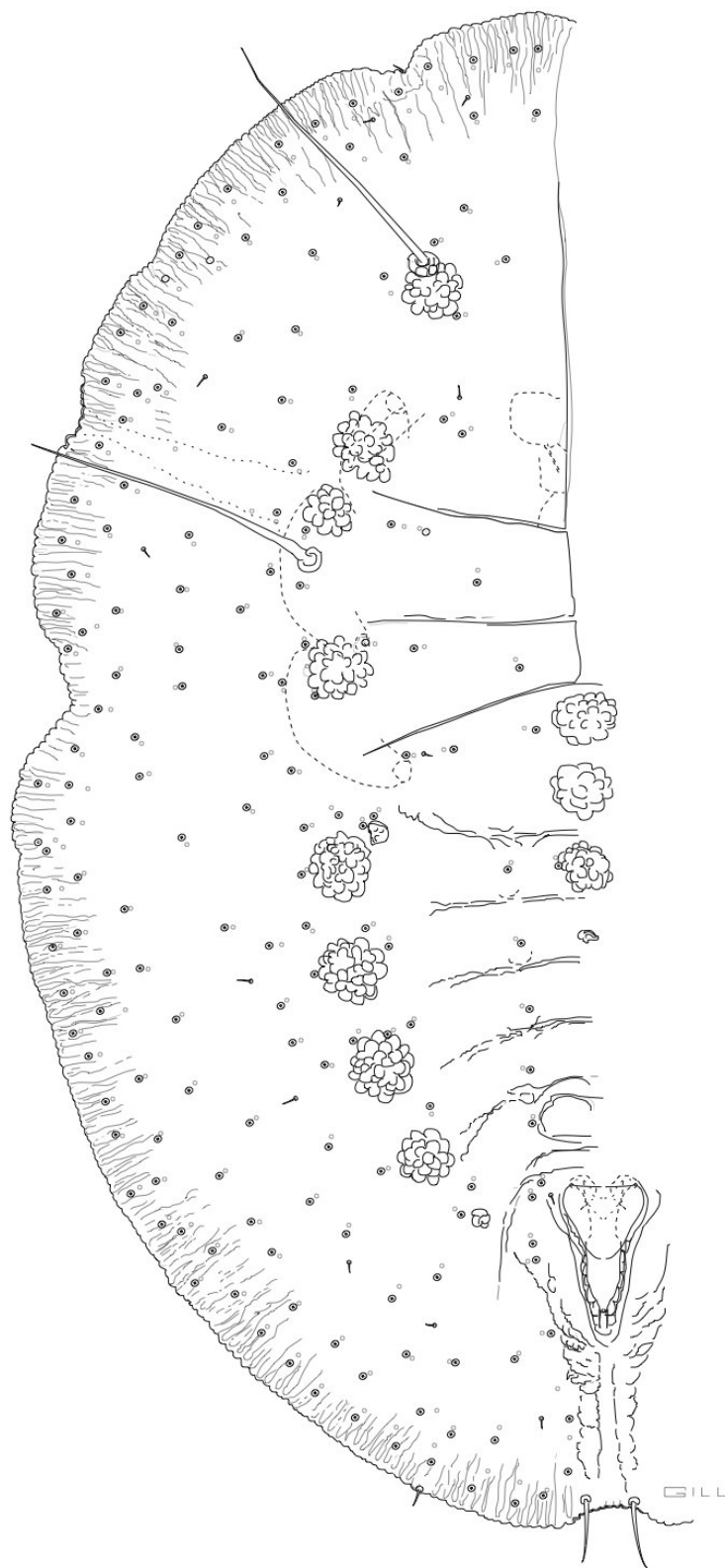


Figure 23. *Bemisia berbericola* (Cockerell), Avenal, Kings County, Calif., II-6-80, ex *Quercus* sp., Gilbert/Dunncliff, colls. (Reprinted by permission from Springer Science+Business Media B.V.).

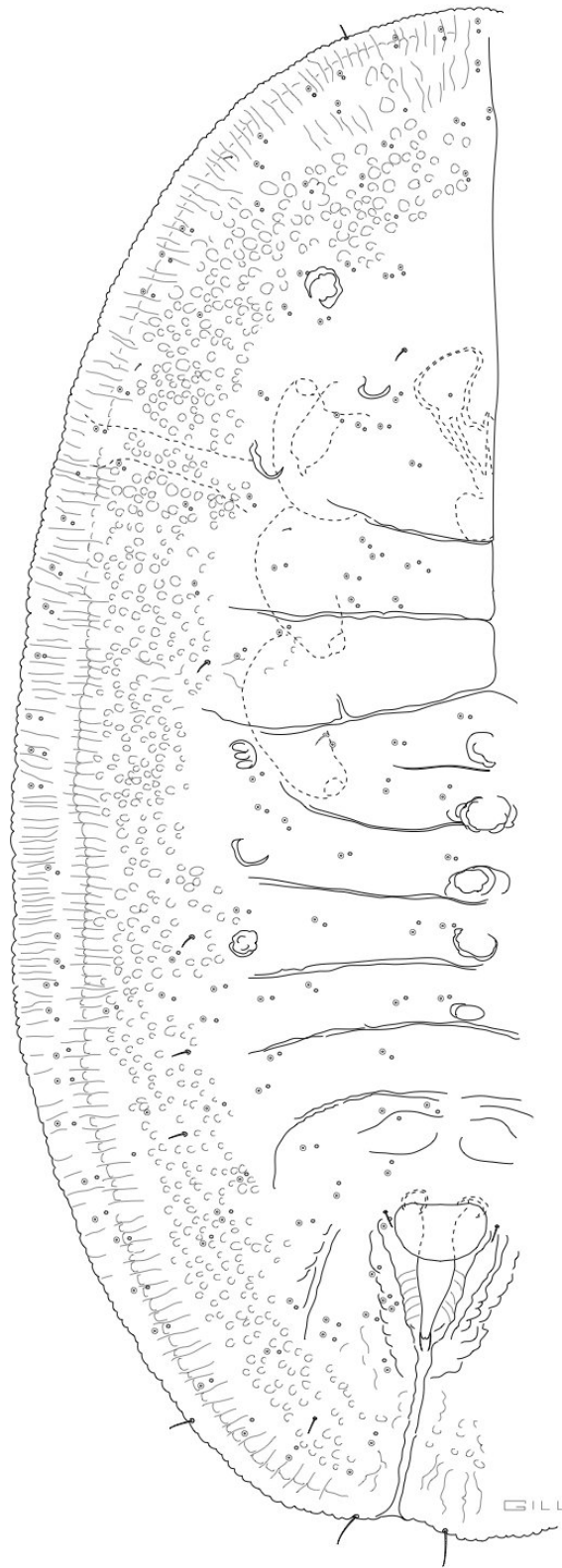


Figure 24. *Bemisia berbericola* (Cockerell), Hwy 128, 13 mi. E/O Rutherford, Napa County, California, 16-V-1968, ex. *Adenostoma fasciculatum*, T. Kono, coll.

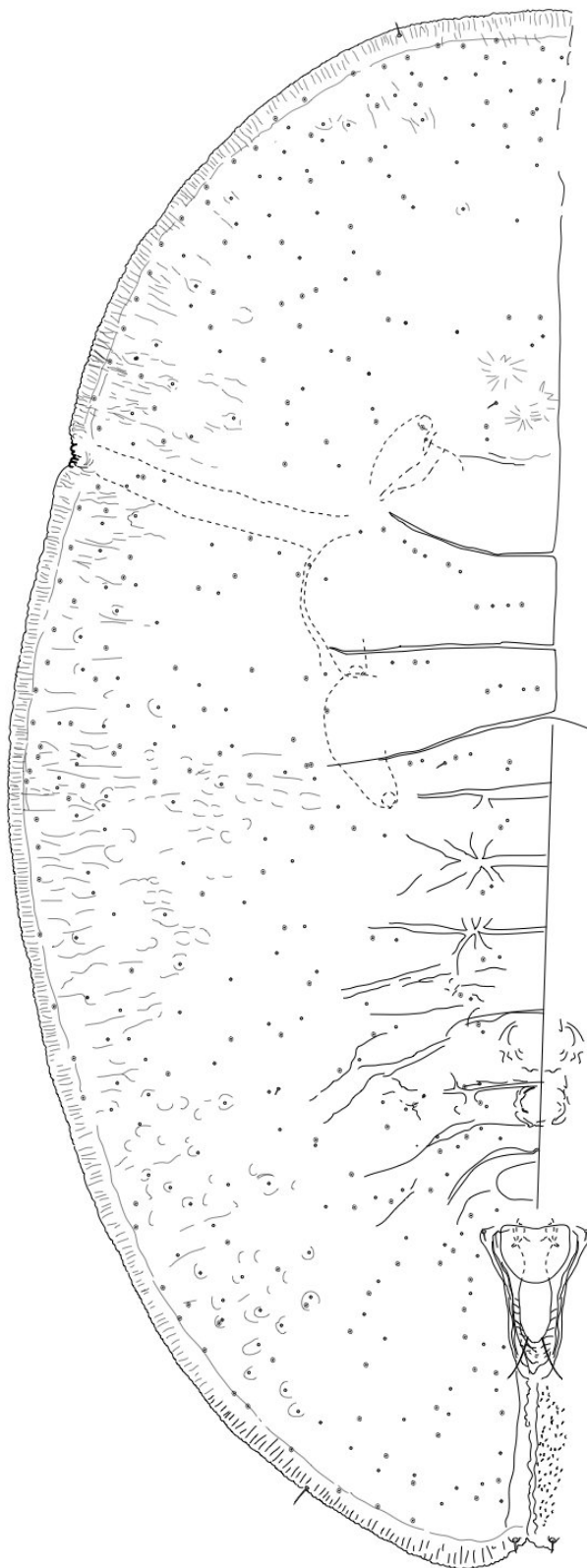


Figure 25. Type material, *Bemisia caudasculptura* Quaintance and Baker, Cholula, Mexico, Dec. 1910, ex. *Fraxinus* sp., USNM# 6517.

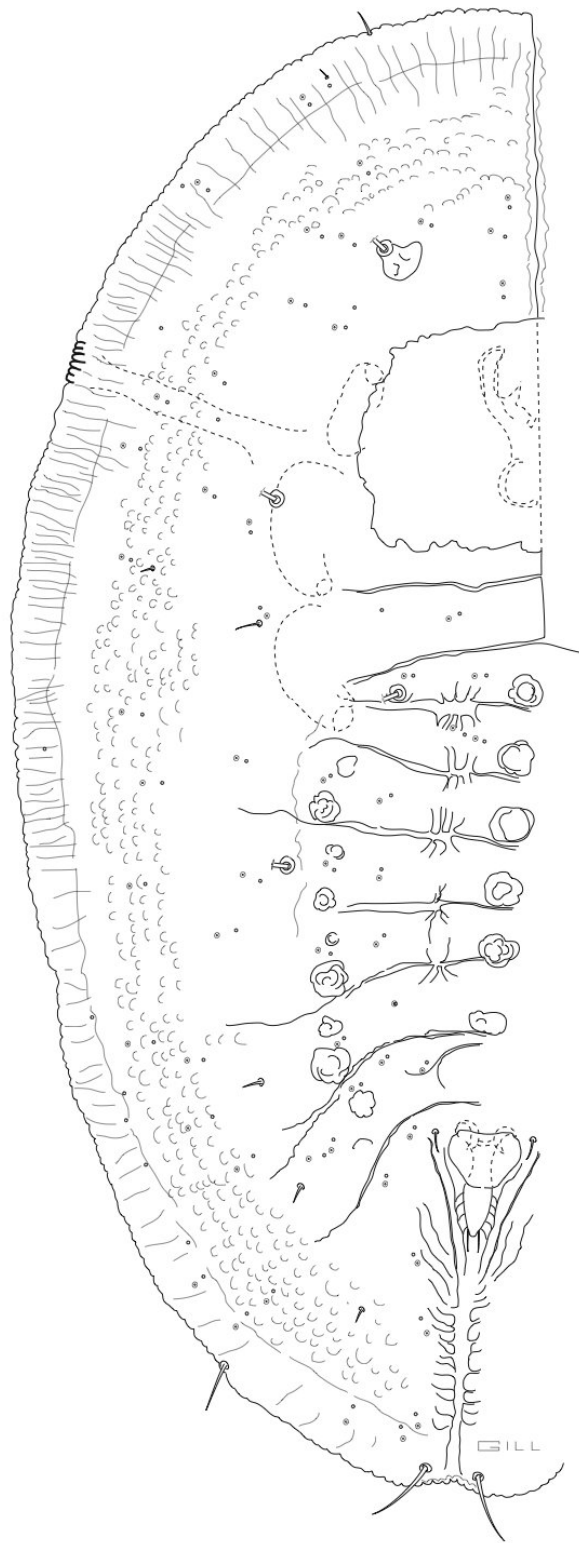


Figure 26. *Bemisia porteri* Corbett, Taiwan, Tari, XII-1993, ex. *Bauhinia variegata*, K.C. Chow, coll., Det. By C.-C. Ko.

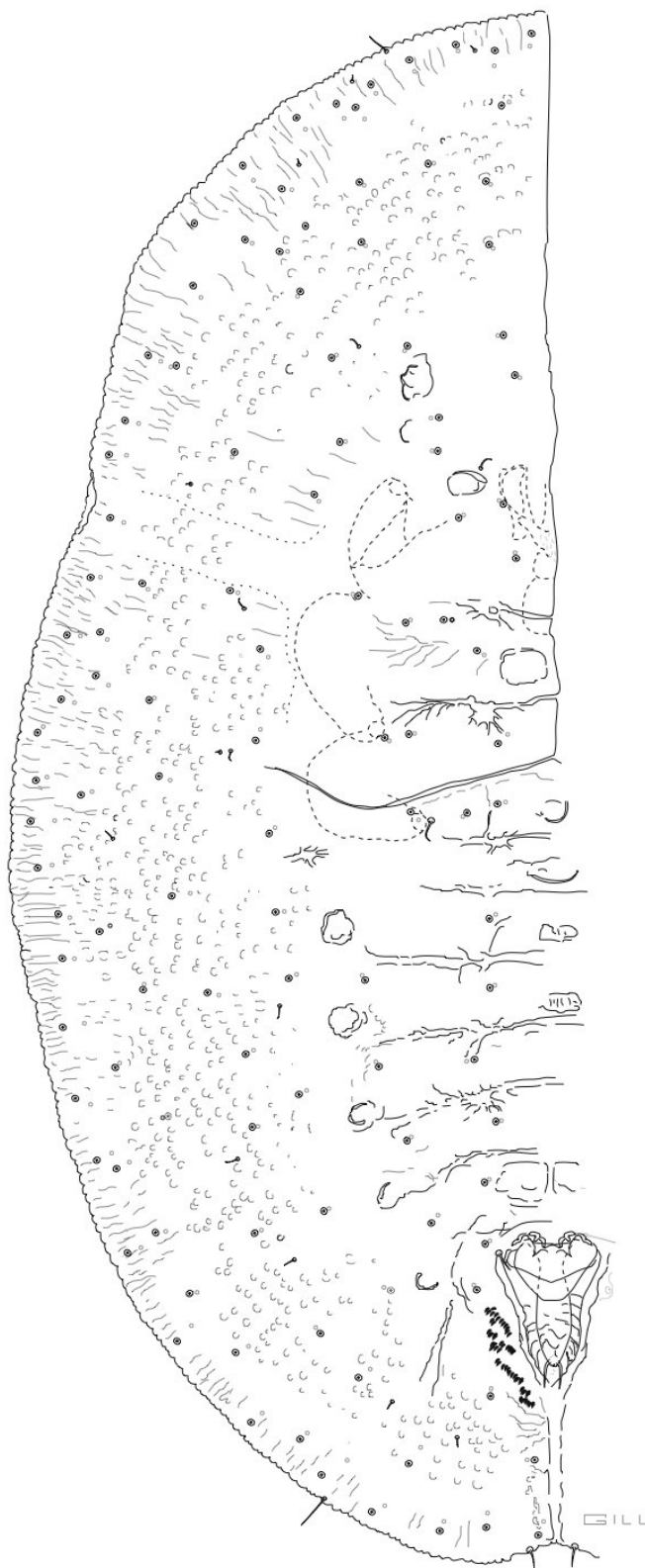


Figure 27. Paratype, *Bemisia confusa* Danzig, Caucasian Black Sea Coast, Lazarevskaya, ex: *Psoralea bituminosa*, Aug. 12, 1960, E. Danzig, coll.

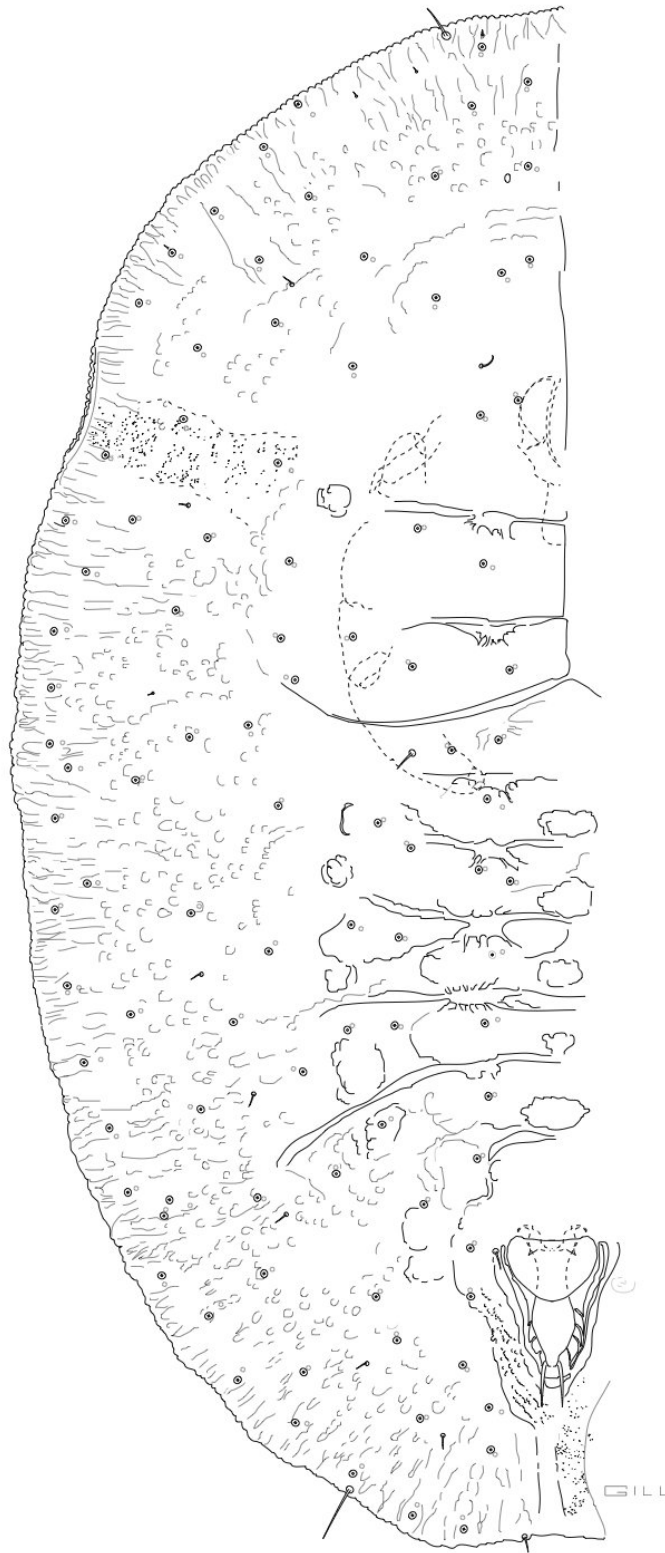


Figure 28. Paratype, *Bemisia eoa* Danzig, Southern Maritime Territory, Khasan District Kedrovaya pad' Reservation, ex. *Ulmus propinqua*, 31-VII-61, E. Danzig, coll.

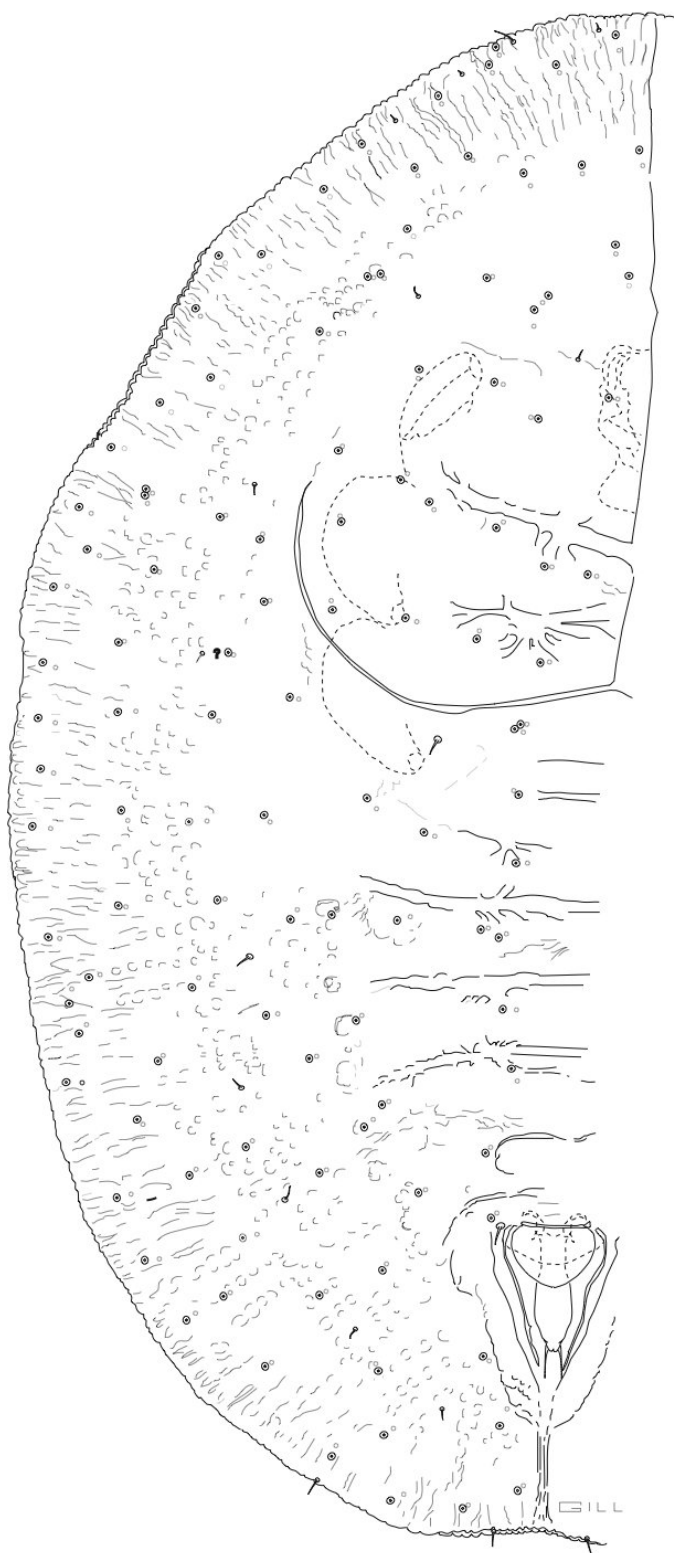


Figure 29. Paratype, *Bemisia silvatica* Danzig, Zelenyy Mys USSR , ex: *Frangula alnus*, E. Danzig, coll.

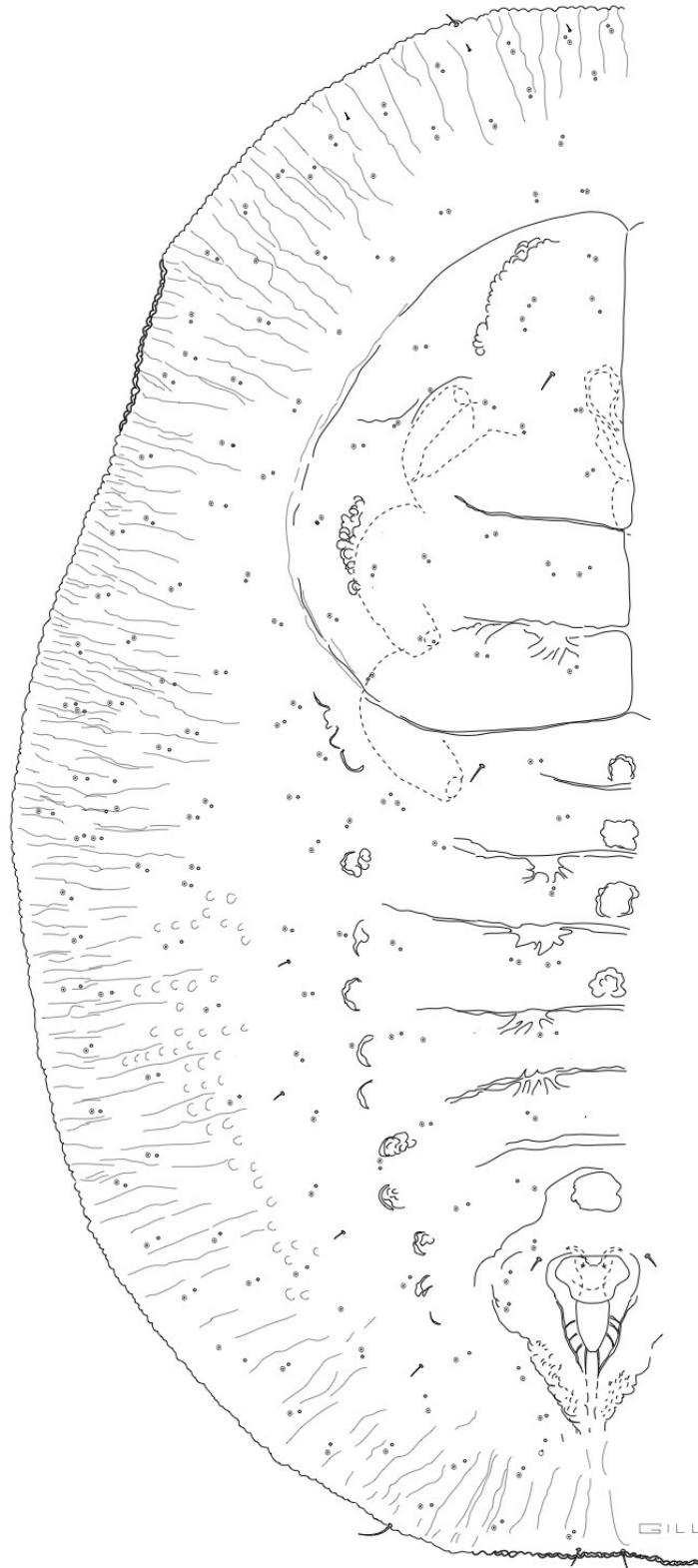


Figure 30. *Asterobemisia carpini* (Koch), Italy, quar. at San Francisco, California, 5-II-1965, CDFA#65C5-3, ex. *Rubus* sp., H. Bowden, coll., Det. L.M. Russell

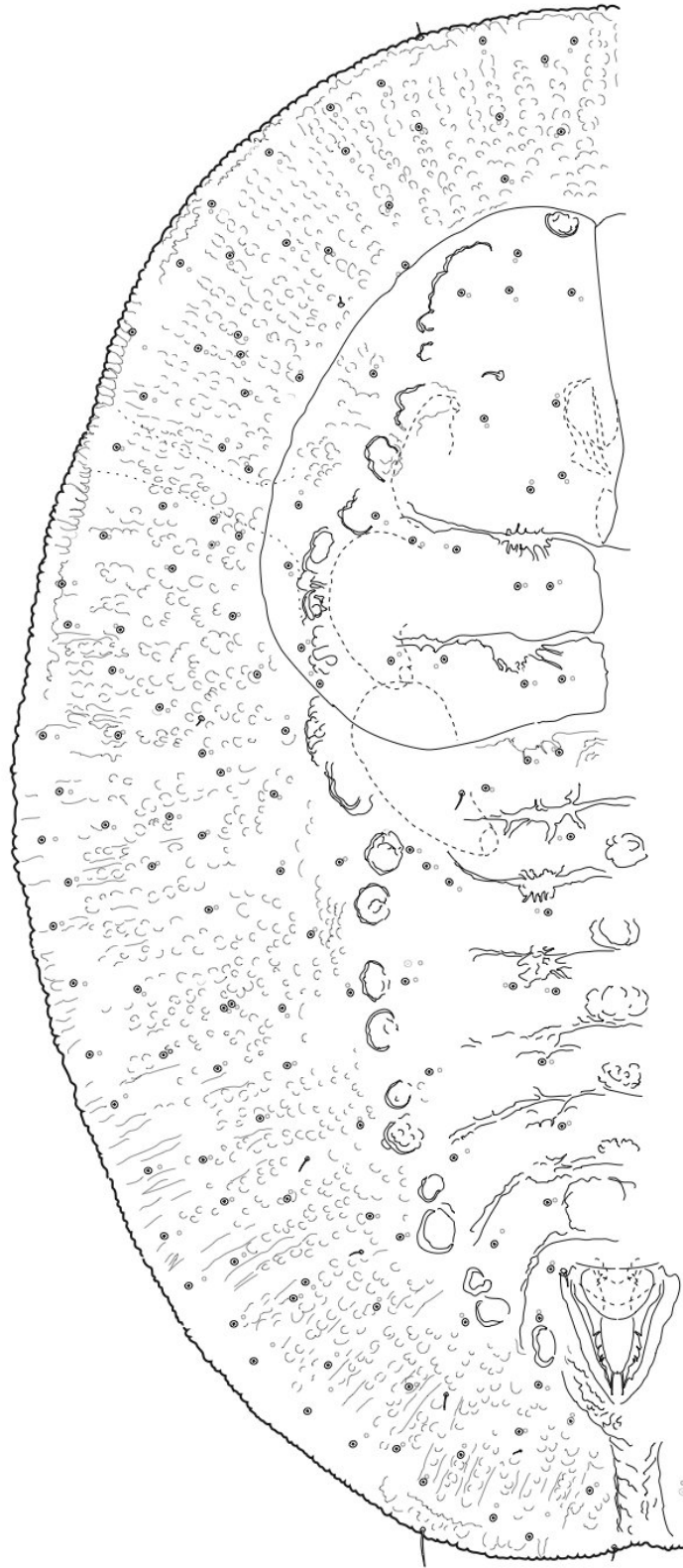


Figure 31. *Bemisia shinanoensis* Kuwana, data not available.

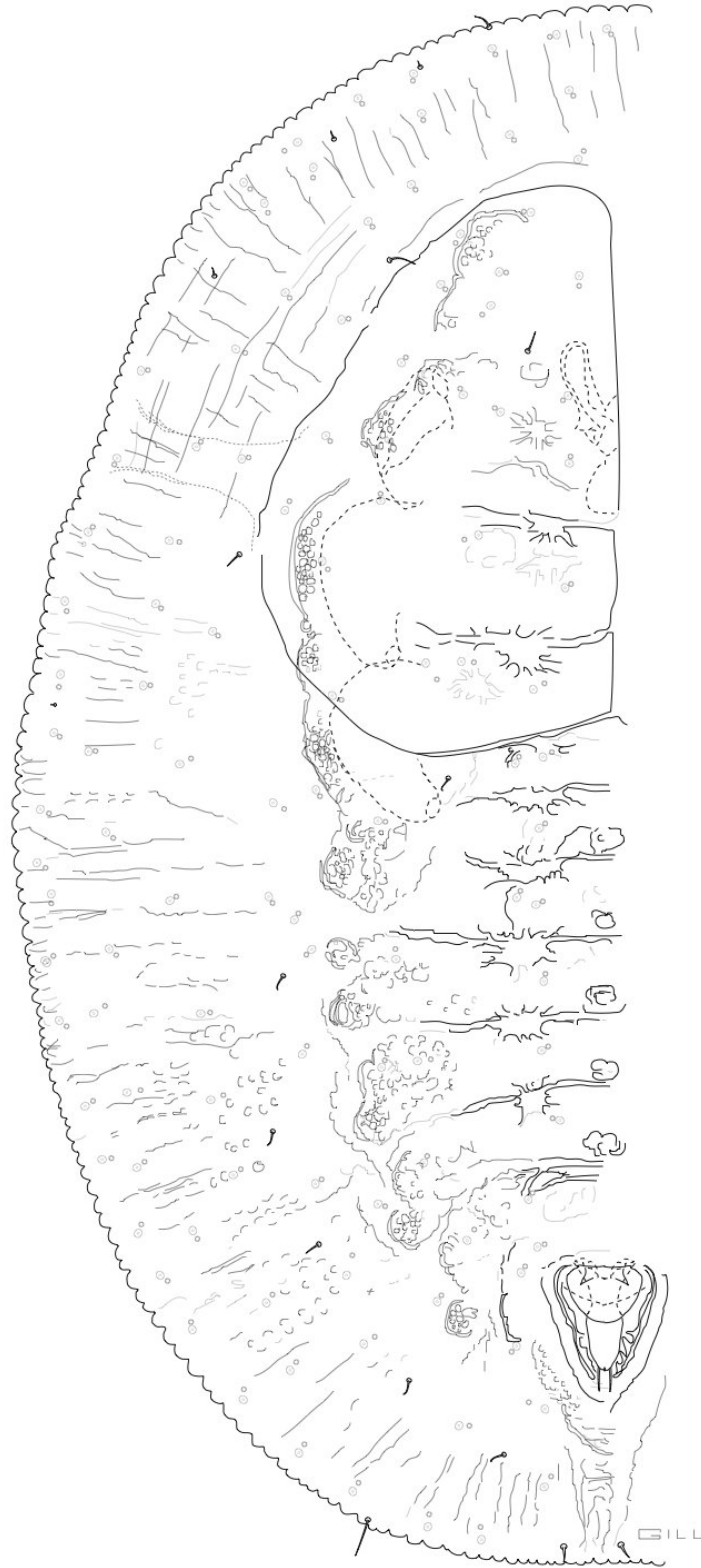


Figure 32. Paratype, *Asterobemisia takahashii*, Southern Maritime Territory, Khasan District, Kedrovaya pad' reservation, V-29-62, E. Danzig, coll.

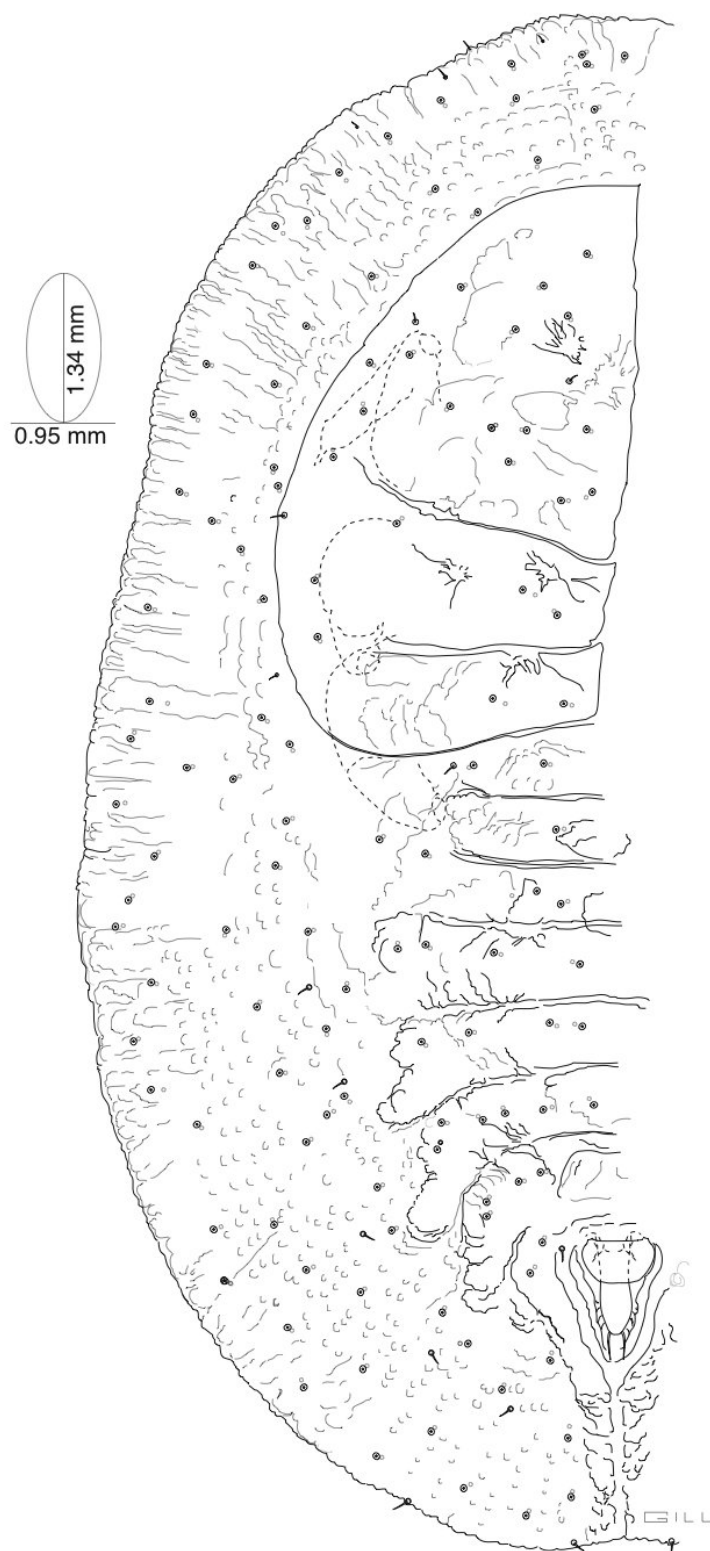


Figure 33. *Neobemisia trifolii* Danzig, Southern Maritime Territory, Chernyatino Suyfuno Valley, ex. *Trifolium lupinaster*, E.M. Danzig, coll.

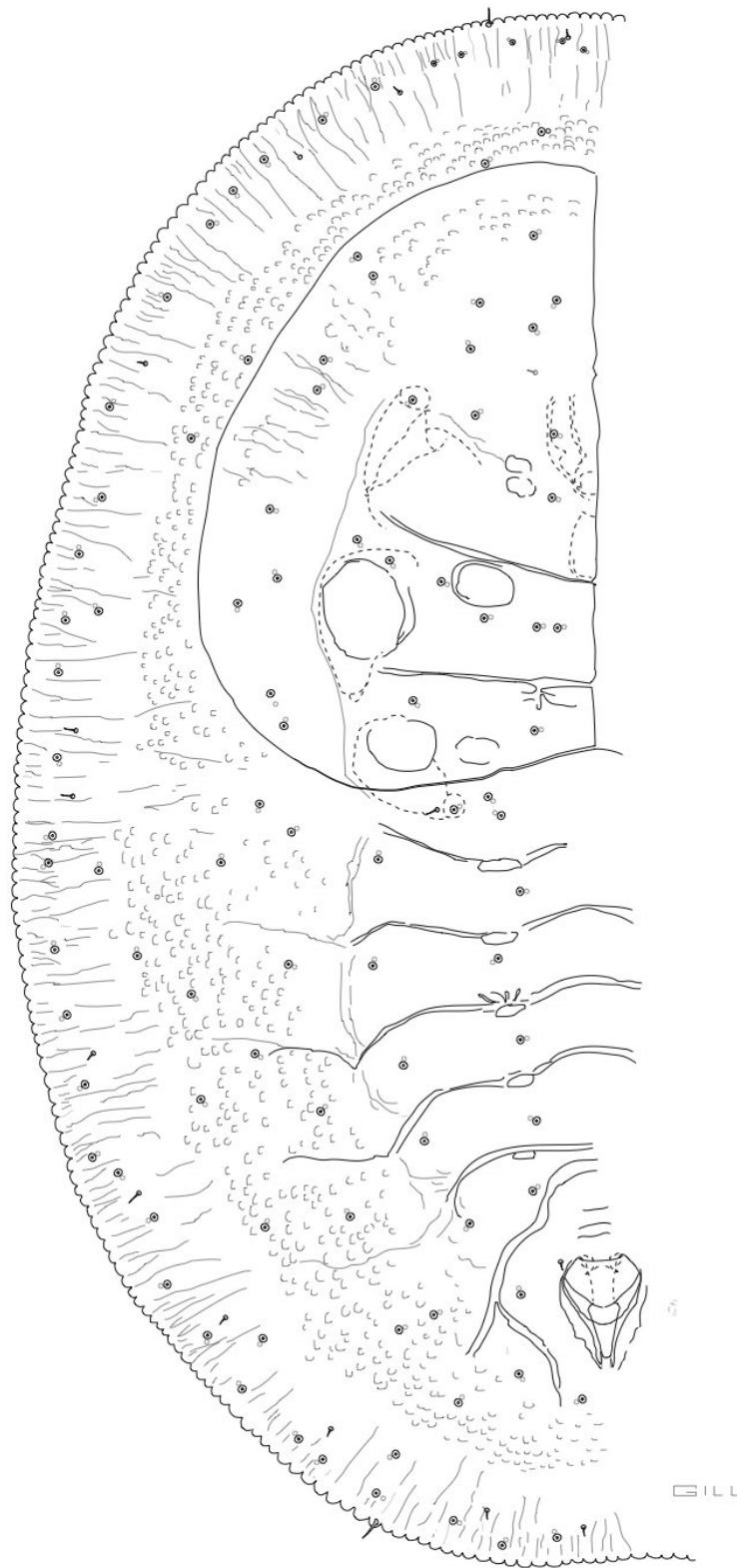


Figure 34. Paratype, *Neobemisia atraphaxius* Danzig, Dzhabul Province, spurs of the Chu-Ili Mtns., ex: *Atraphaxis*, 15-IX-57, Ye Sugonyayev, coll.

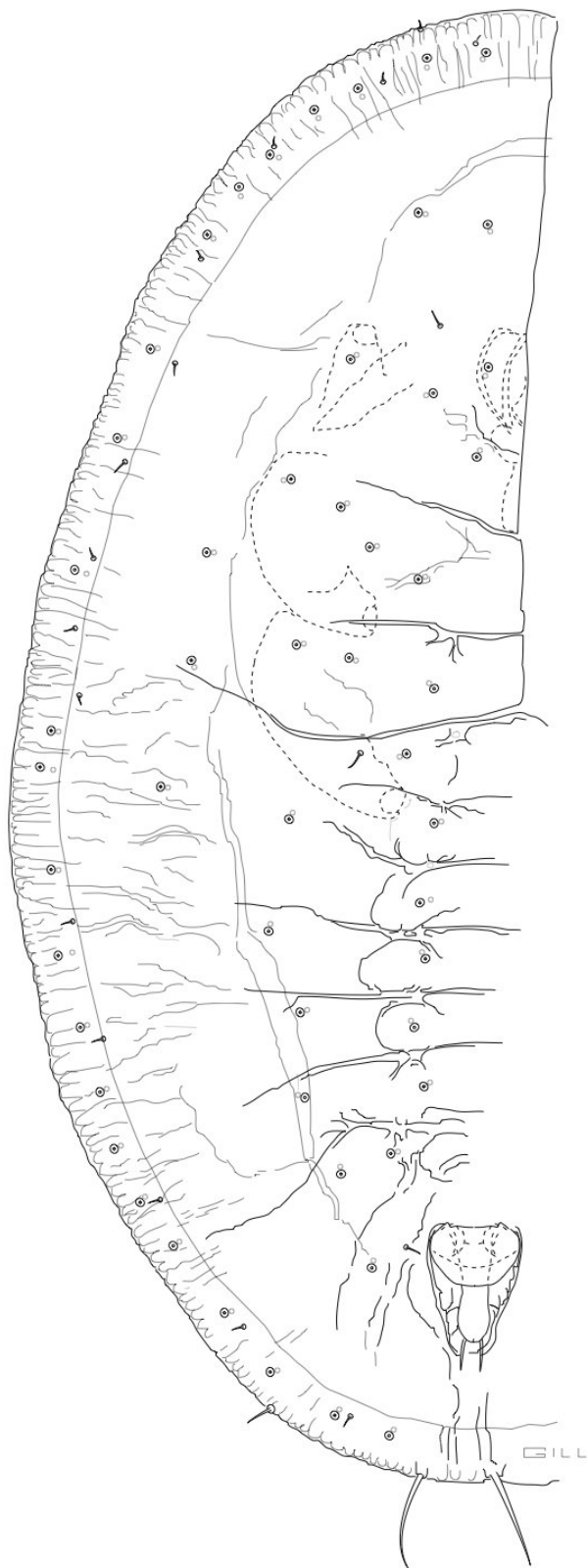


Figure 35. Paratype, *Bemisia rosae* Danzig, 25 km s/o Orapa?, 10-VI-78, ex: rose, E. Danzig, coll.

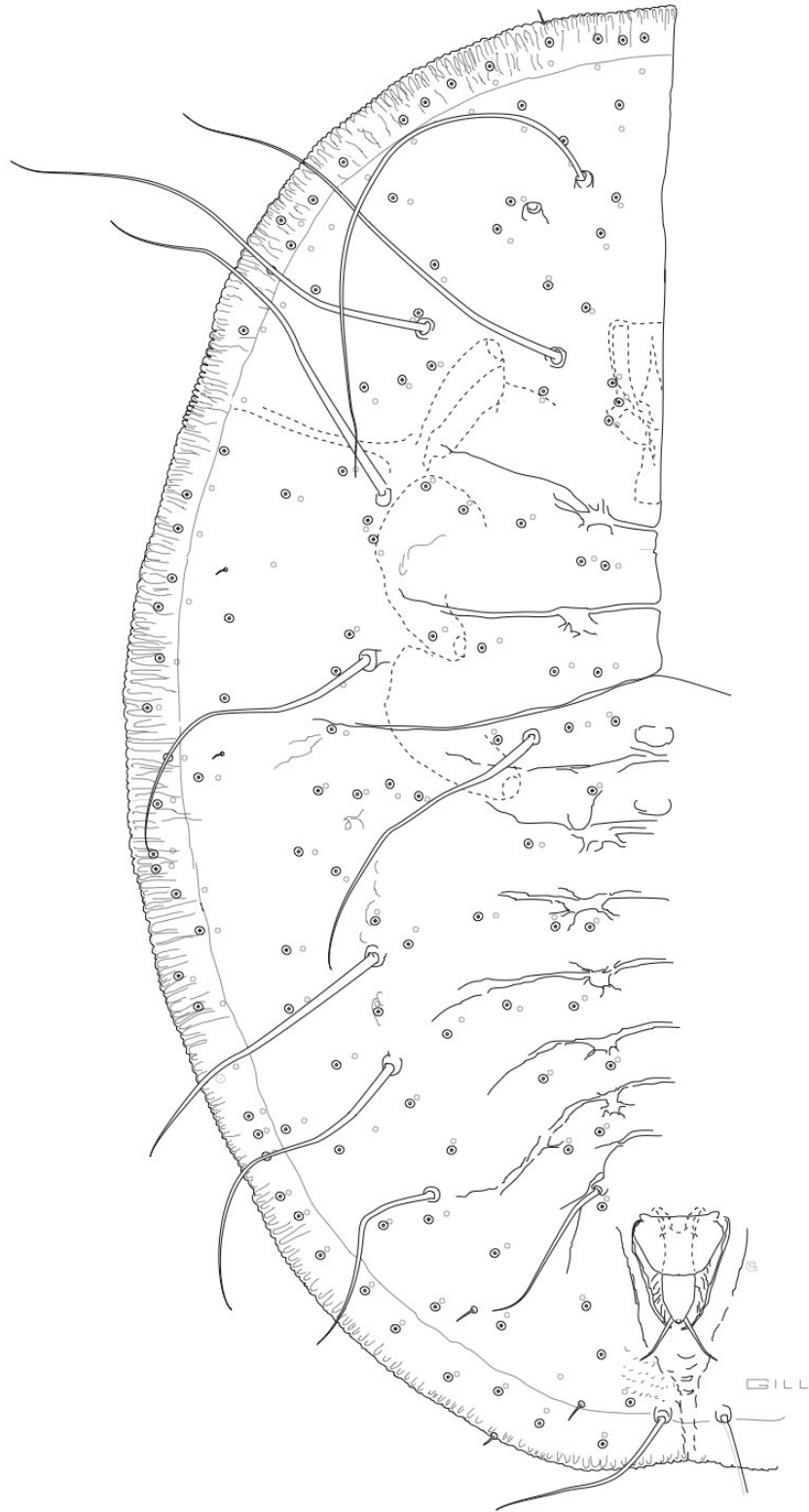


Figure 36. Paratype, *Bemisia mesasiatica* Danzig, Kirgizia Chatkal Range, Nanay, ex. *Armeniaca* sp., 22-VII-60, Sugonyayev, coll.

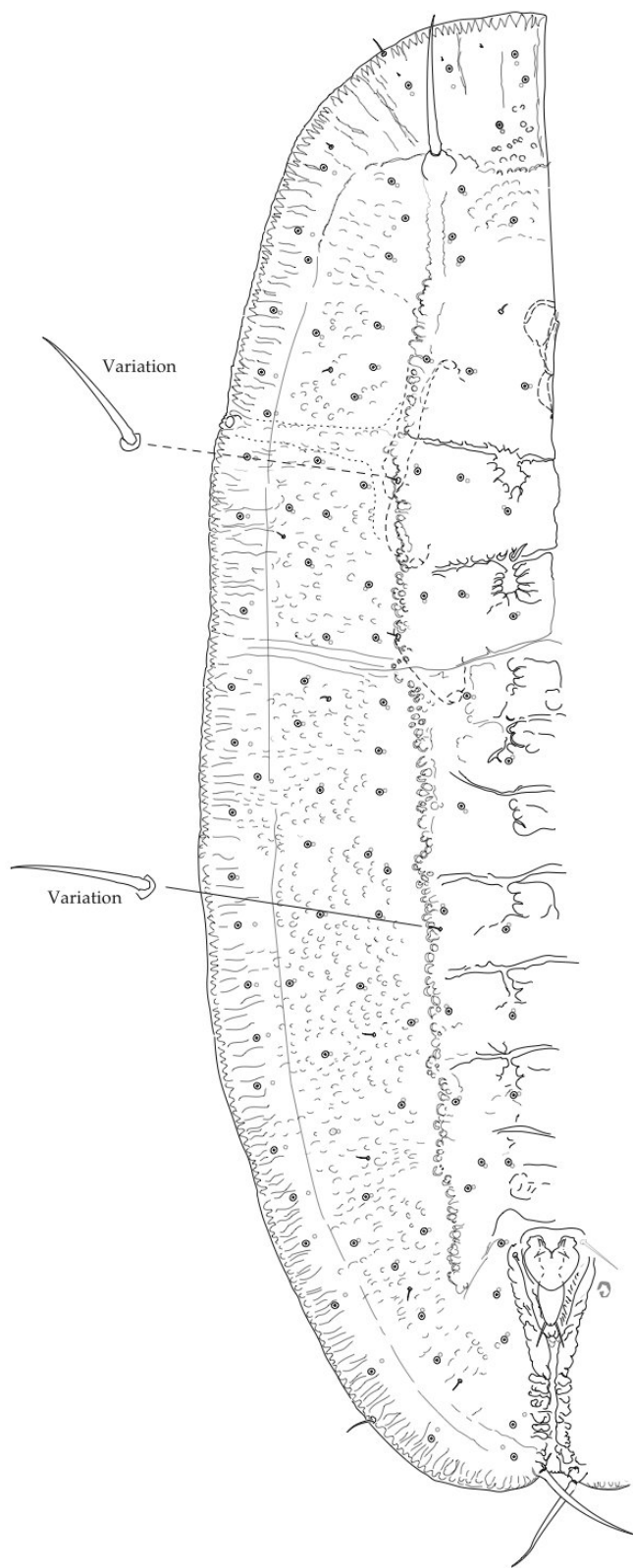


Figure 37. *Bemisia giffardi* Kotinsky, Pawaa, Oahu, HI, IX-27-82, ex *Citrus* sp., Bernarr Kumashiro, coll.

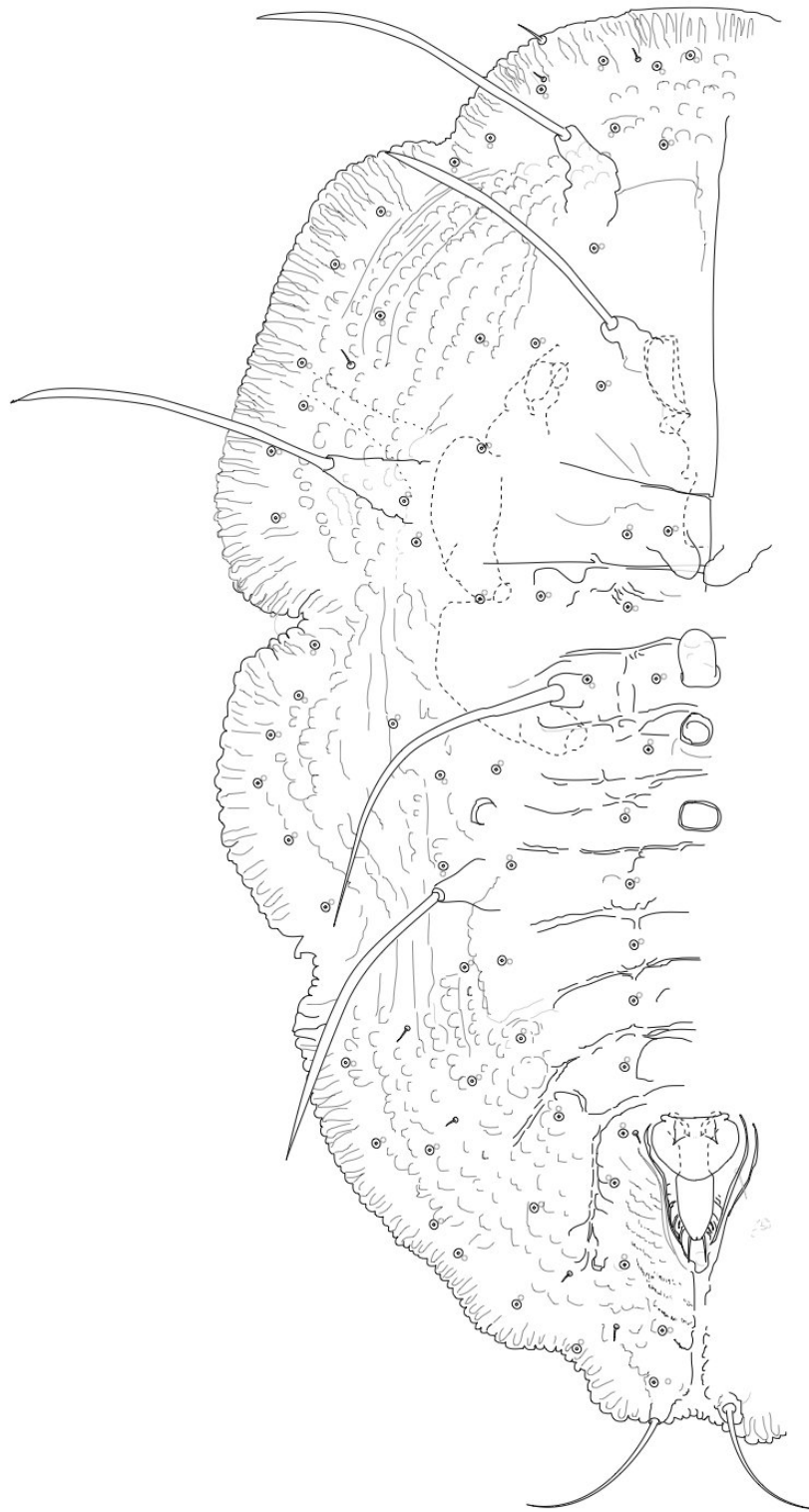


Figure 38. *Bemisia centroamericana* Martin, Belize, Cayo, Chiquibul Forest, Las Cuevas, on waste ground, 06 Nov. '94, J. Martin, coll. #6464, ex. *Bocconia arborea*, (Papaveraceae).

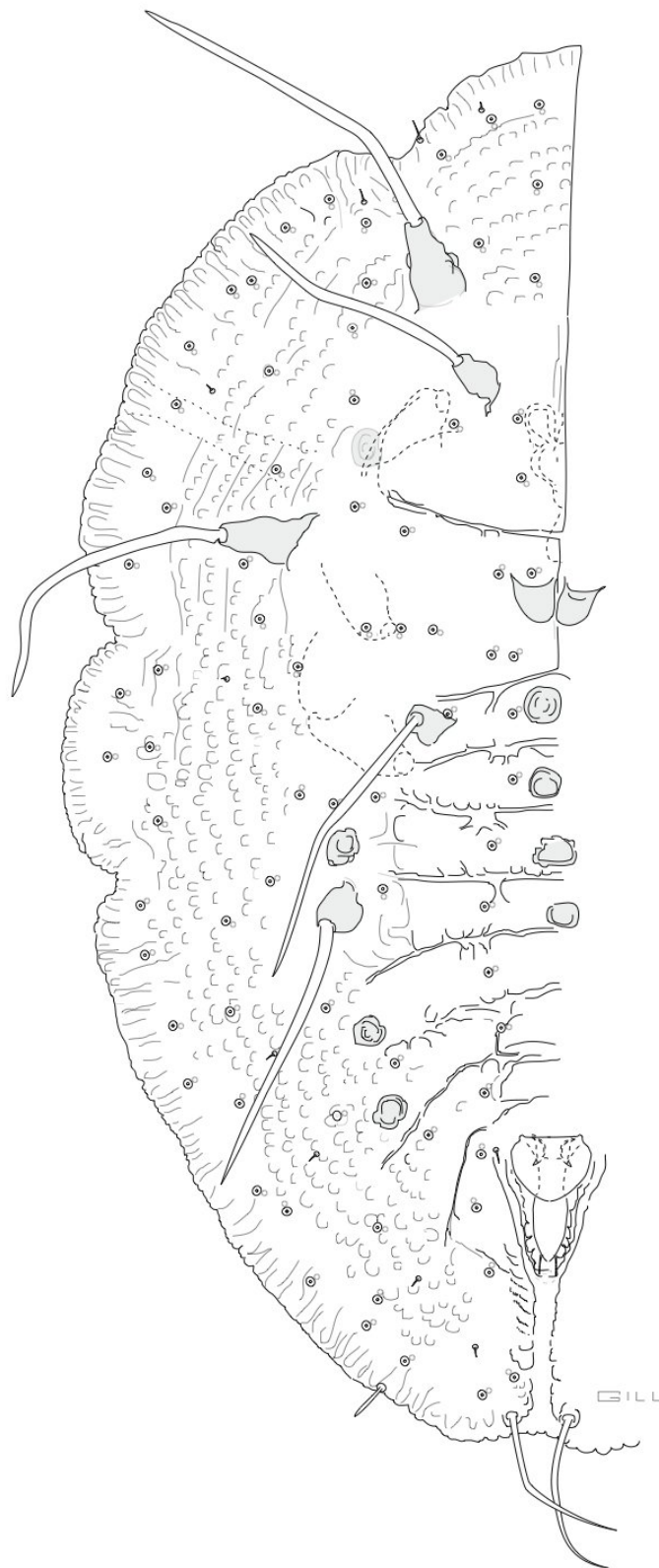


Figure 39. *Bemisia centroamericana* Martin, Guatemala, Centro Retalhuleu, Cat. # 9, Feb. 94-02, ex. tomaté, Brown/Frolich/Caballero colls.

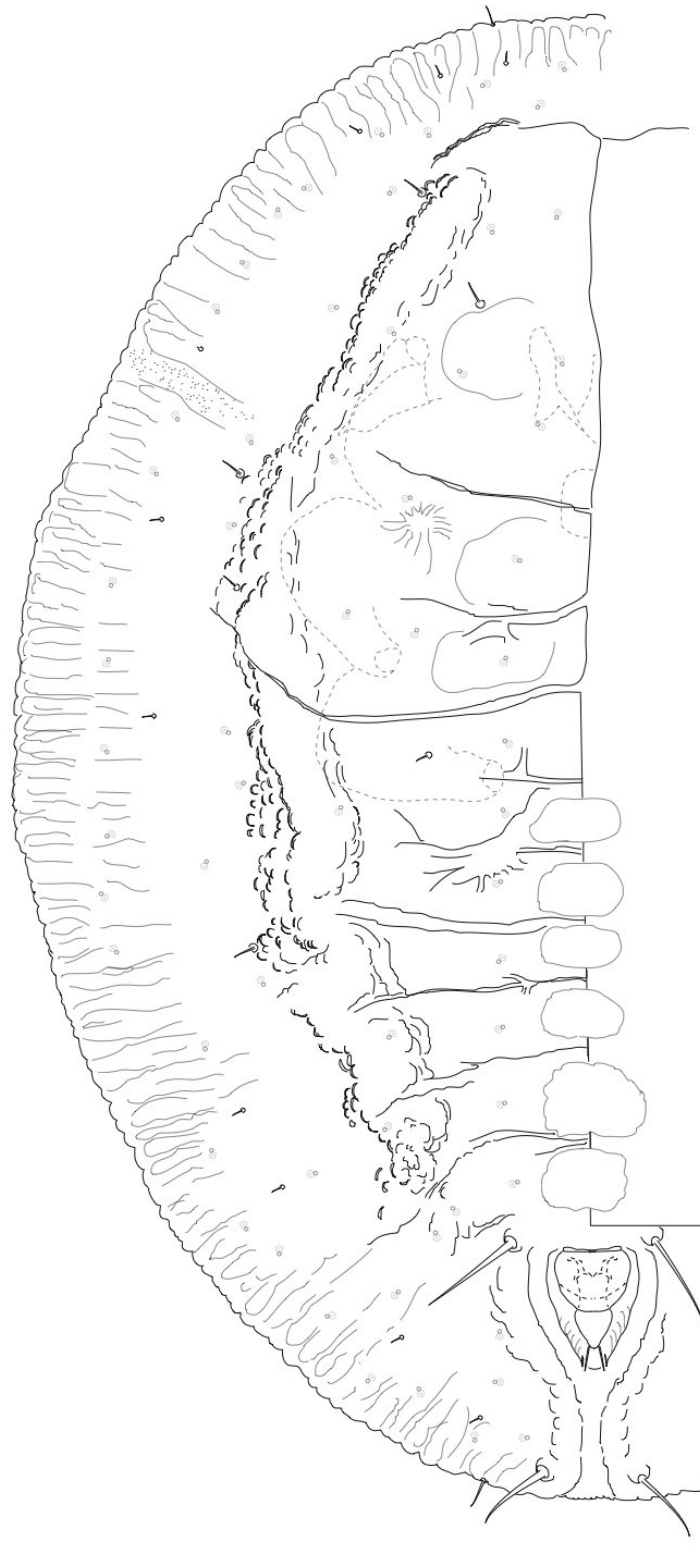


Figure 40. *Bemisia flocculosa* Gill and Holder, New Zealand: MC, Christchurch, Botanical Gardens, natives, section, Site 2, 19 Mar 2004, NPPRL Ref. 03/2004/1050, On *Melicytus* aff. *obovatus* leaf, Coll. P.Holder/ M.Bullians.

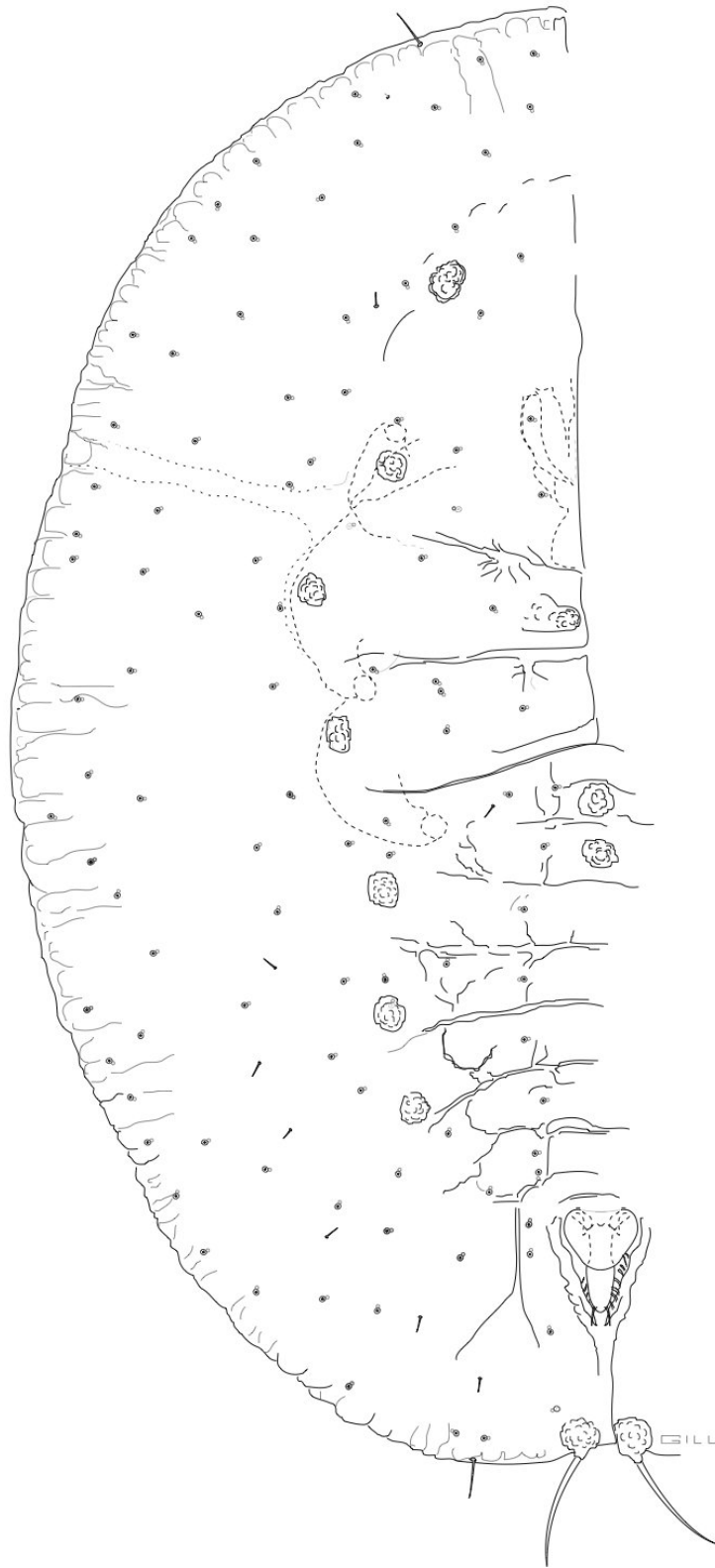


Figure 41. *Bemisia* sp. unknown, Mangareva, Gambiers Is., So. side Mt. Mokoto, 1000 ft. elevation, 3-vi-34, A. Anderson, coll.

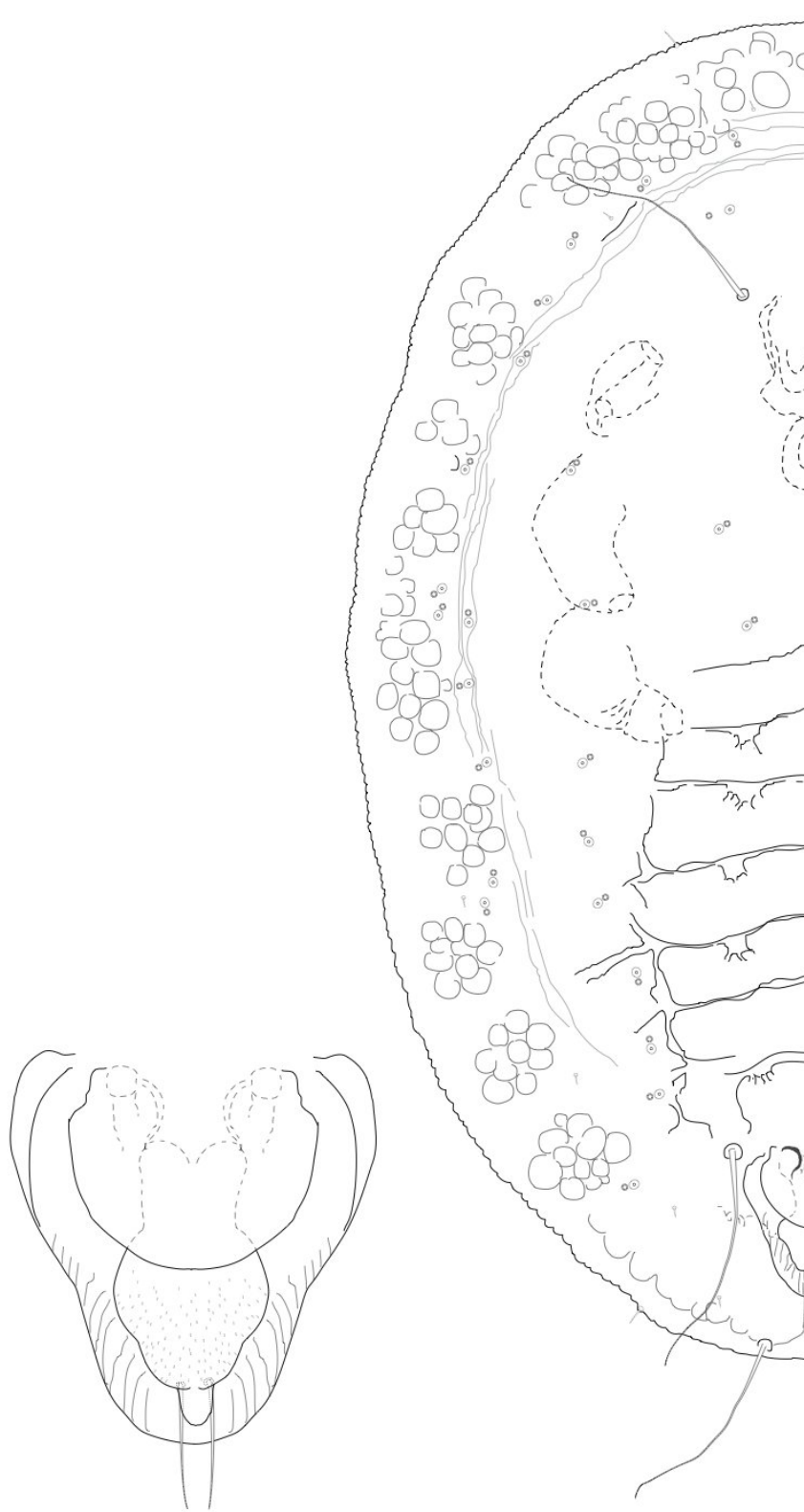


Figure 42. *Lipaleyrodes emiliae* Chen and Ko, Yungho, Taiwan, 23-VII-2003, ex. *Euphorbia*, C.-C. Ko, coll.

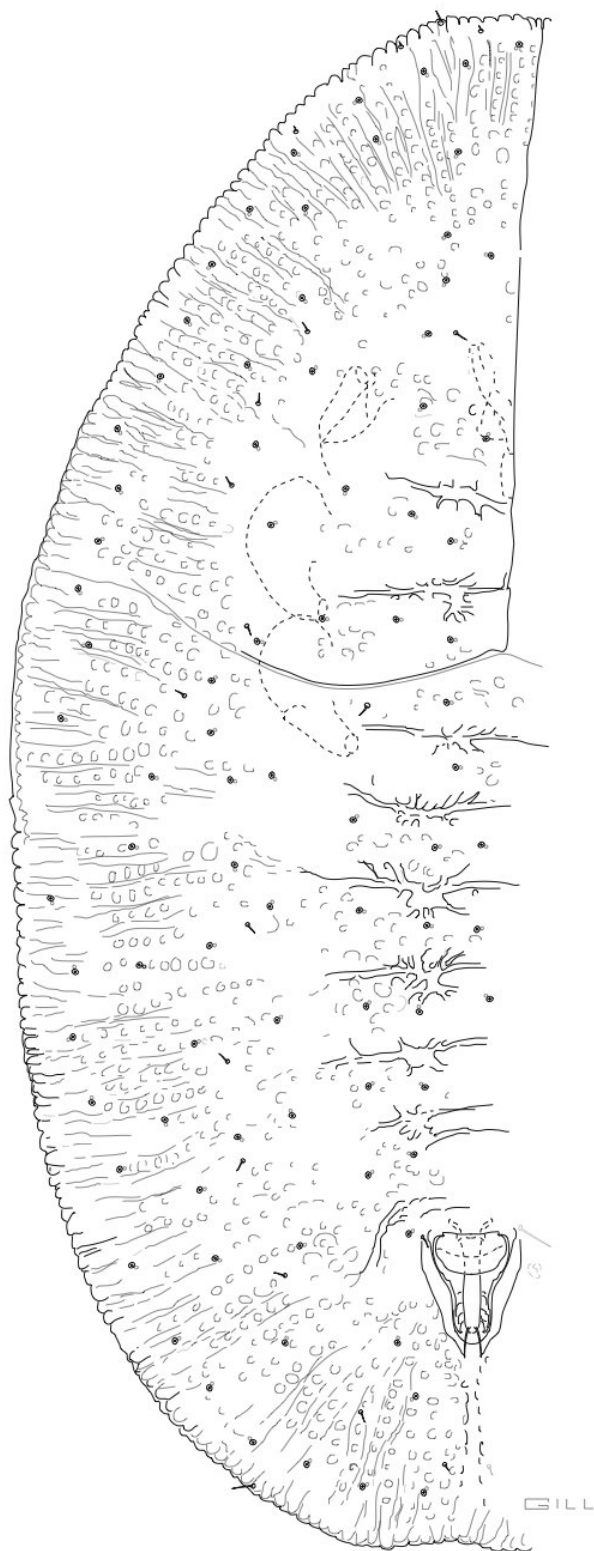


Figure 43. *Bemisia subdecepiens* Martin, Kangaroo Island, So. Australia, 17-II-90, ex: *Melaleuca*, J.H. Martin, coll., JHM #5652.

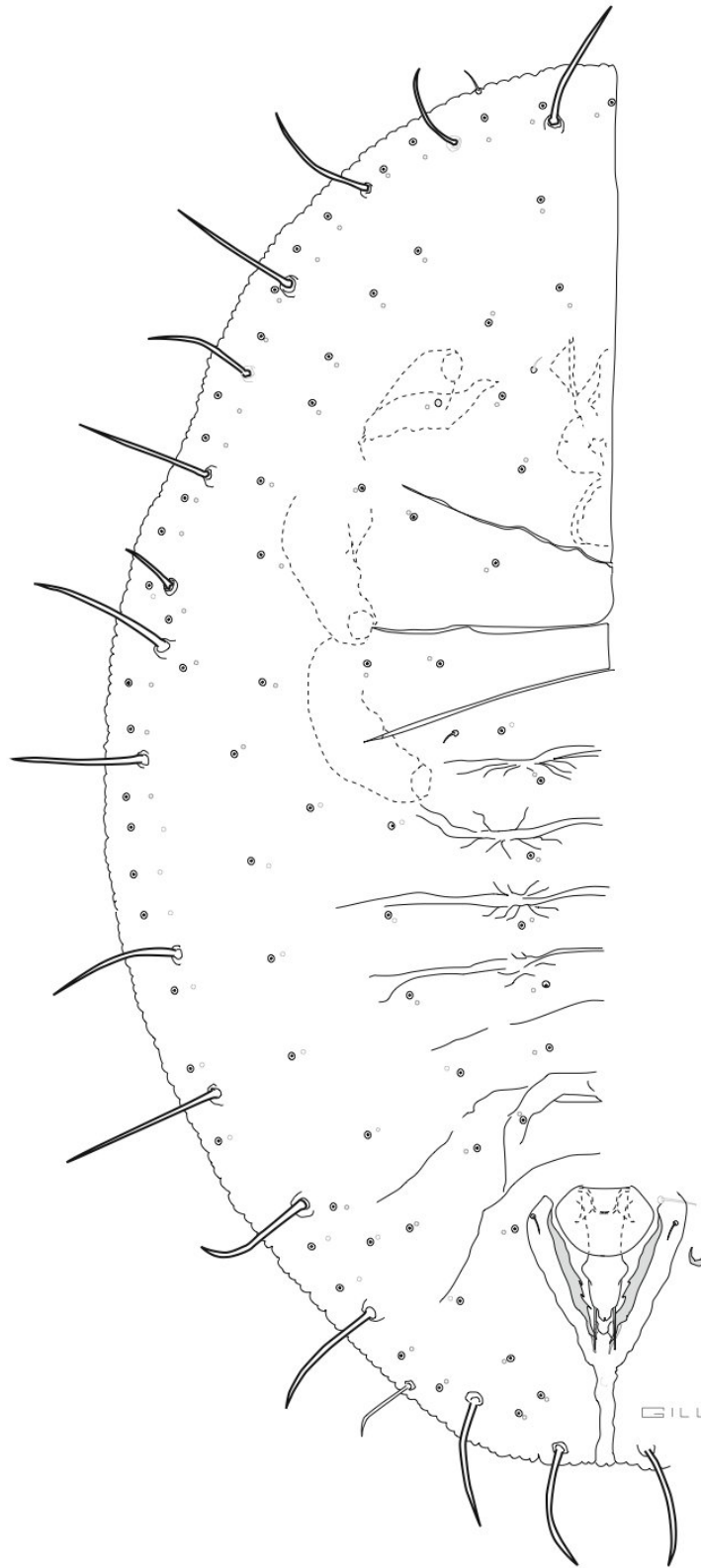


Figure 44. Holotype, *Bemisia combreticula* Bink-Moenen, Tchad, Bebedjian, 27-VII-1972, ex: *Anageissus leiocarpus*

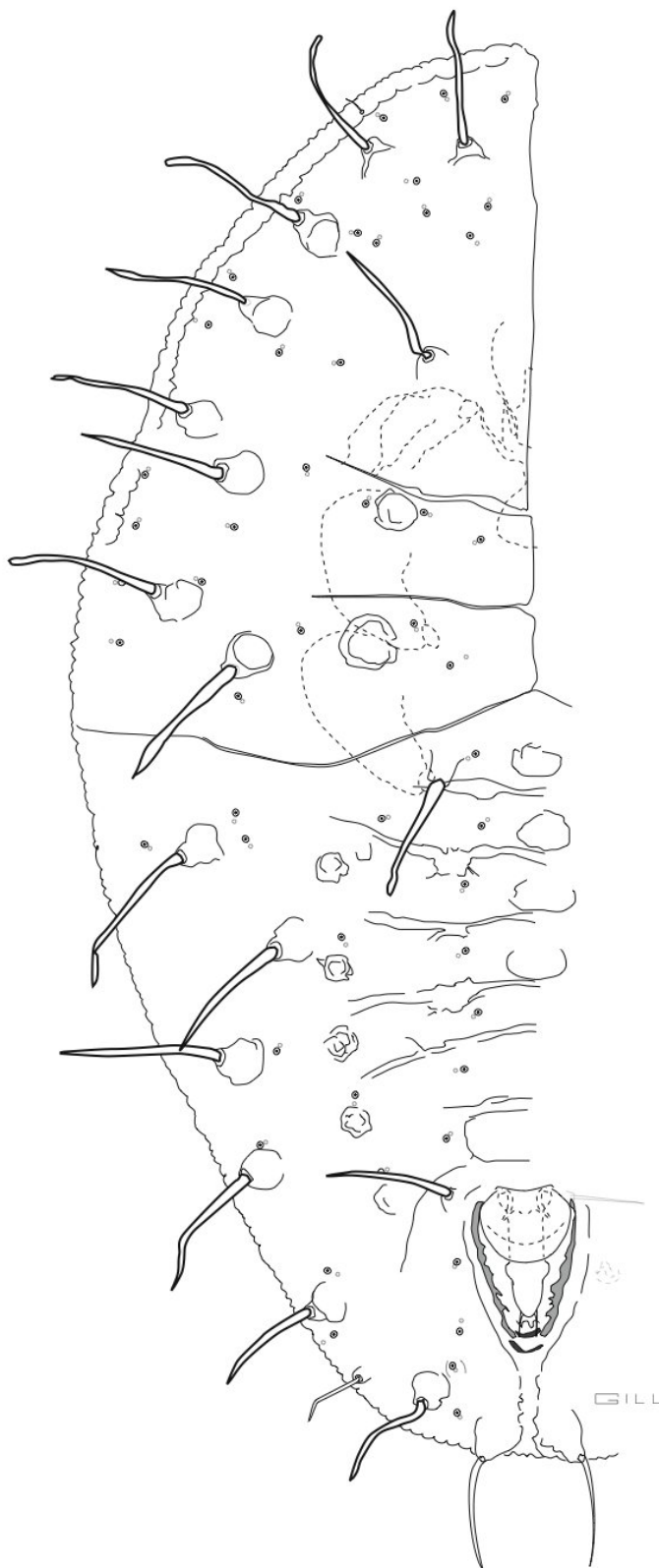


Figure 45. *Bemisia hirta* Bink-Moenen, Sudan: Kordofan, 18-IV-81, ex. *Boscia senegalensis*, J. Martin, coll.



Figure 46. *Parabemisia myricae* (Kuwana), Santa Ana, Orange Co., Calif., X-6-78, ex: Gardenia, CDFA #78J12-1, McRoberts/Garrett, colls.

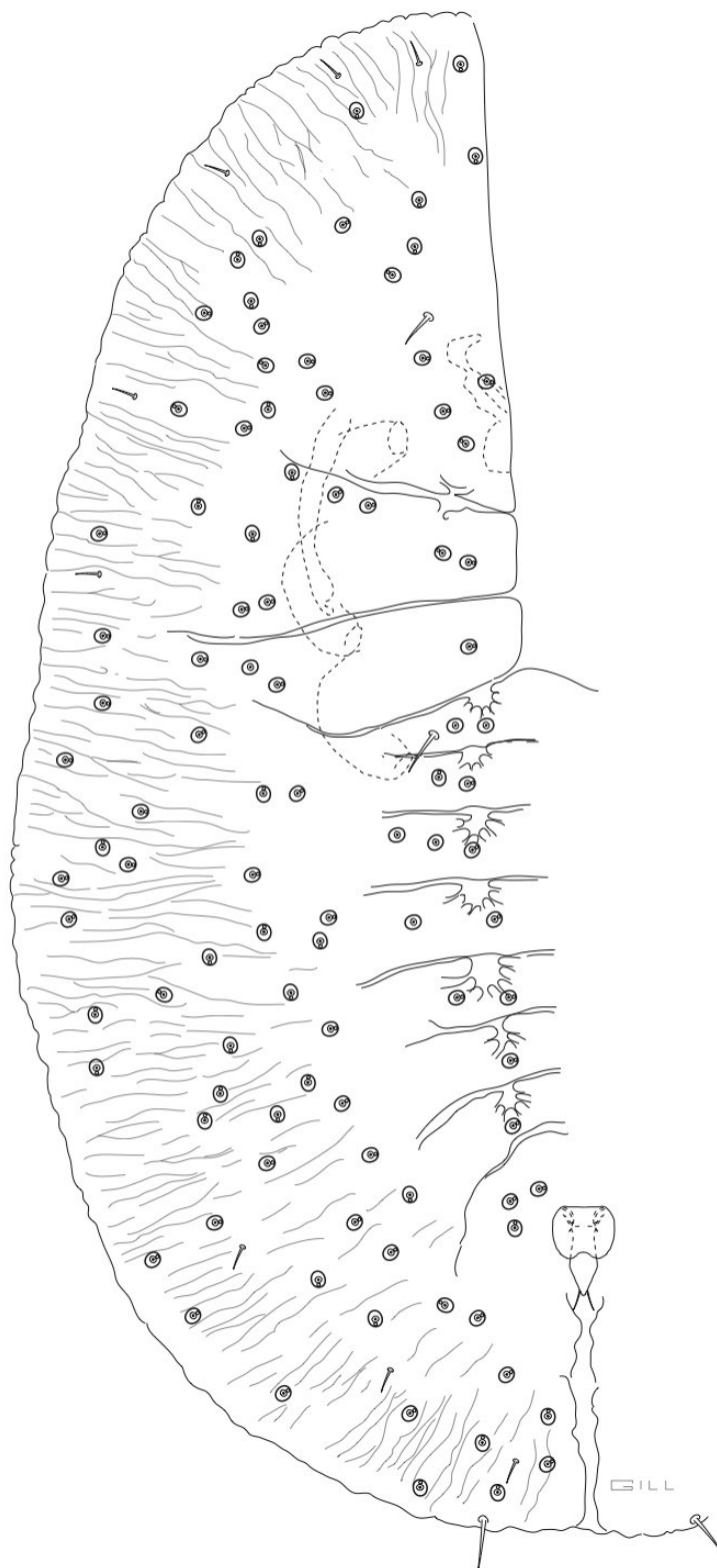


Figure 47. *Bemisia pongamiae* Takahashi, Taiwan, Taipei, 6-IX-1985, ex. *Pongamia pinnata*, C.C. Ko, coll.

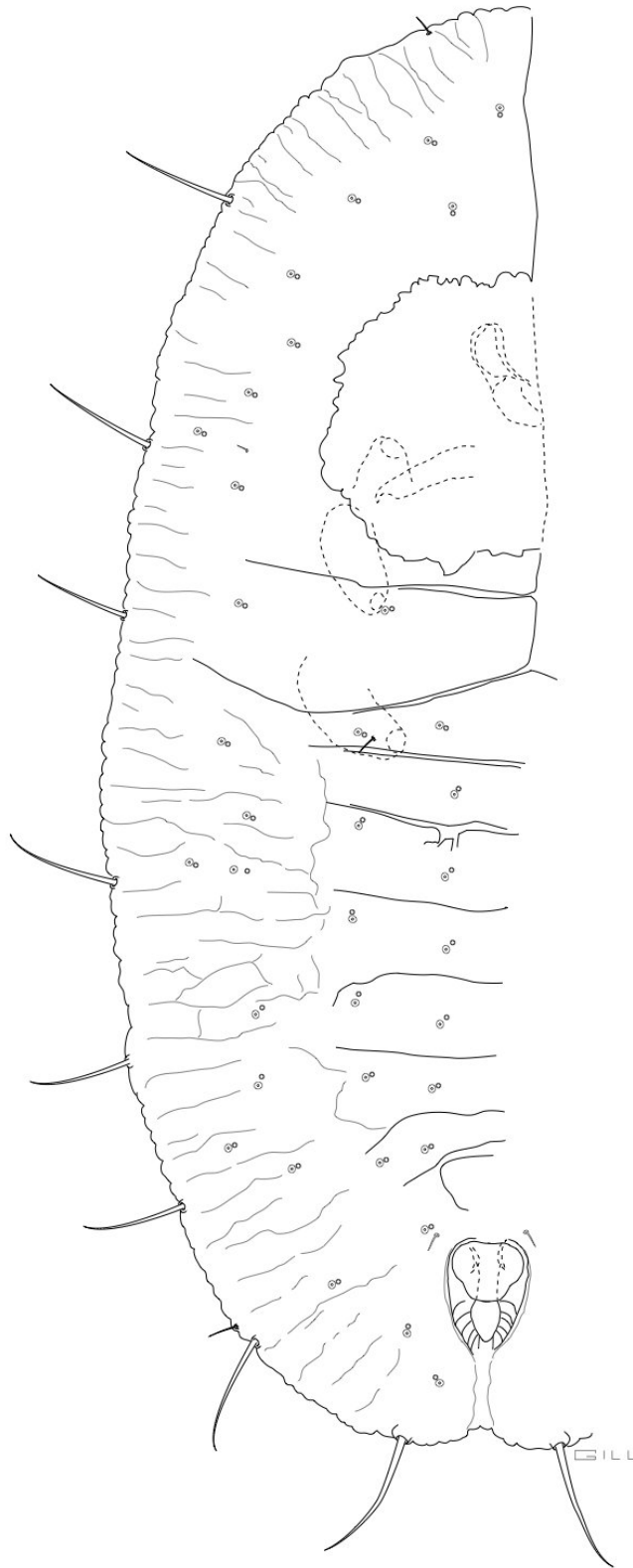


Figure 48. *Metabemisia filicis* Mound, TAIWAN, Jihyuetan, 27-XII-1995, ex. *Tectaria decurrens*, K.C. Chou, coll.

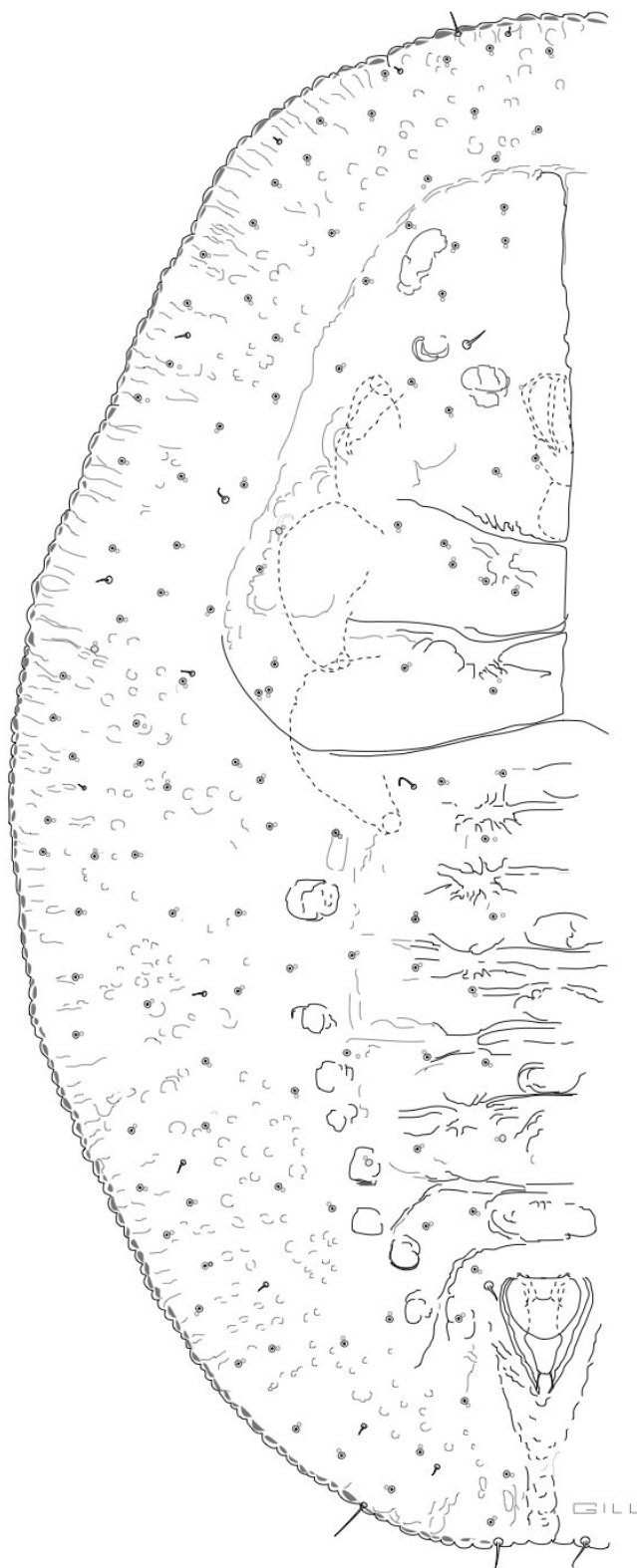


Figure 49. *Bemisiella lespedezae* Danzig, Paratype, Southern Maritime Territory, Khasan District, Kedrovaya pad' Reservation, ex: *Lespedeza bicolor*, July 27, 1960, E. Danzig, coll.

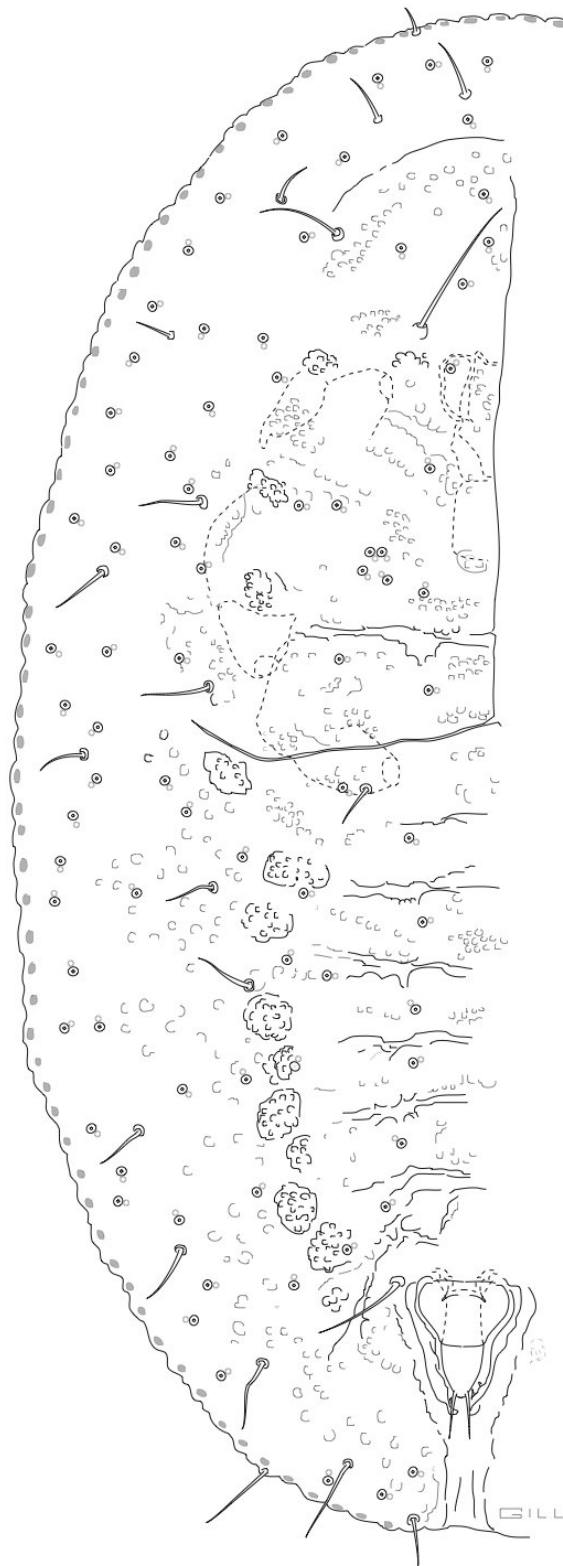


Figure 50. *Bemisiella artemisiae* Danzig, Paratype, Southern Maritime Territory, Khasan District, Kedrovvaya pad' reservation, ex: *Artemisia*, July 27, 1961, E. Danzig, coll.

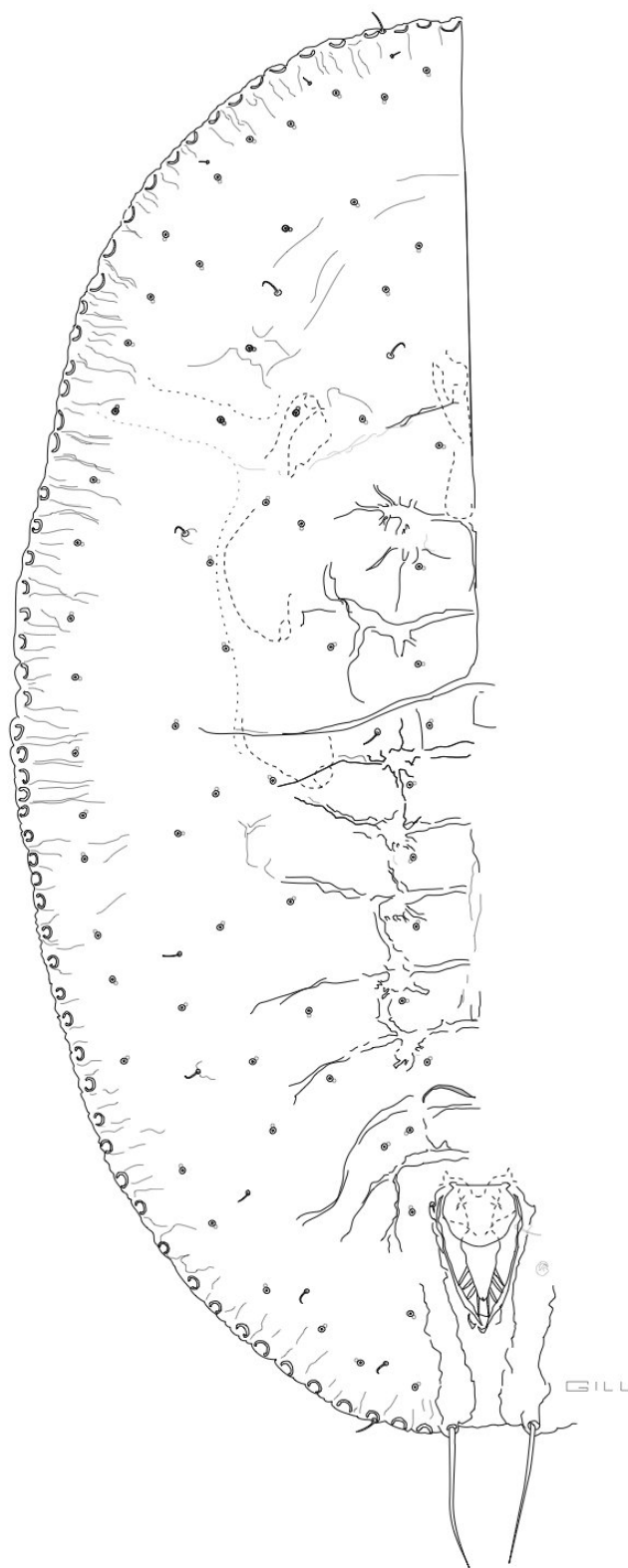


Figure 51. *Bemisia tabaci* complex specimen, Sudan: Kassala Prov., Jebel, Kassala, 6.iv.1981, ex: creeping grass, Slide #2, Specimen #1, Jon Martin, coll., JHM #3259

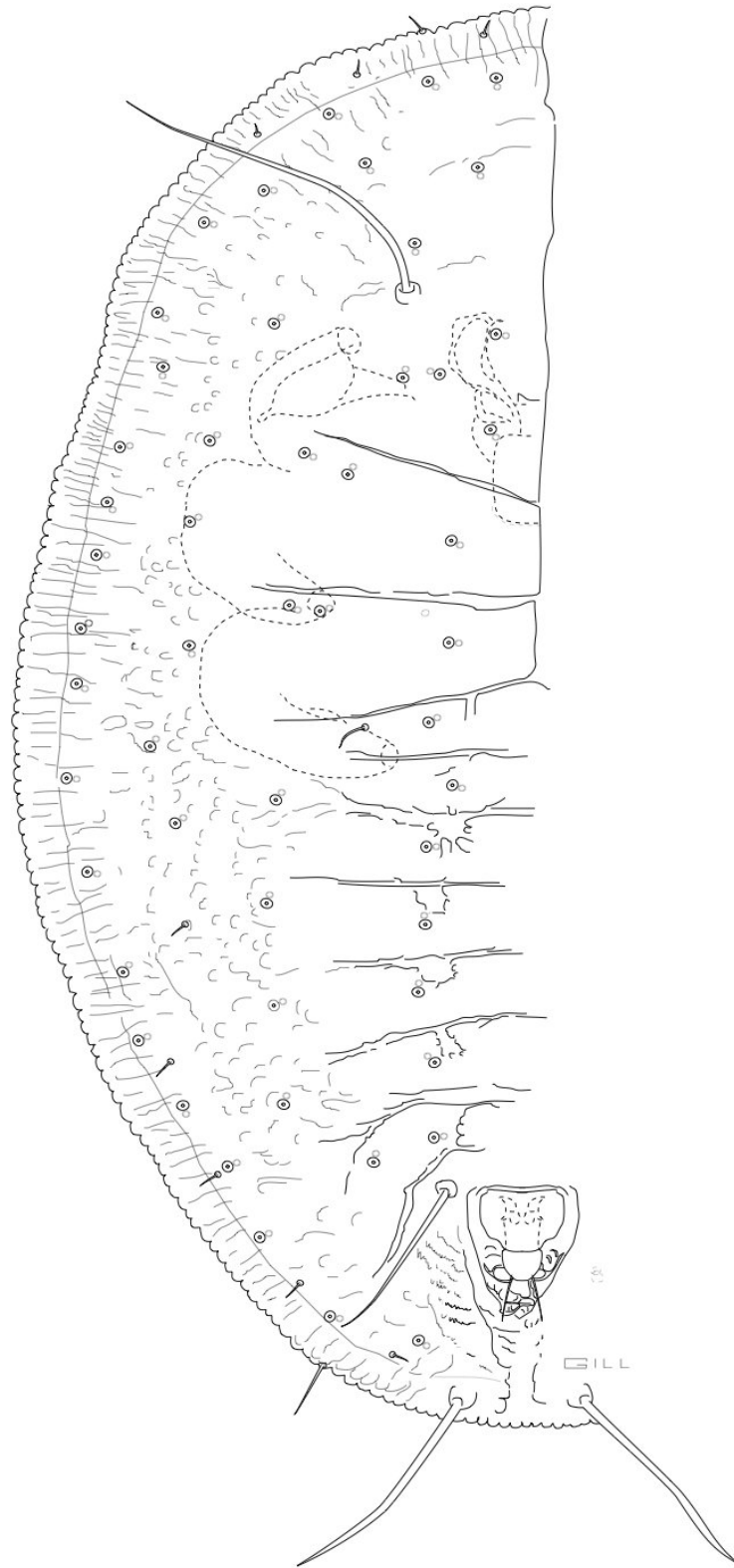


Figure 52. *Pealius azaleae* (Baker and Moles), Portland, Multnomah County, Oregon, VII-24-74, ex. *Rhododendron mucronatum*, R.L. Furniss, coll.

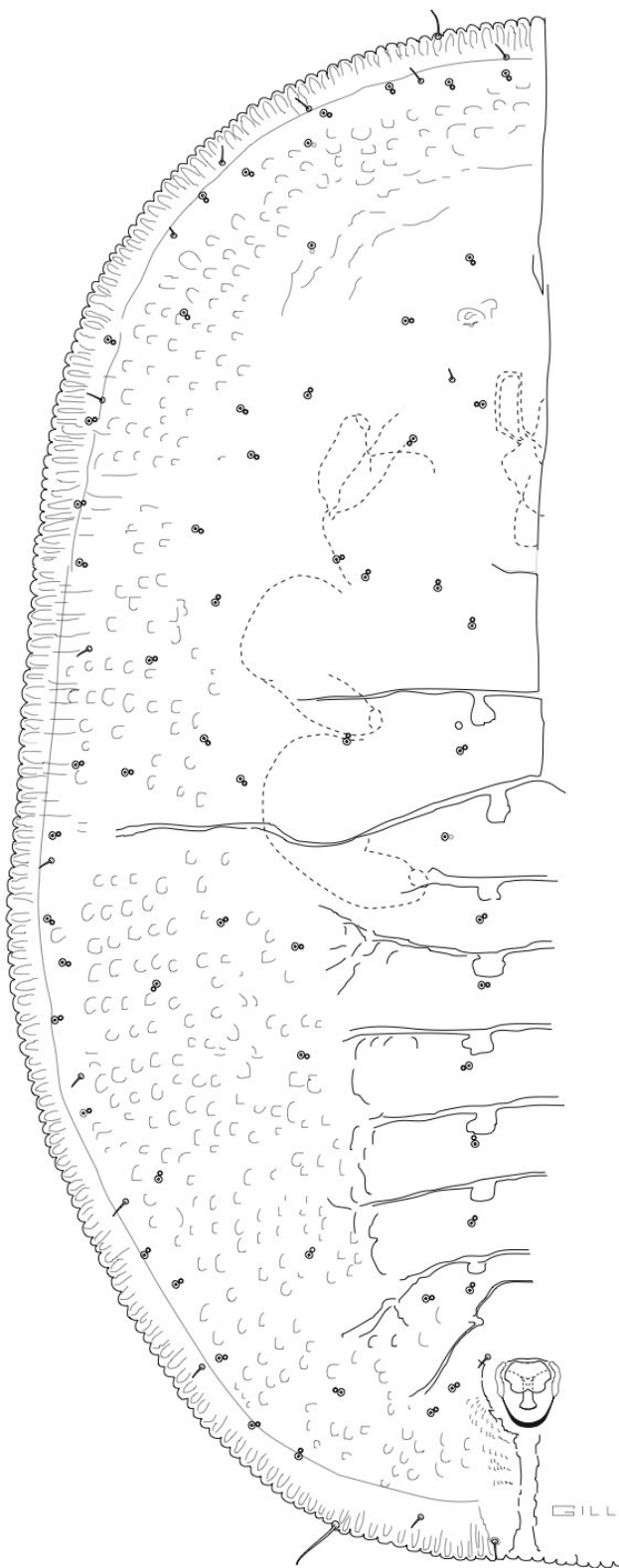


Figure 53. *Pealius maskelli* (Bemis), w/o Drytown on Hwy 16, Amador Co. Calif., III-30-76, ex *Quercus* sp., E. Paddock and R. Gill, colls.

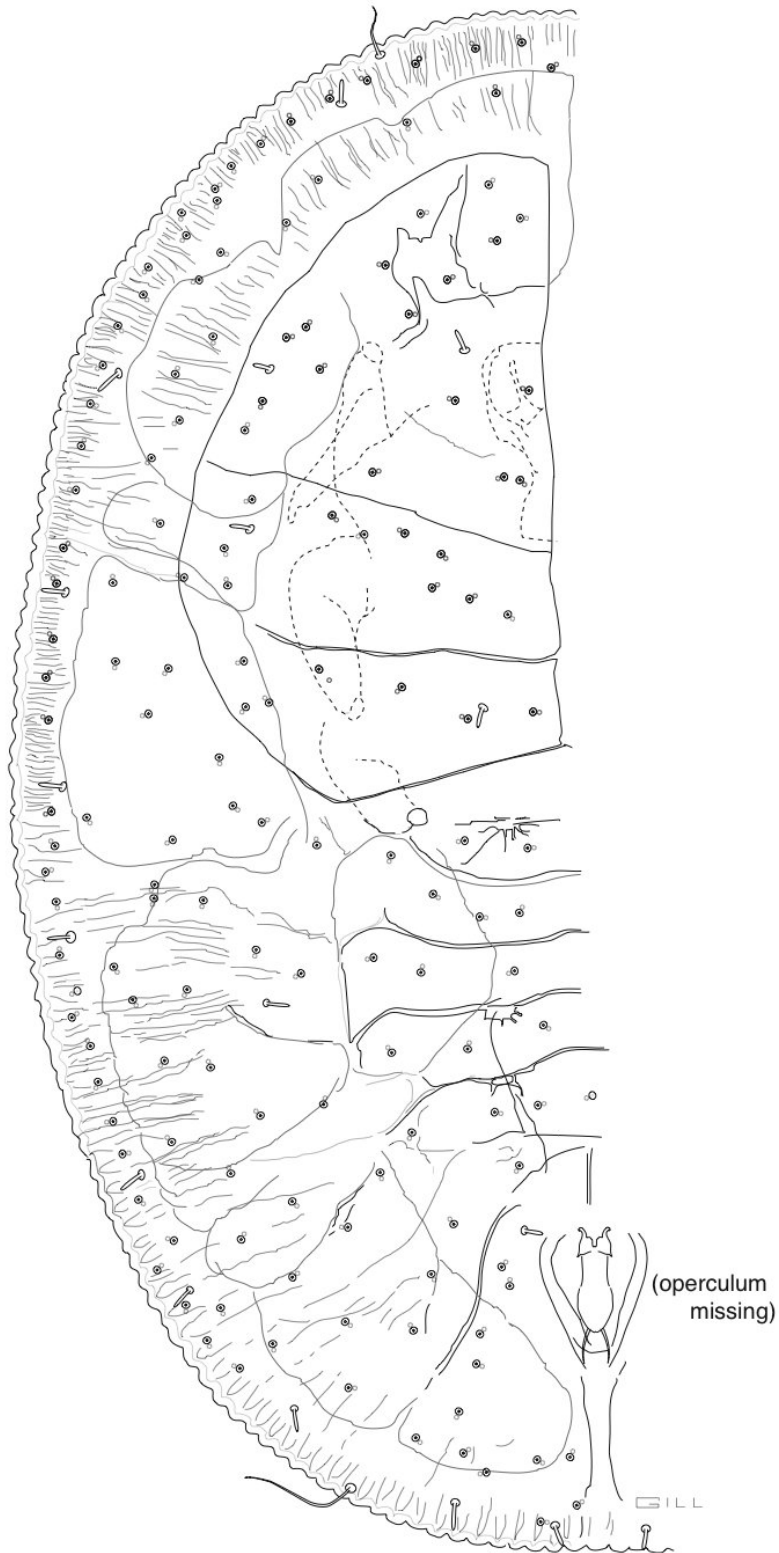


Figure 54. *Rosanovia hulthemiae* Danzig, Paratype, South Kazakstan, Saryagach, ex. *Hulthemia berberifolia*, 10-10-1958, E.M. Danzig, coll.

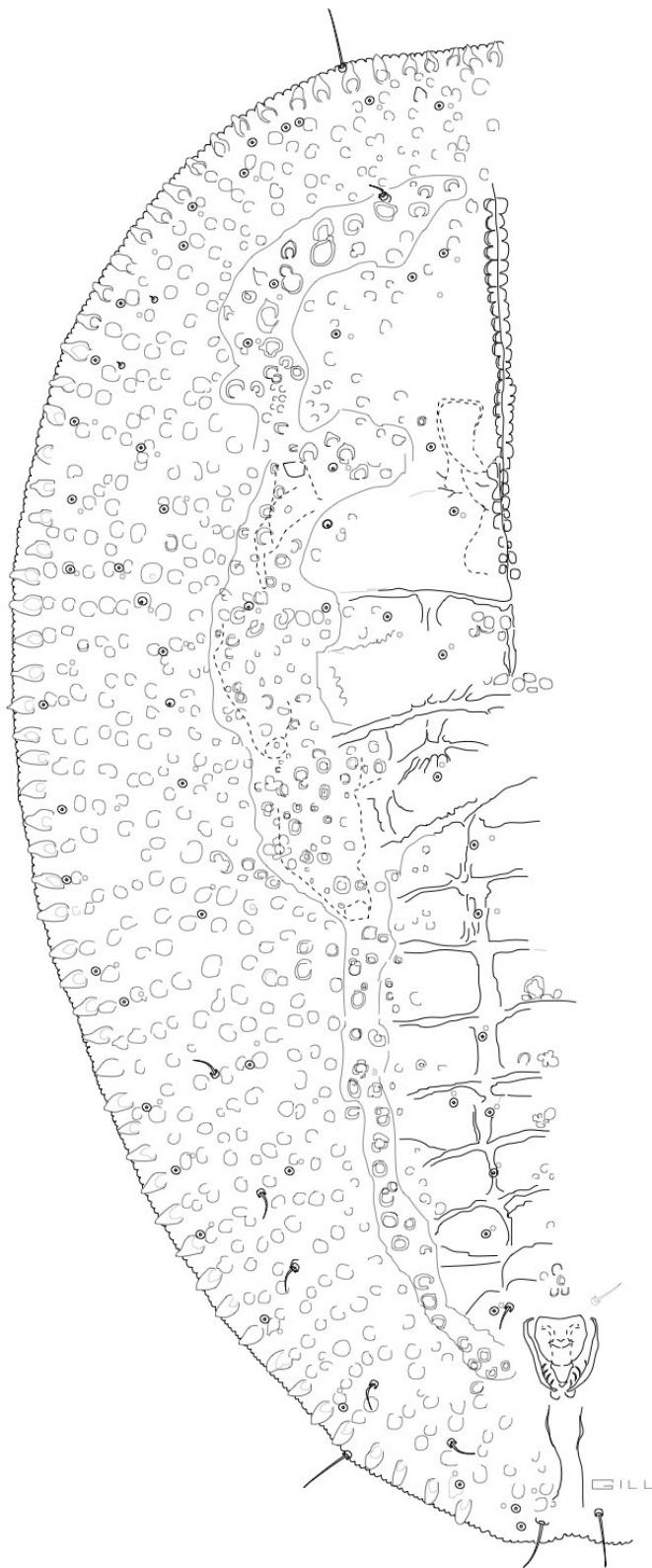


Figure 55. *Bemisia* sp. (??), Barro Colorado Is., Panama Canal Zone, 12 March 1983, ex. *Macherium floribundum*, Leguminosae. J.H. Martin, coll #3981.

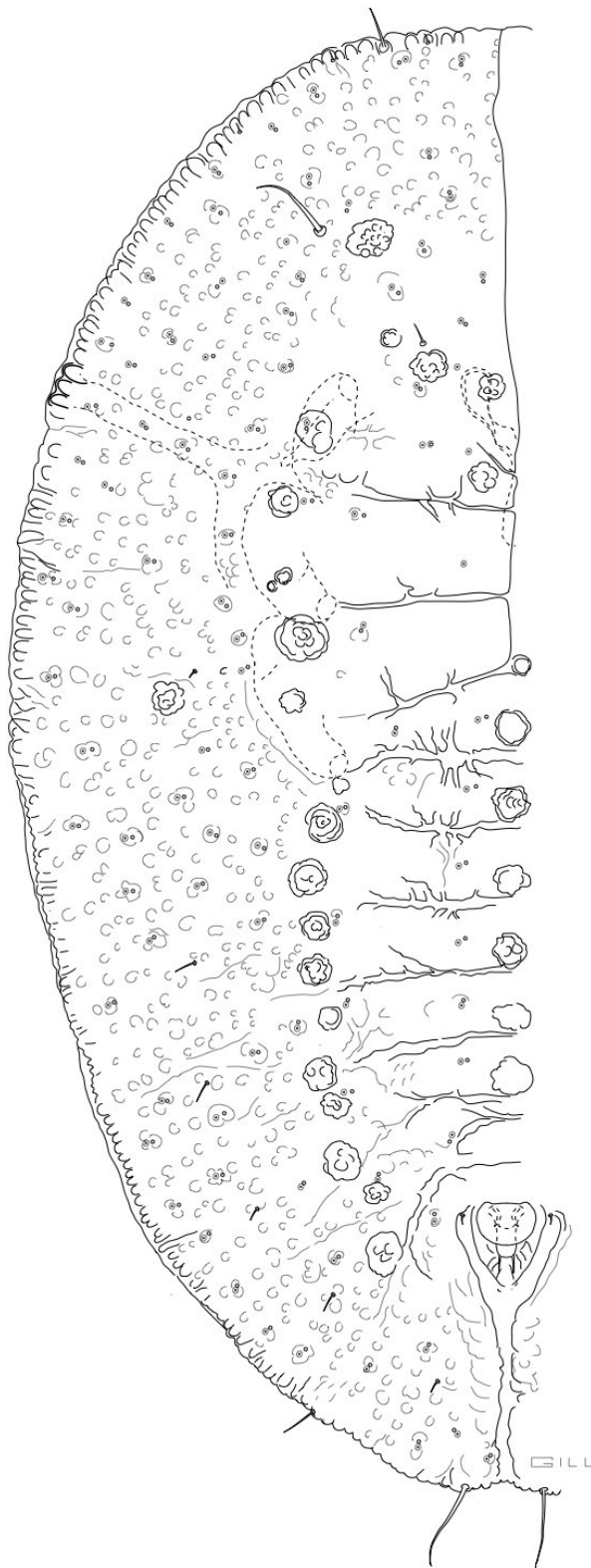


Figure 56. *Bemisia* sp. (??), Gambo Pond, Panama Canal Zone, March 25, 1993 ex. *Erythrina fusca*, J. Martin, coll., JHM #4133.

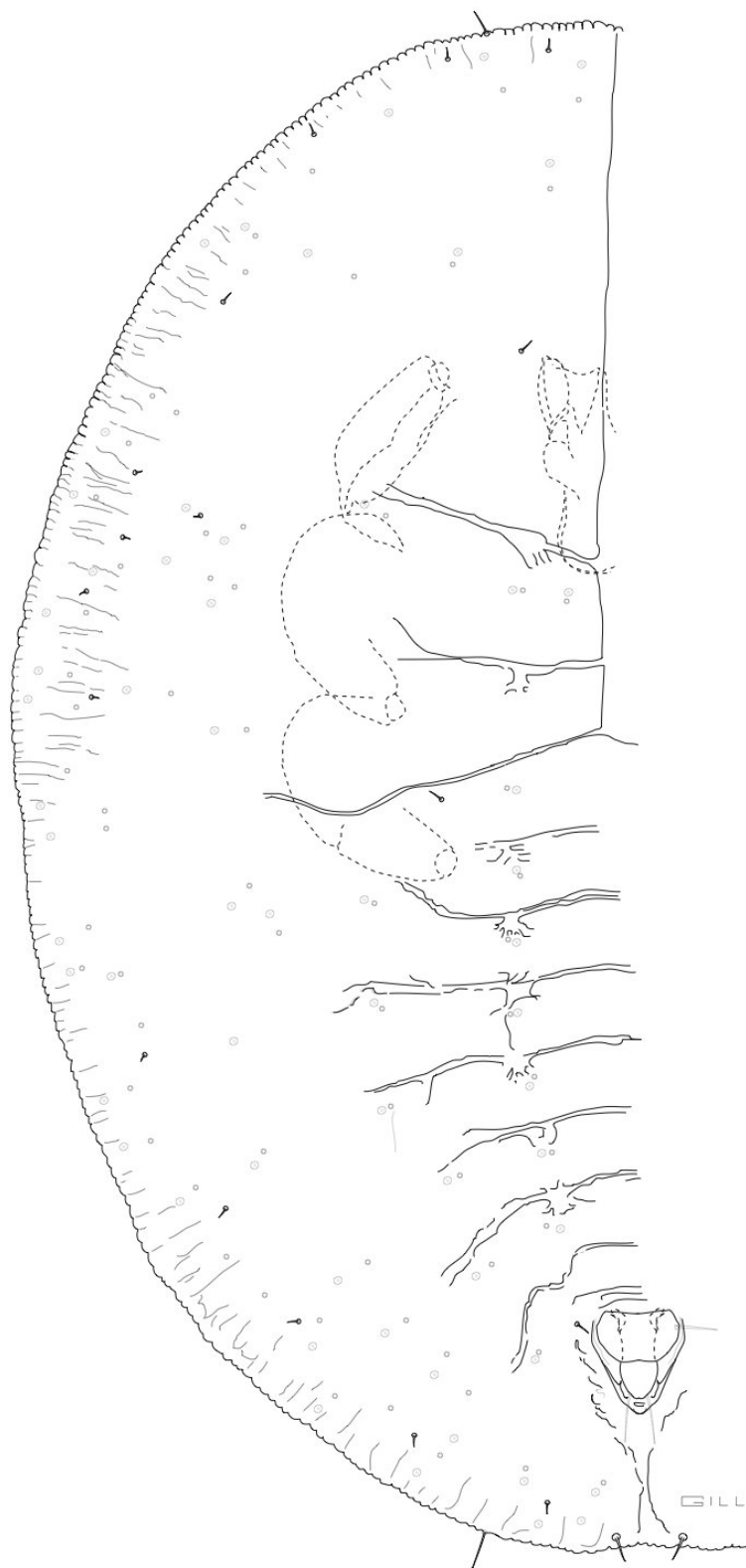


Figure 57. *Aleyrodes spiraeoides* Quaintance, Salinas, Monterey Co., Calif., VIII-86, ex. rose, W. C. Walsh, coll.

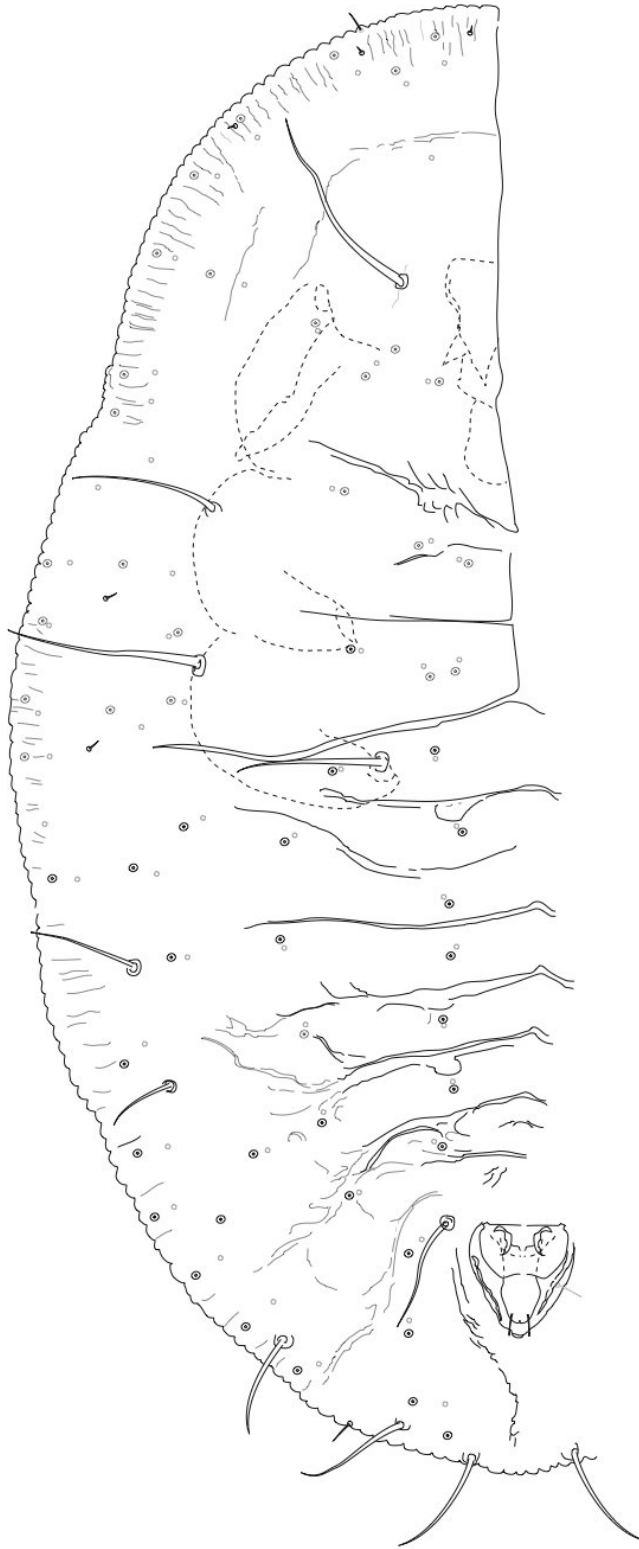


Figure 58. *Aleyrodes spiraeoides* Quaintance, Stockton, San Joaquin Co. Calif., VII-4-84, ex. *Lycopersicon esculentum*, T. Gantenbein, coll.

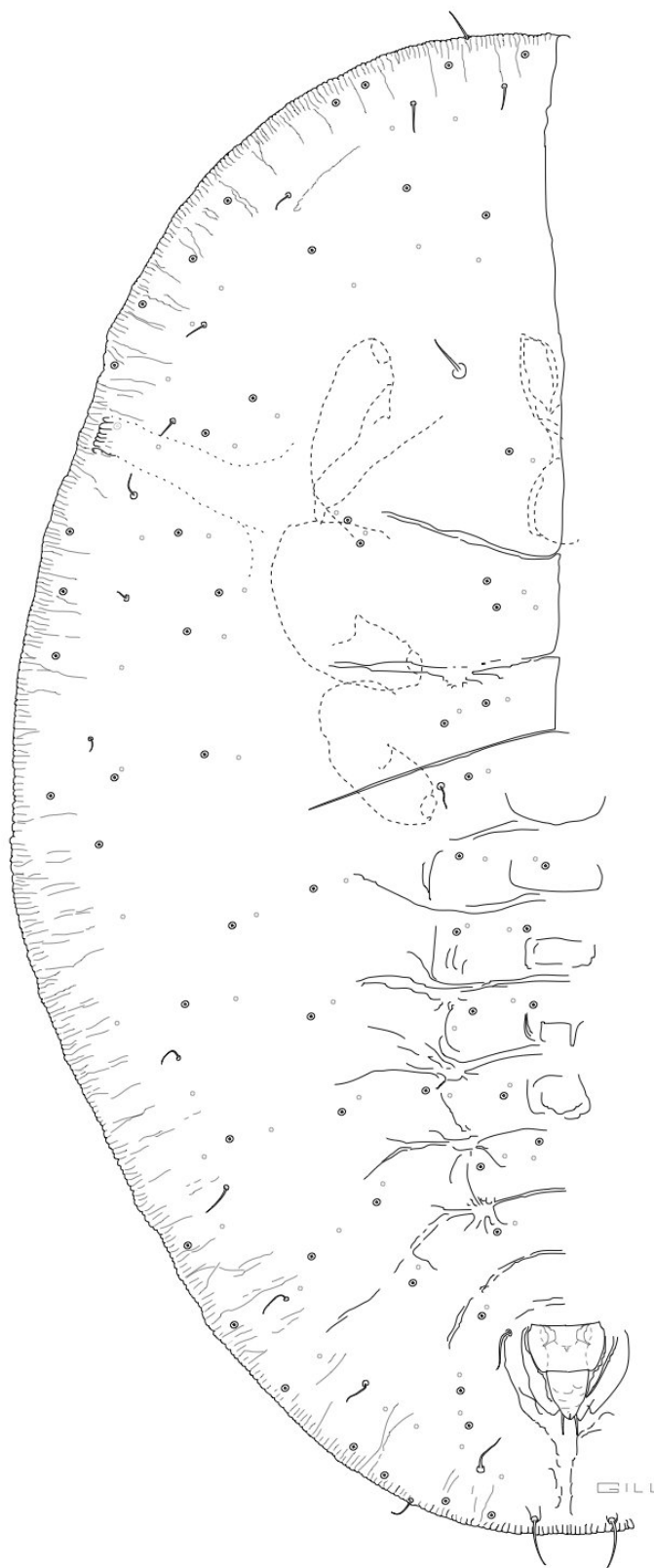


Figure 59. *Aleyrodes philadelphi* Danzig, Vladivostok, Okeanskaya, ex. *Philadelphus tenuifolius*, 18-vii-61, E.M. Danzig, coll.

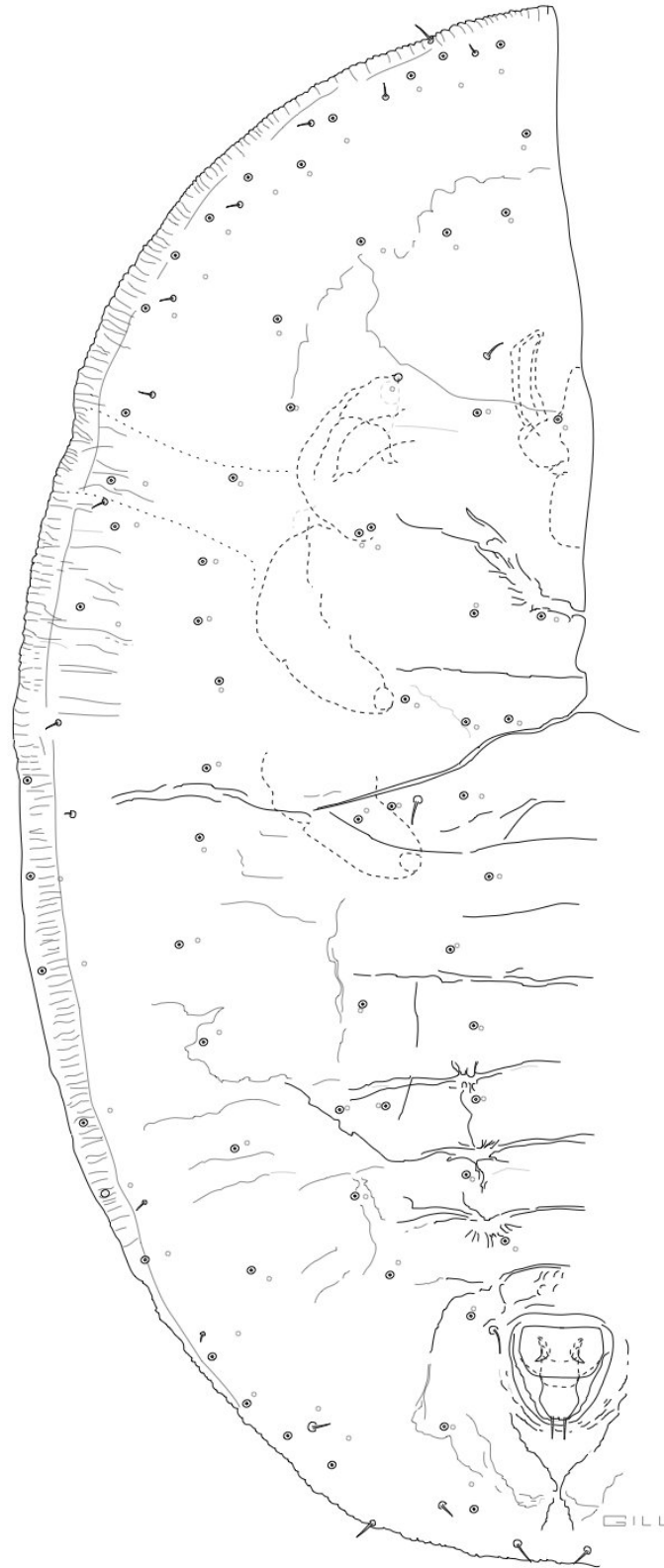


Figure 60. *Aleyrodes zygia* Danzig, Southern Maritime Territory, upper reaches of Chapigou, ex. *Euphorbia* sp., 1-vii-62, E.M. Danzig.

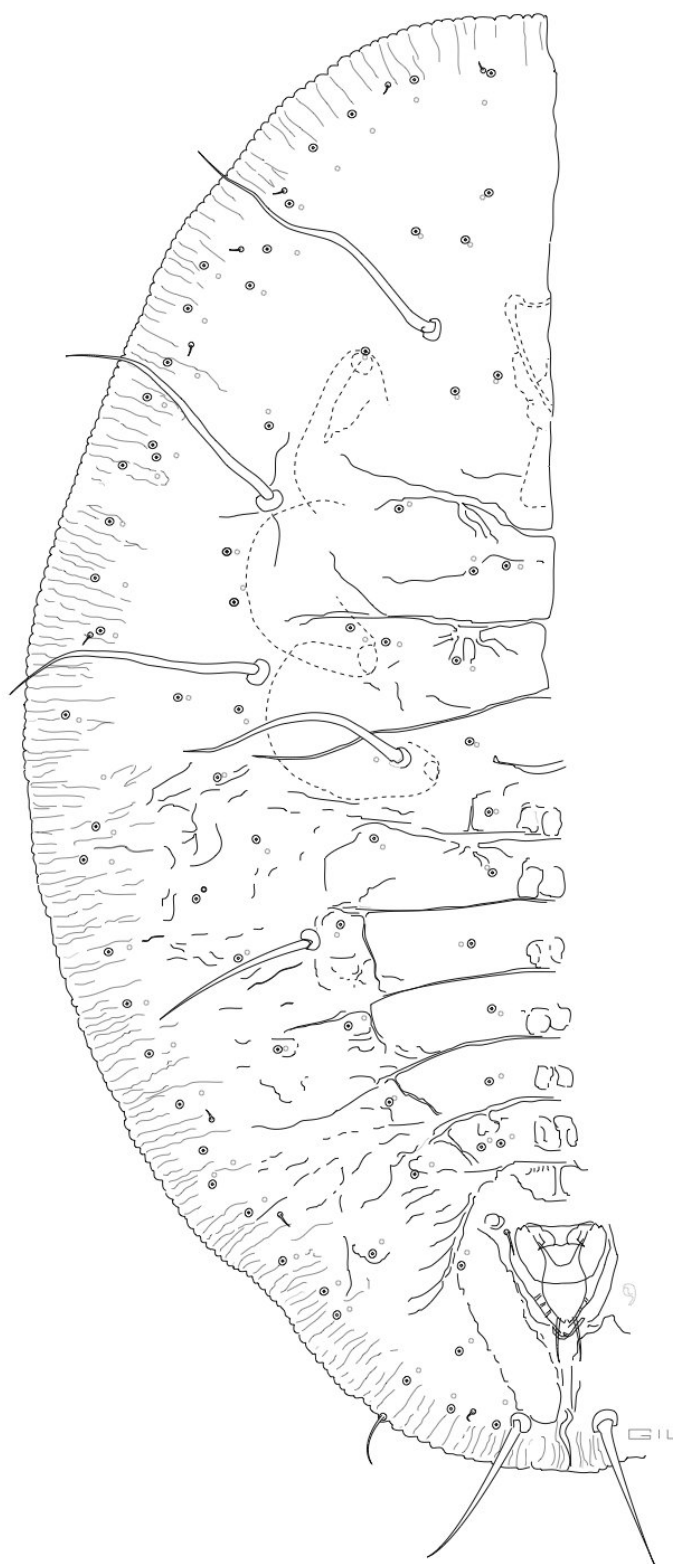


Figure 61. *Aleyrodes borchsenii* Danzig, Southern Maritime Territory, Khasa District, Kedrovaya padi reservation, ex: *Urtica* sp., August 1961, E. Danzig, coll.

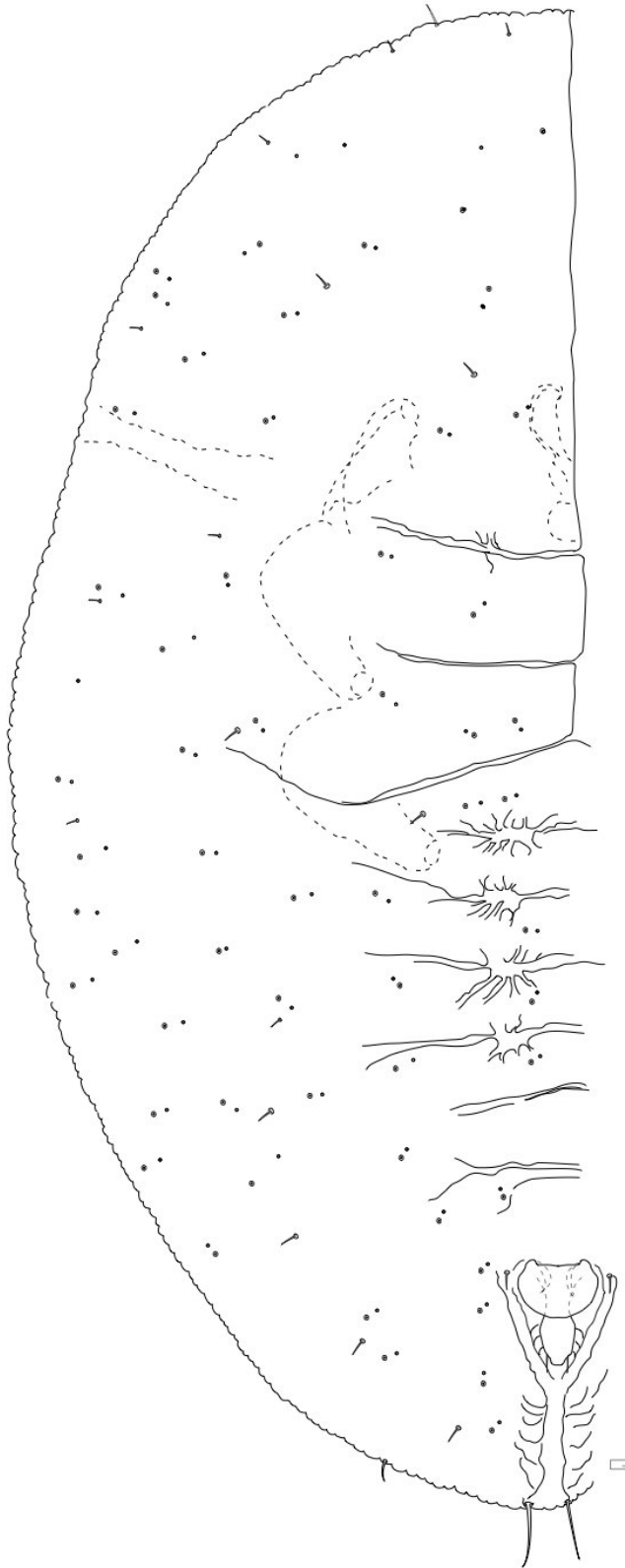


Figure 62. *Bemisia afer* complex, Canary Islands, Tenerife, Barranco, de las Moradas, at 7-900m, 18 May 1997, ex. *Hypericum grandifolium*, J. Martin, coll., JHM # 7041.

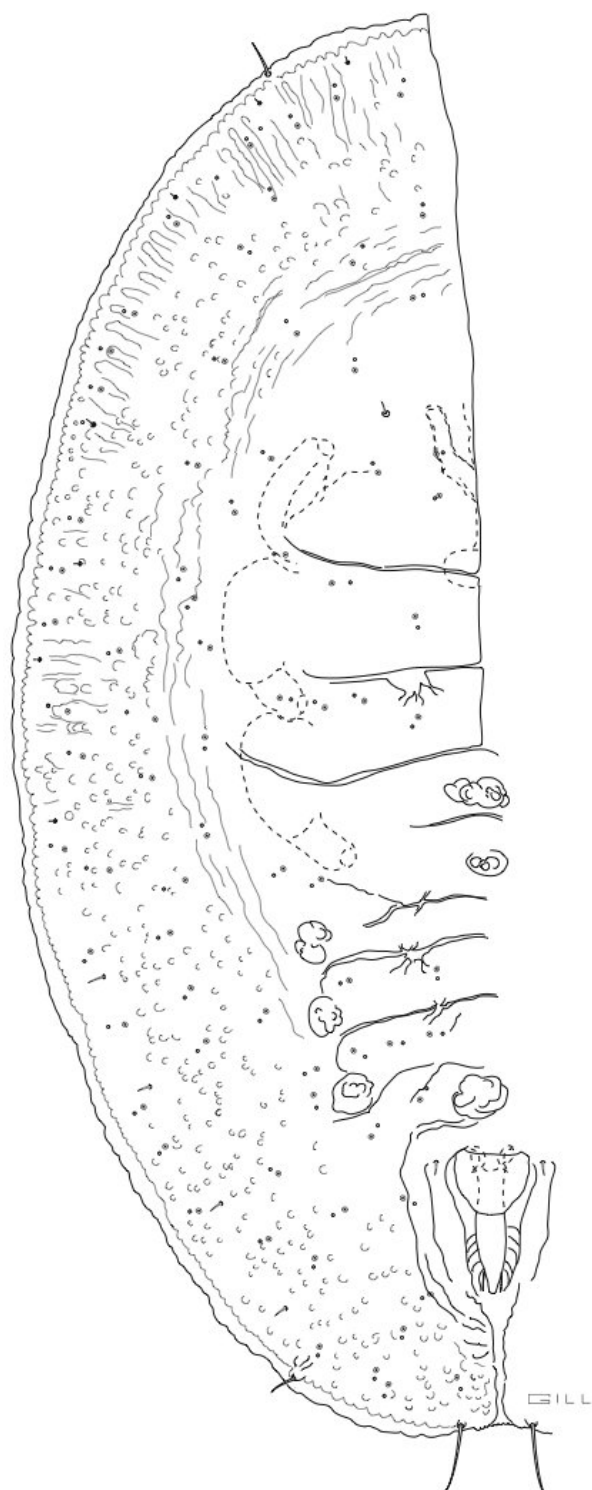


Figure 63. *Bemisia afer* complex, Canary Islands, La Palma, Pto Nao, ex. *Euphorbia balsamifera*, 22-VI-1997, E. Hernandez-Suarez, coll.

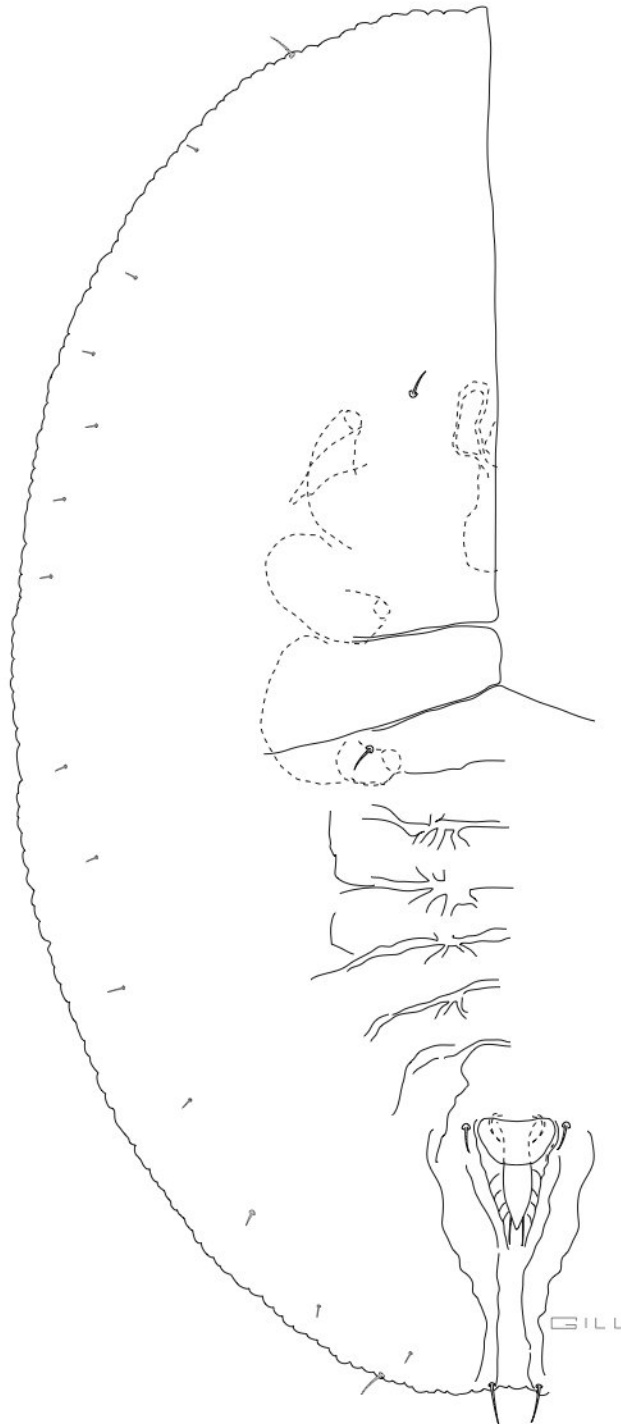


Figure 64. *Bemisia afer* complex, Canary Islands, Las Palmas, Zarata, ex. *Euphorbia balsamifera* and *E. regis-jubae* foliage, 4-i-2001, C.M. Malumphy, coll., CM#2001-4, BMNH (6) 2001-28. This illustration is less detailed than others, and is meant only to show general body shape and setal patterns.

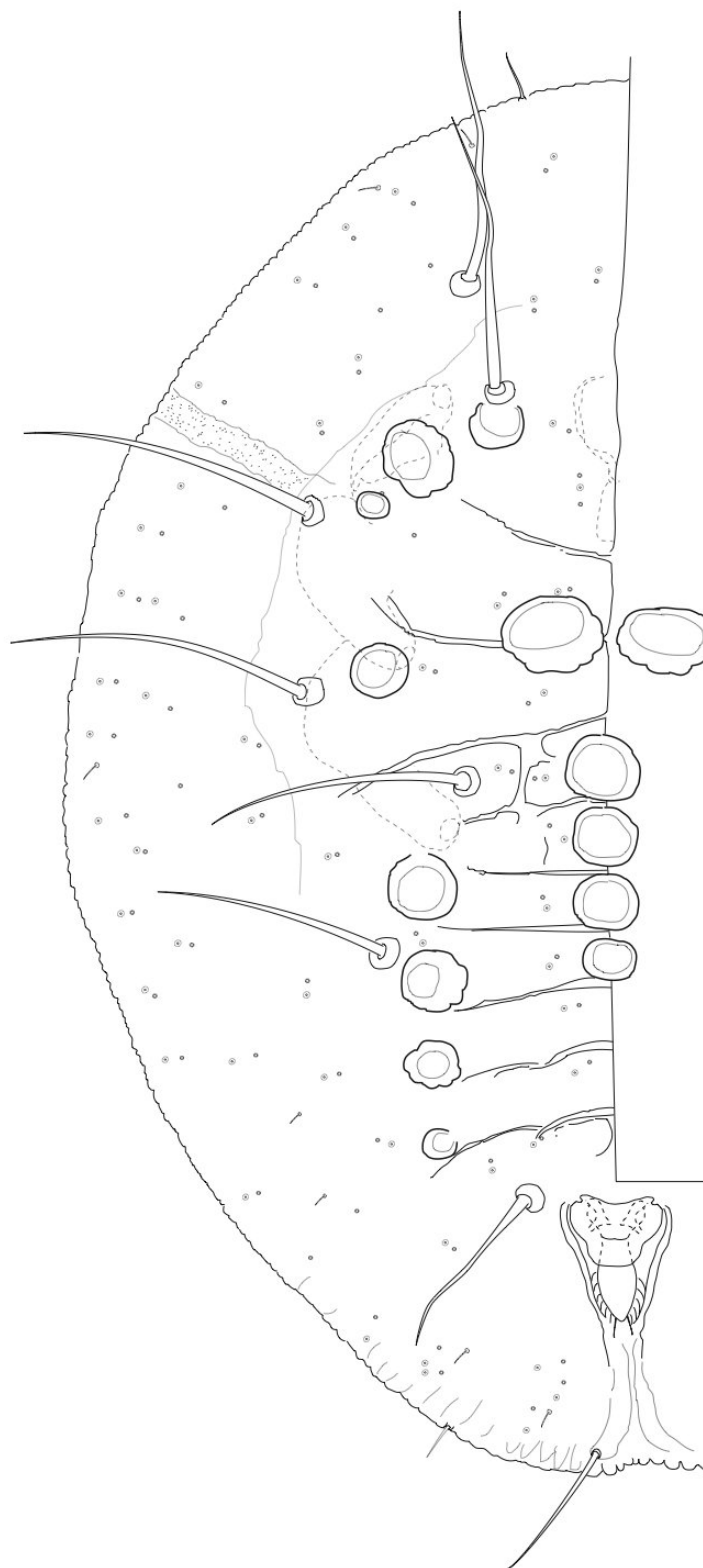


Figure 65. *Bemisia afer* complex, Canary Islands, Tenerife; Barranco, de las, Moradas nr. Ico de los Vinos, approx 700-900 m, 18 May, 1997, ex. *Gesnouinia arborea*, J.H. Martin, coll. #7049.

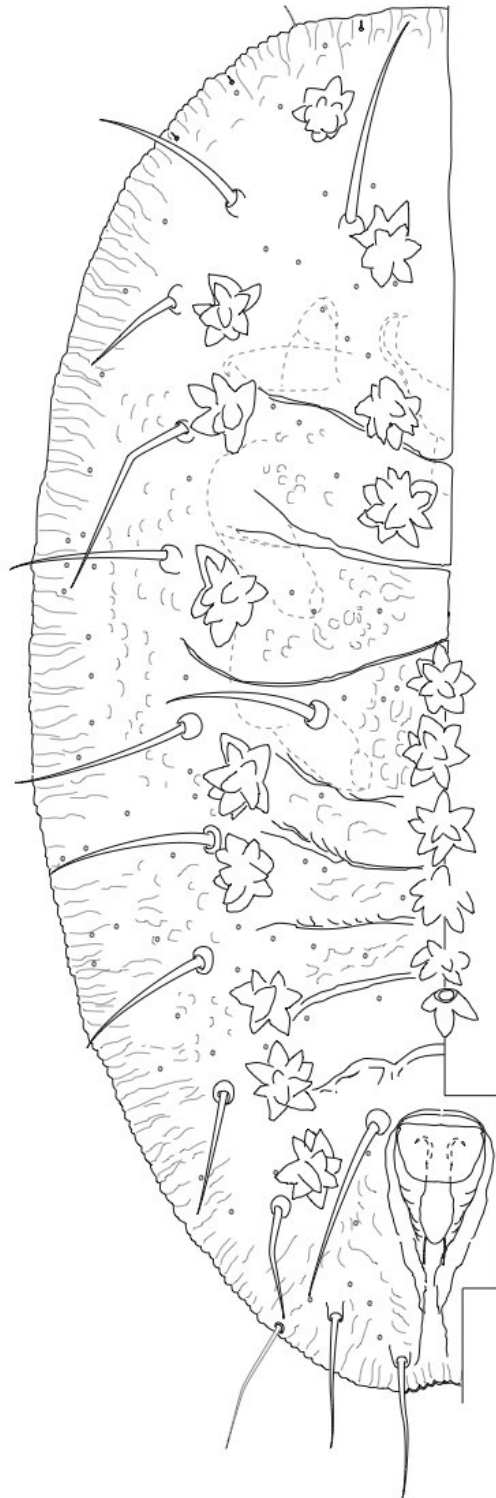


Figure 66. *Bemisia afer* complex, Canary Islands, Tenerife, Guimar, Bco de Badajos, January 1998, ex. *Bencomia caudata*, E. H-Suarez, coll.

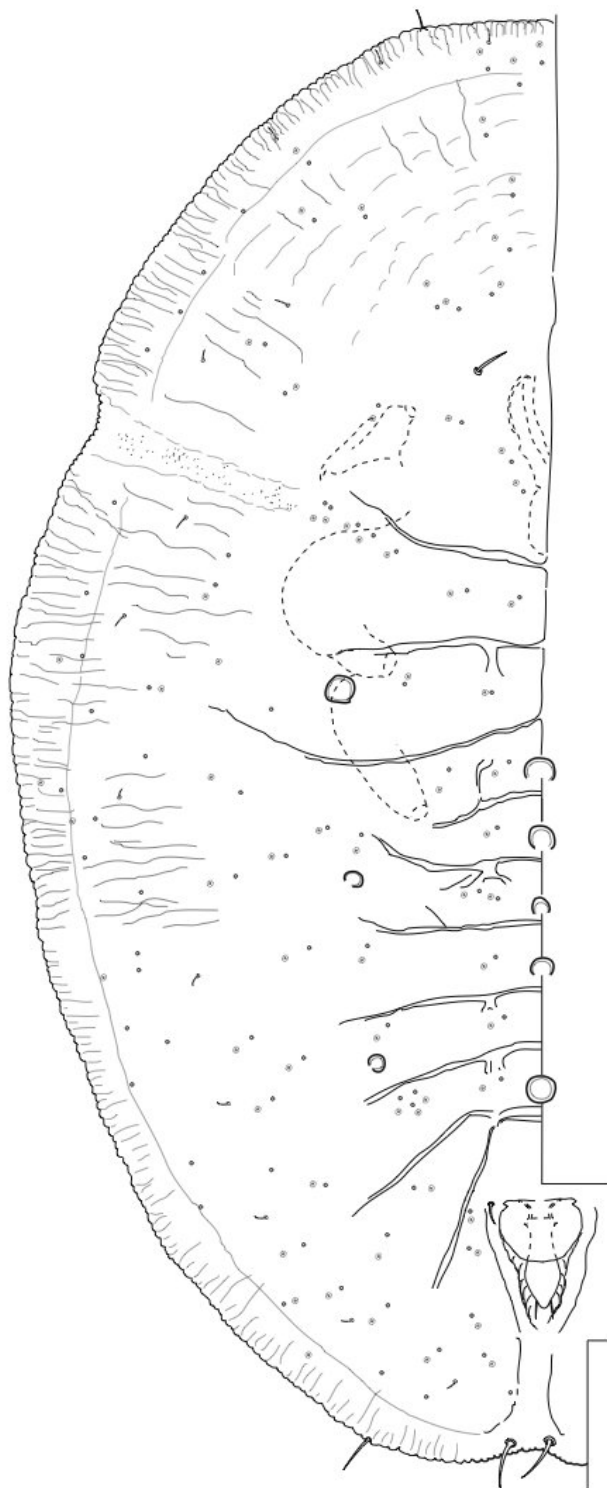


Figure 67. *Bemisia afer* complex, Canary Islands, Tenerife: Guimar, Bco de Badajos, 25 Nov. 2000, ex. *Bencomia caudata*, -upper surfaces, J.H.Martin, coll.

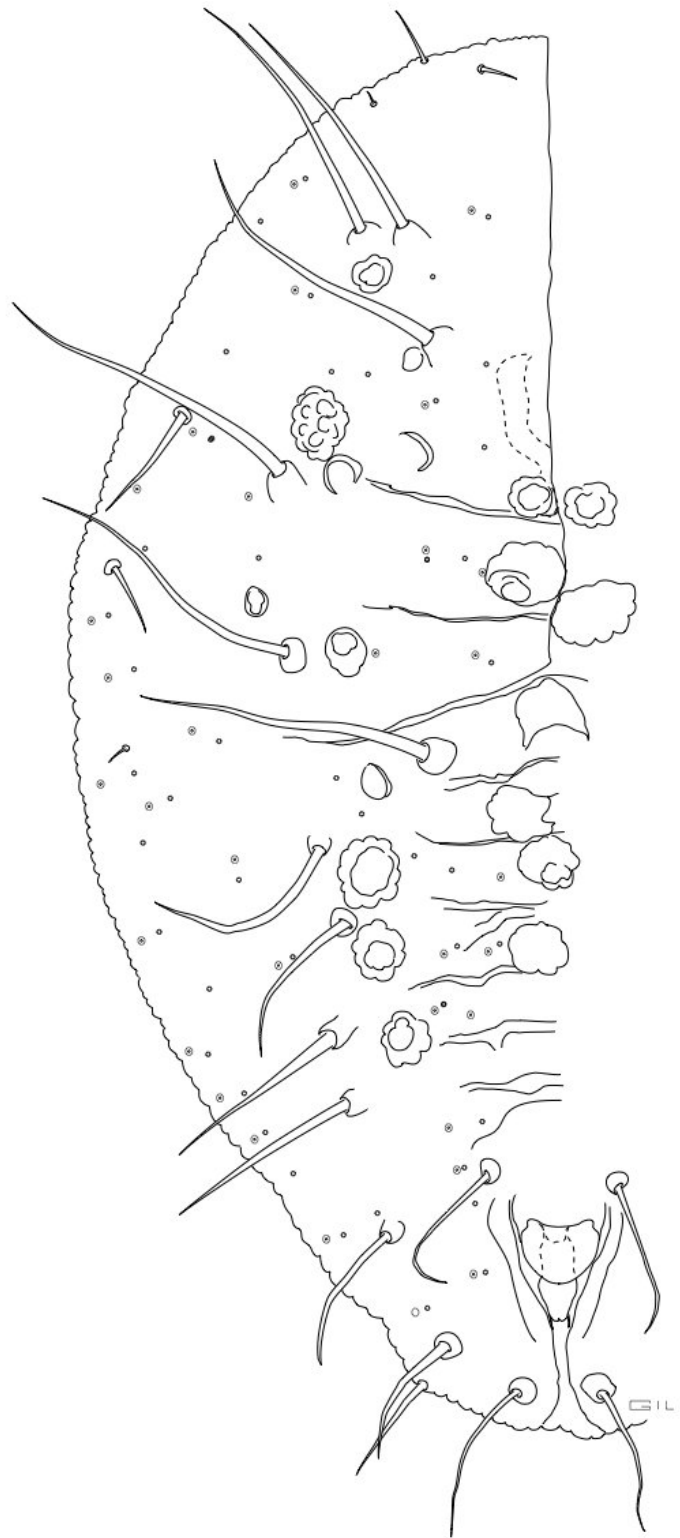


Figure 68. *Bemisia afer* complex, Canary Islands, Tenerife, Barranco, de las, Moradas, nr., Icod de los Vinos, at 7-900m, 18 May 1997, ex. *Cistus* sp., J. Martin, coll., JHM # 7046.

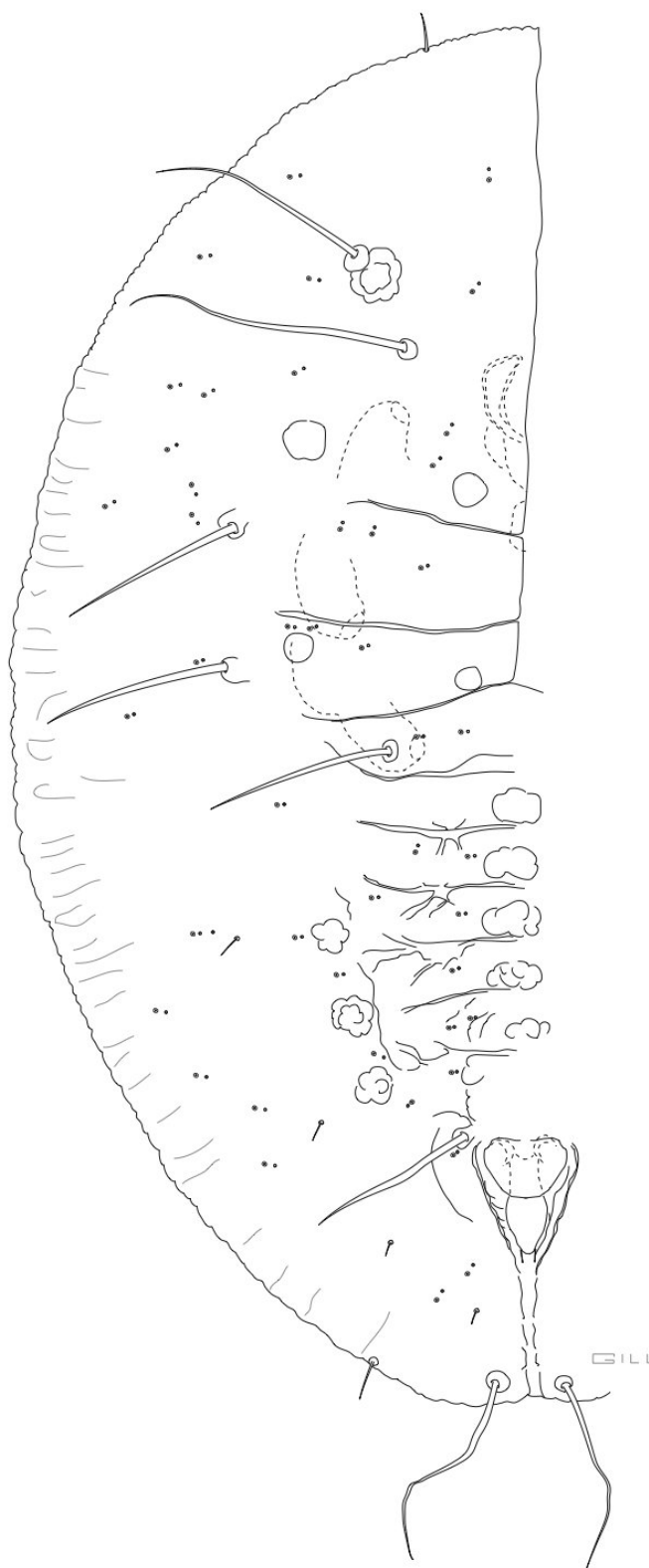


Figure 69. *Bemisia afer* complex, Canary Islands, La Palma, Ctr. Barbuento, ex. *Rubus* sp., 21-VI-1997, E. Hernandez-Suarez, coll.

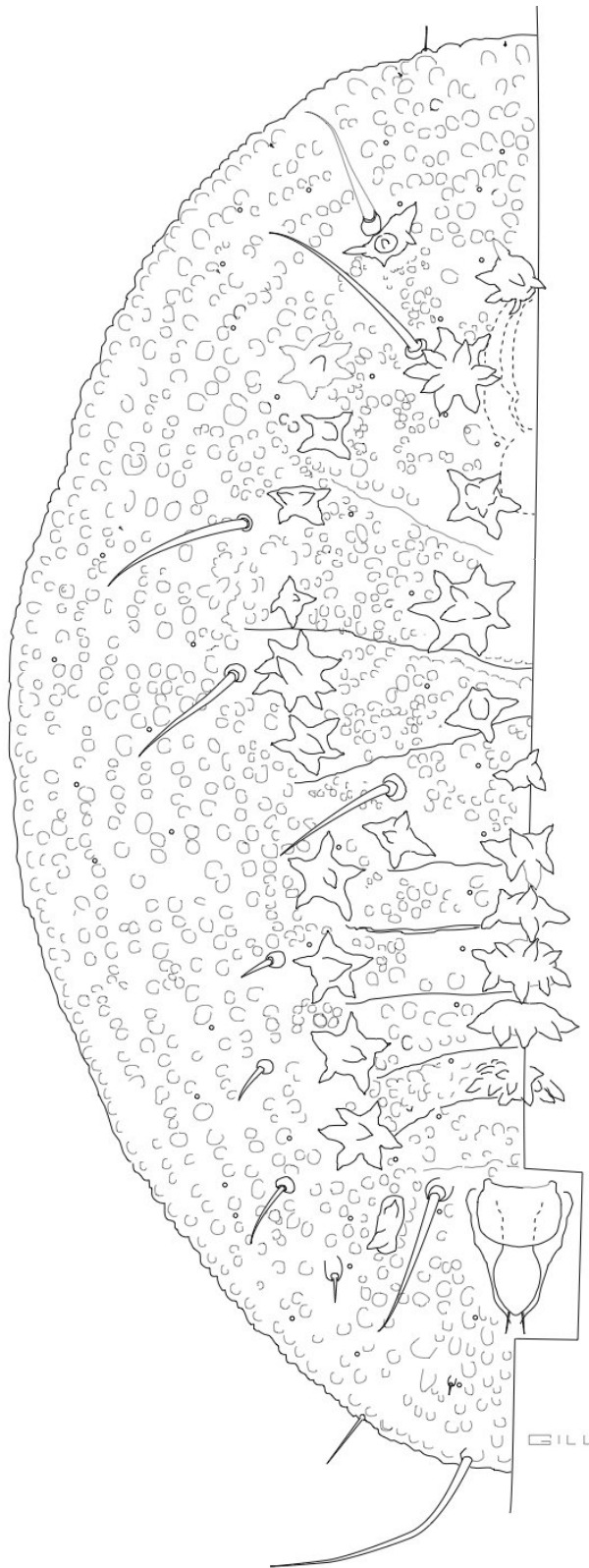


Figure 70. *Bemisia afer* complex, Canary Islands, Tenerife, Barranco de los Moradas, nr. Icod de los Vinos, approx 700-900 m., 18 May 1997, ex *Rubus fruticosus* grp., J.H. Martin, coll., JHM #7047.

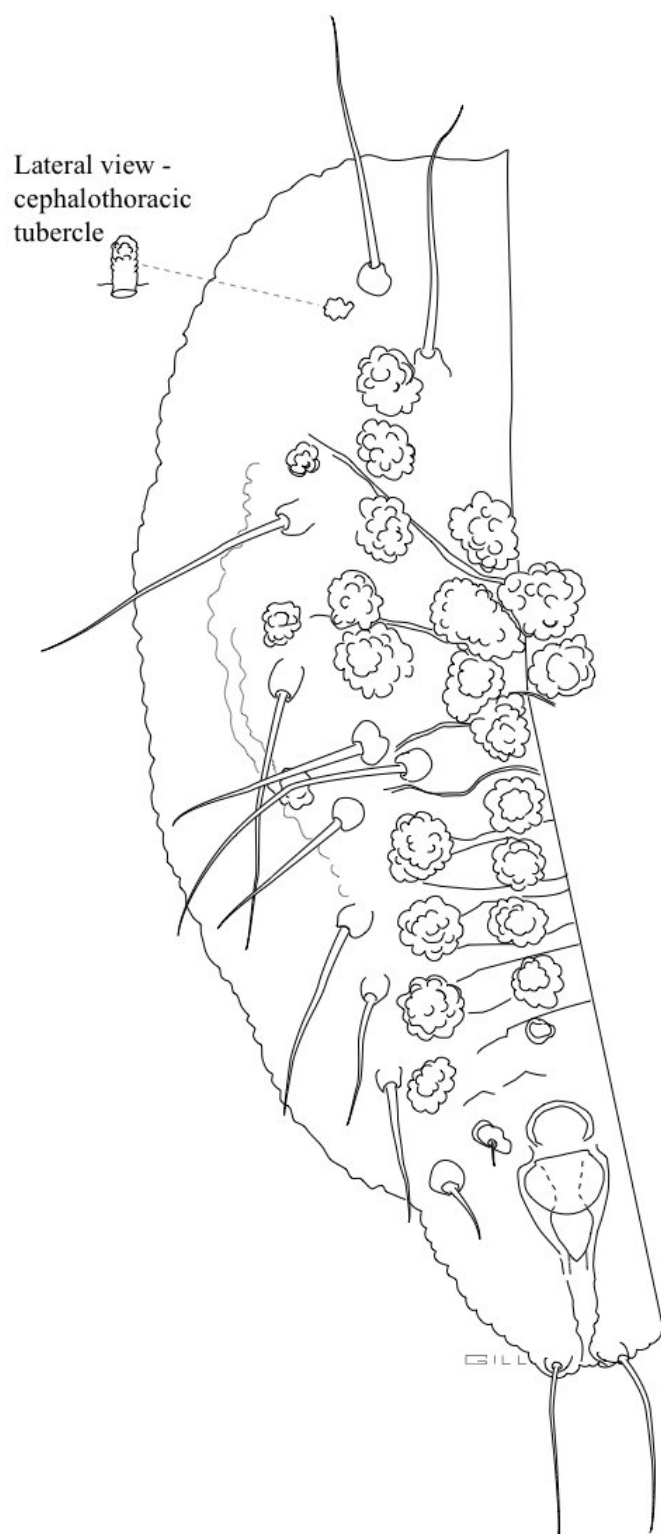


Figure 71. *Bemisia afer* complex, Canary Islands, Tenerife, Barranco de las Moradas, ex. *Eschium* sp., J. Martin, coll., JHM # 7048.

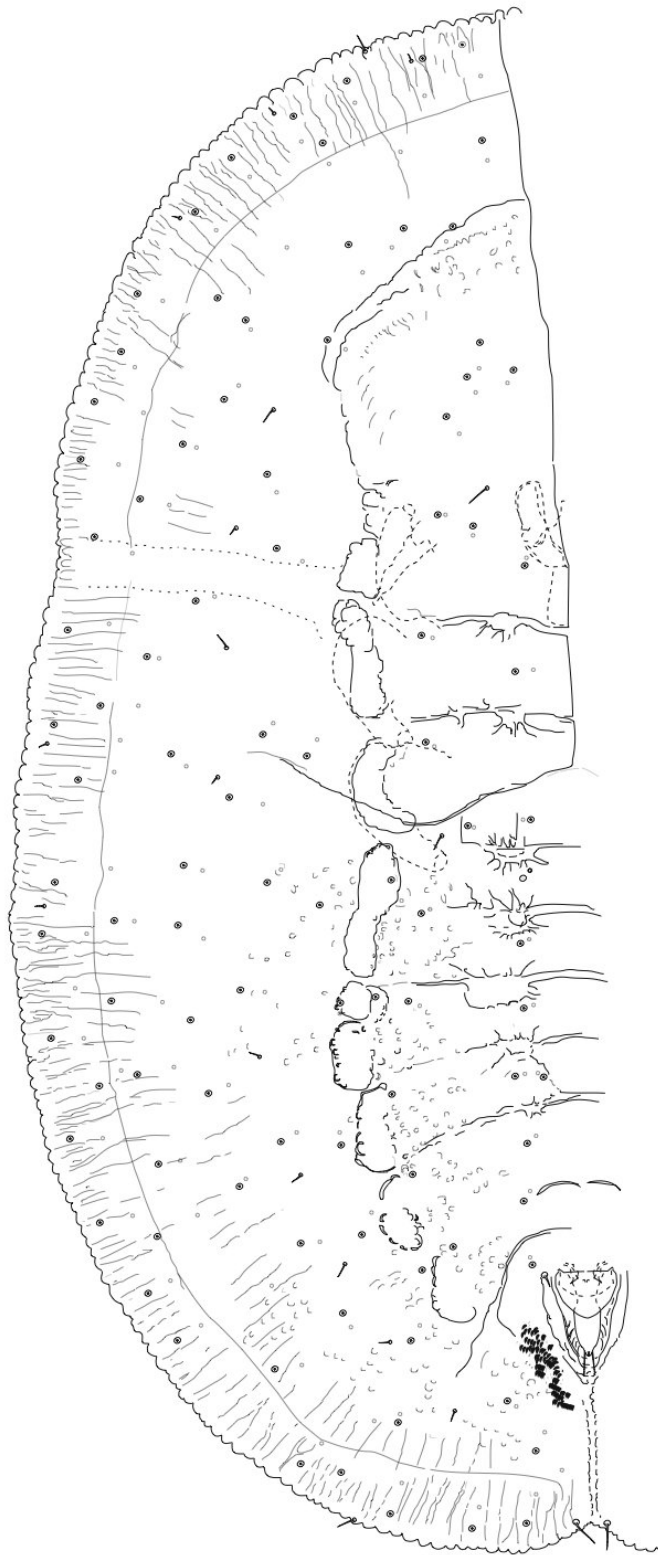


Figure 72. *Bemisia lauracea* Martin et al. , Madeira, Seixal, 6-iii-1992, ex. *Ocotea foetens*, F. Aguiar, coll., #C125.

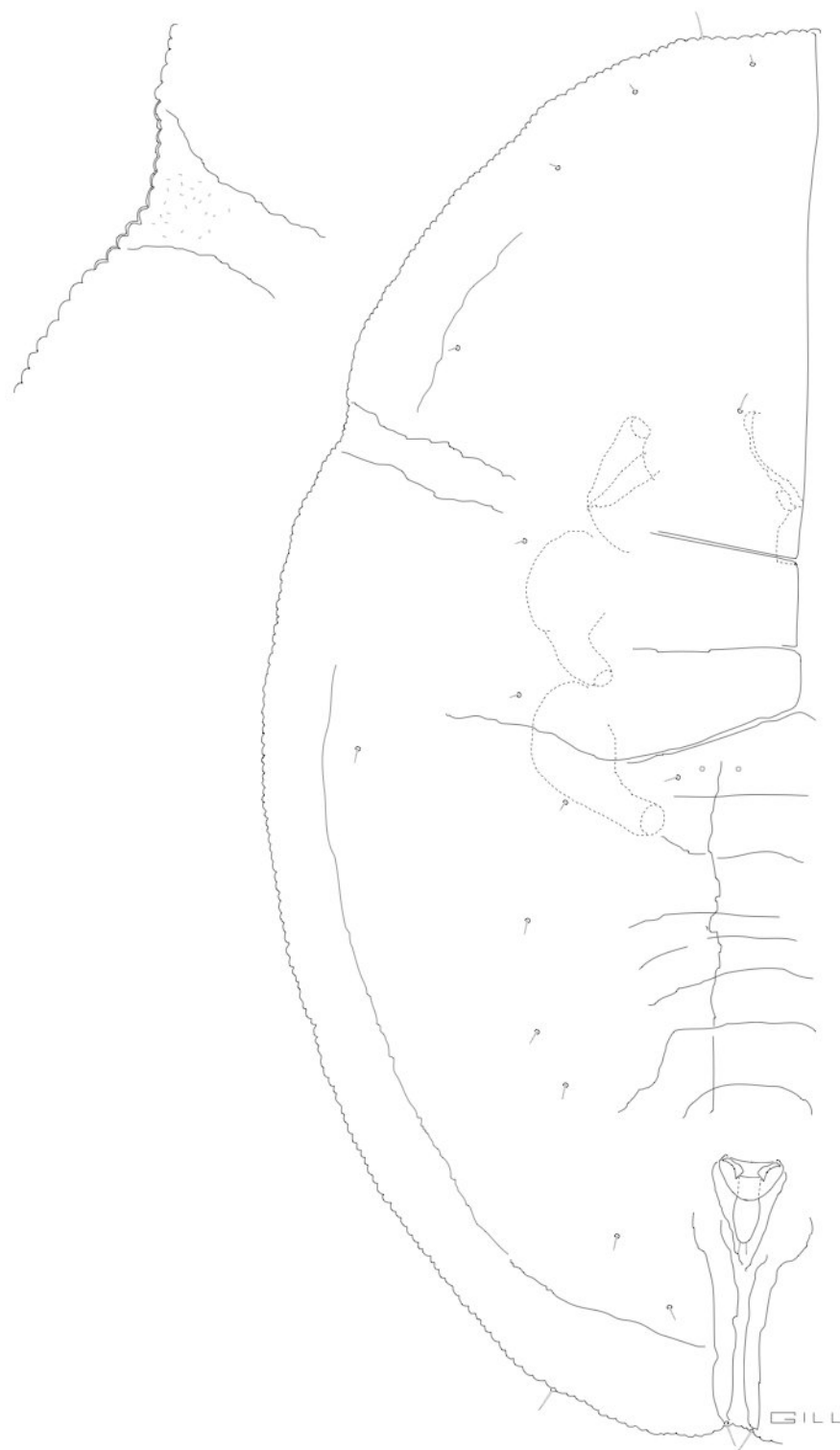


Figure 73. *Bemisia afer* complex, Madeira, Ribiero Frio, 800 m., 28 March 1995, J.H. Martin, A.F. Aguiar coll, ex. *Sonchus fruticosus*, JHM coll. #6543. This illustration is less detailed than others, and is meant only to show general body shape and setal patterns.

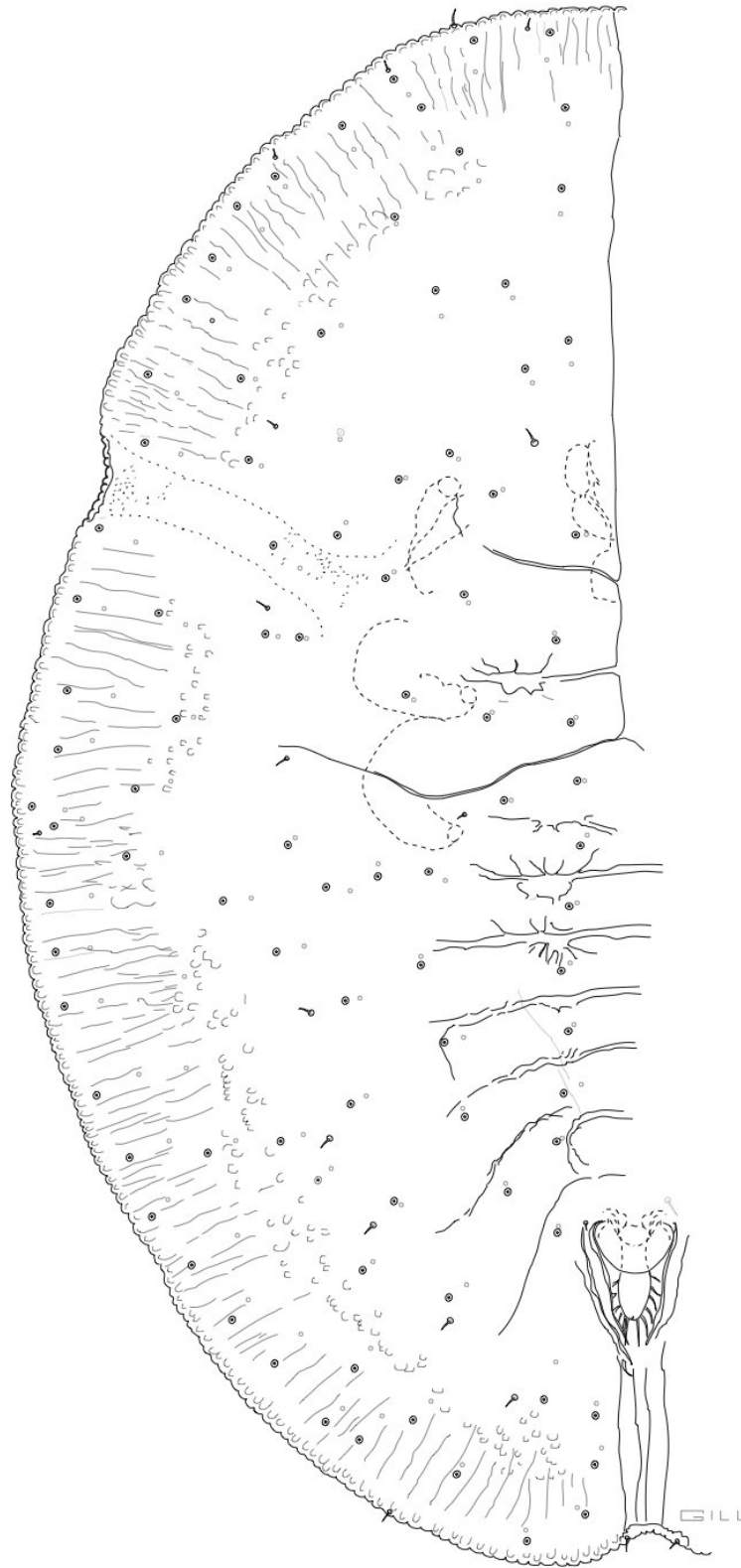


Figure 74. *Bemisia afer* complex, Madeira, Seixal, 6-III-92, ex. *Ocotea foetens.*, (Lauraceae), F. Aguiar, coll. #C125.

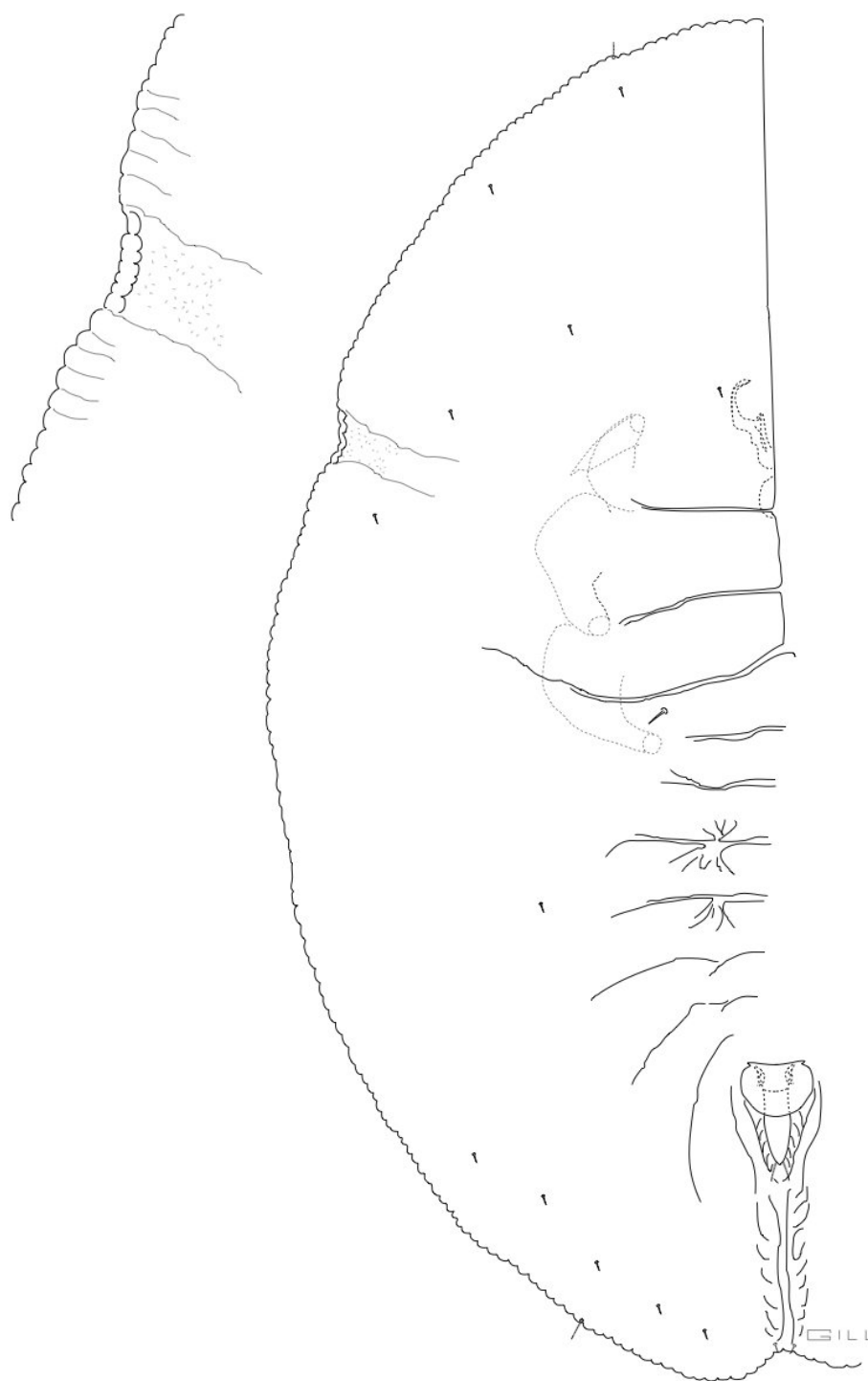


Figure 75. *Bemisia afer* complex, Madeira, Levado do Norte, , Below Bica da Cana, 1000-1100 m, 16 May 1997, ex. *Clethra arborea*, J.H. Martin coll. #7040. This illustration is less detailed than others, and is meant only to show general body shape and setal patterns.

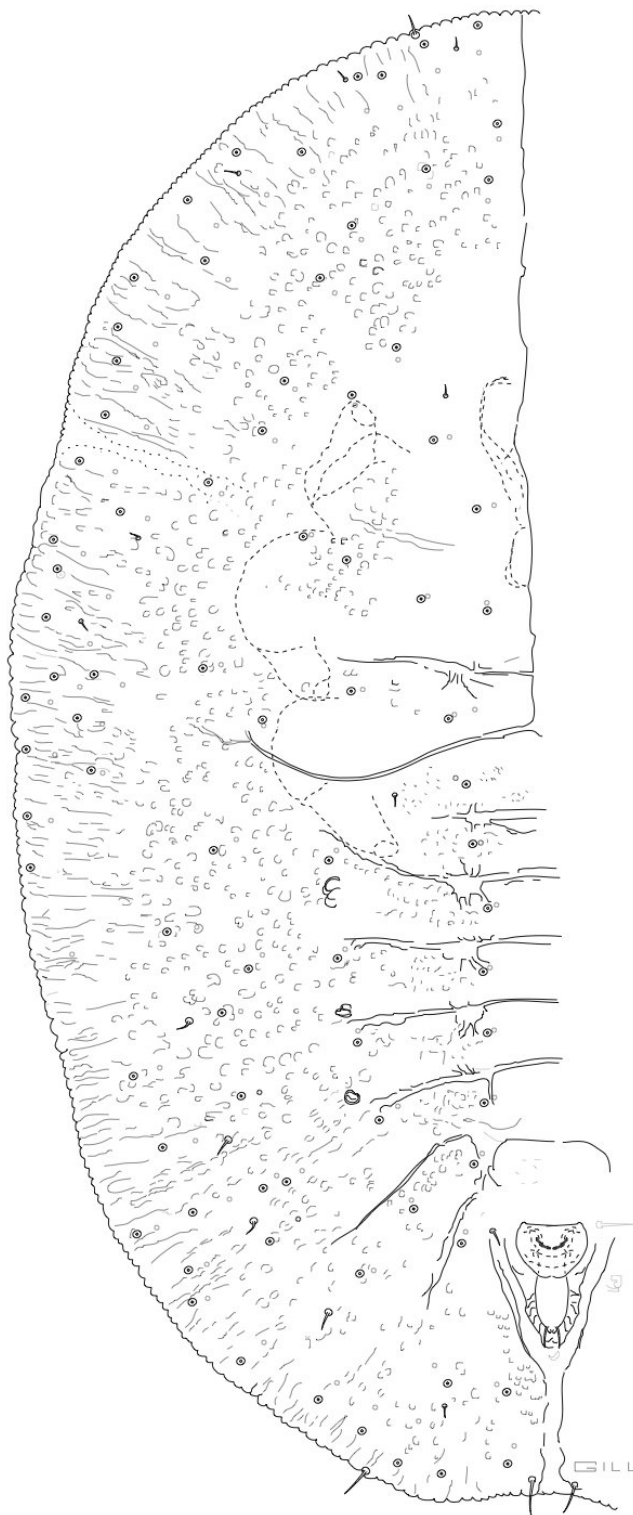


Figure 76. *Bemisia afer* complex, Madeira, Faja do Penedo, 20-iii-1992, ex. *Marcetella madeirensis*, F. Aguiar, coll. # C136.

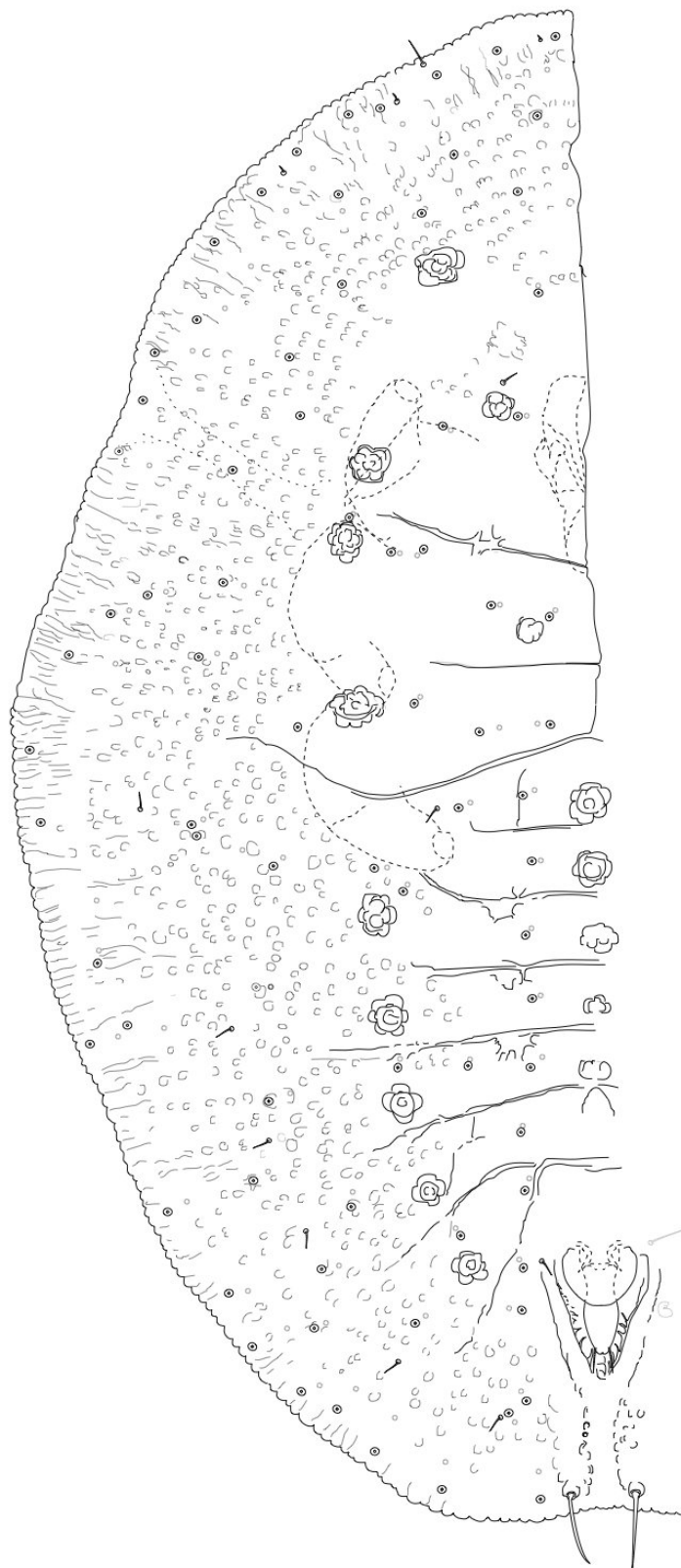


Figure 77. *Bemisia afer* complex, Madeira, Faja do Penedo, 20.iii.92, ex. *Marcetella madeirensis*, F. Aguiar, coll., #C136.

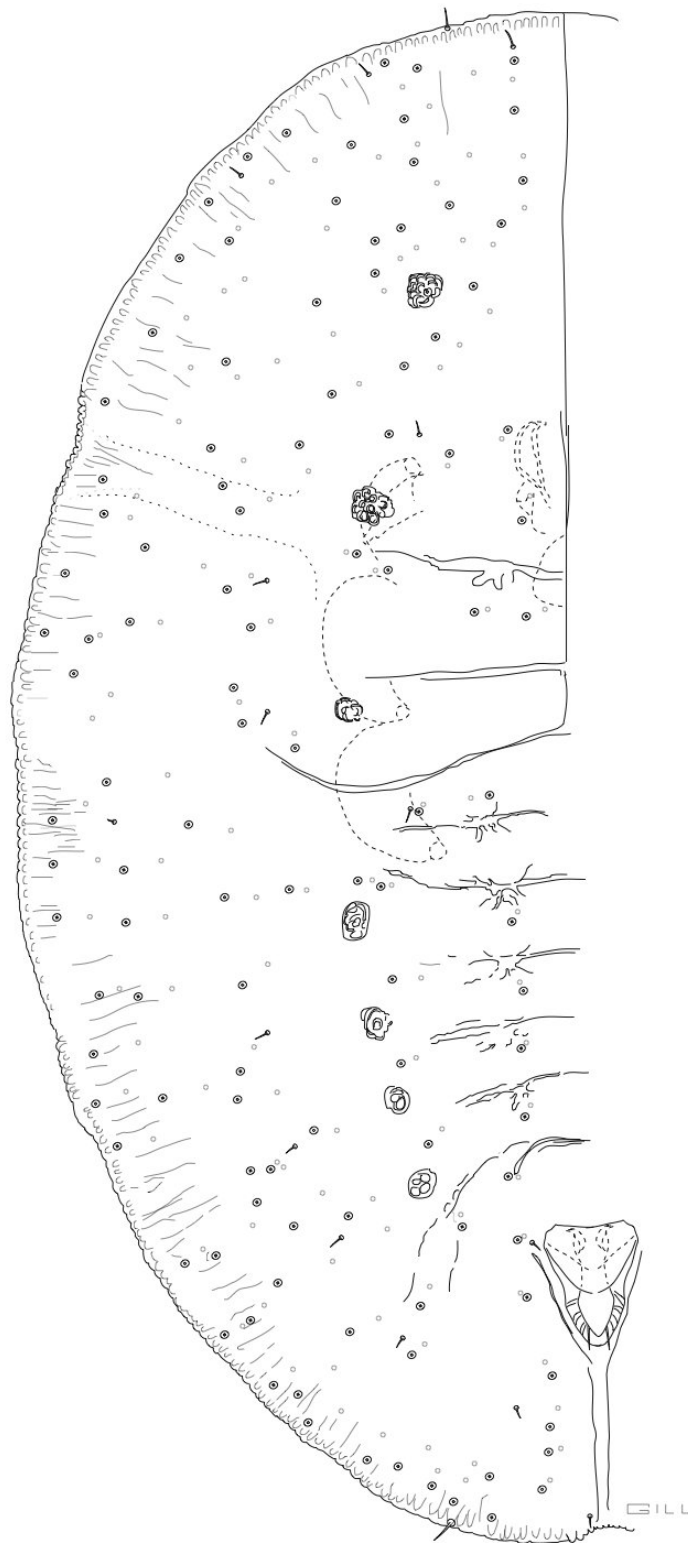


Figure 78. *Bemisia afer* complex, Madeira, Santana, Faja do Niguiera, 15-XII-92, ex. *Myrica toya*, F. Aguiar, coll.

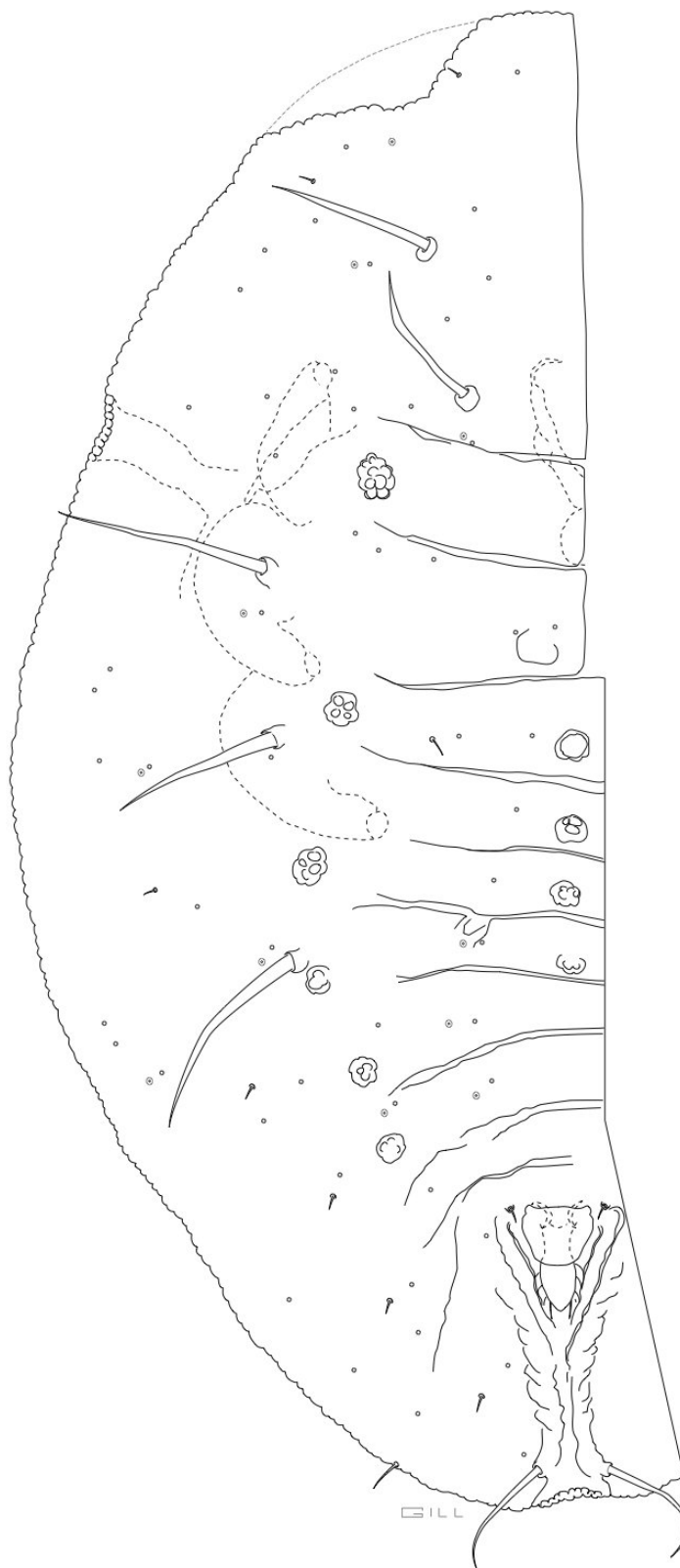


Figure 79. *Bemisia afer* complex, Madeira, Levada above Ribeiro Bonita, nr. Sao Jorge Icod de los Vinos, 01 Apr. 1995, ex. *Sibthorpia peregrina* (Scrophulariaceae), J. Martin and A. Aguiar, colls., JHM # 6590.

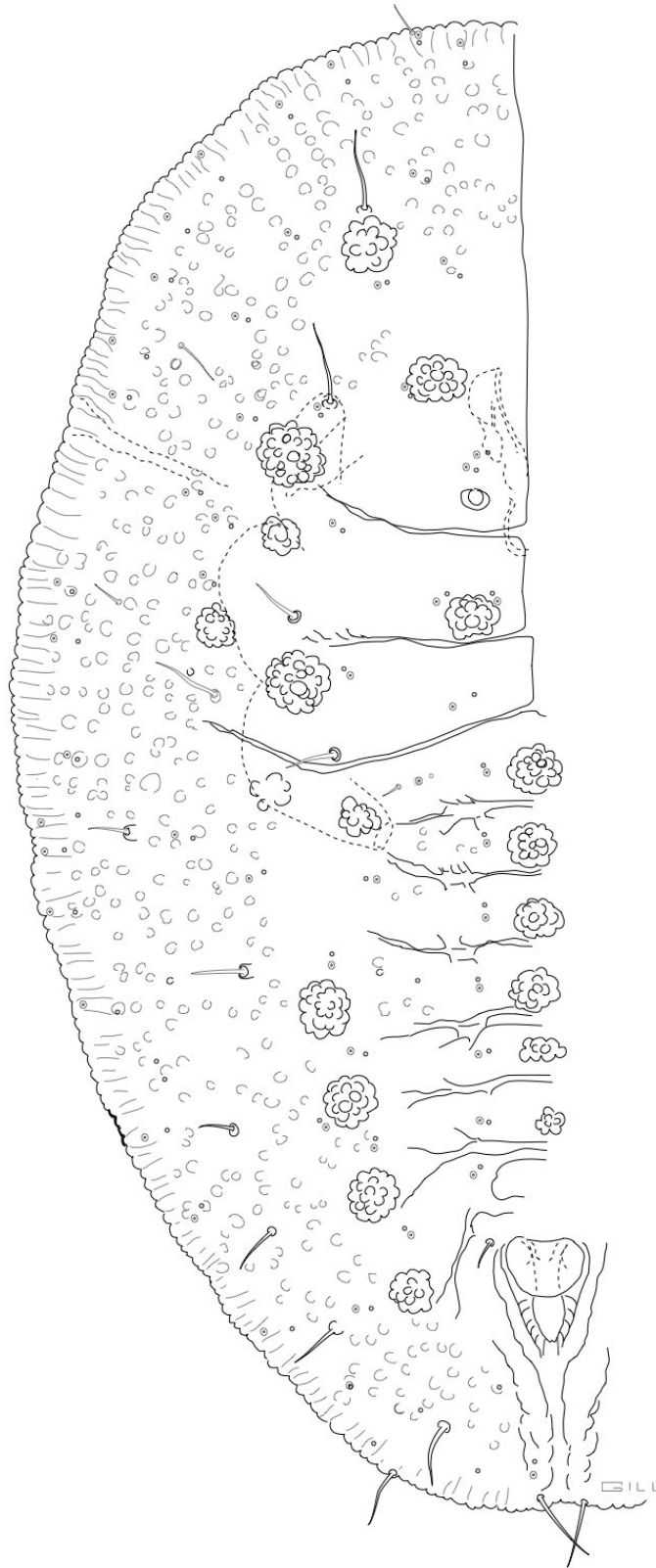


Figure 80. *Bemisia afer* complex, Madeira, Levada above Ribeiro Bonito, nr. Sao Jorge, 550 m, 01 Apr. 1996, ex. *Chamaespartium* sp.?, Leguminosae, Martin and Aguiar, colls., JHM #6583.

