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SOME BURROWING DIASPIDIDS FROM EASTERN ASIA (HOMOPTERA: COCCOIDEA)

By SADAO TAKAGI

Abstract

TAKAGI, S., 2003. Some burrowing diaspidids from eastern Asia (Homoptera: Coccoidea). *Ins. matsum. n. s.* 60: 67–173, 64 figs.

Twenty-five species of scale insects belonging to 18 genera, four tribes, and two subfamilies of the family Diaspididae from Malaysia, the Philippines, Singapore, and Japan are dealt with. Twenty-four species and 14 genera are described as new. The females of all the 25 species are cryptic on the plant body, burrowing into the epidermis of the bark or leaves, under the dense cover of trichomes on the lower surface of the leaves, or among the dense erect hairs on the twigs. Morphological modifications in the adult females are not uniform. Generally, the trullae are dentate or serrate and the dorsal ducts are few and slender. These tendencies are apparently associated with burrowing, but are not without exception. The marginal glanduliferous processes of the pygidium are much reduced in some species, but are well represented in others. Two species are highly advanced burrowing forms in view of the fact that the adult females form extraordinarily large burrows, in which the male crawlers with much shortened legs stay to complete their metamorphosis. One species is an unusual form of uncertain relationship, but the other shows little morphological modification except for the body shape as compared with non-burrowing related forms. Burrowing starts in the second-instar female, which is similar to the adult female especially in the pygidial appendages. In some species, the second-instar males also burrow, and they are homomorphic, being similar to the adult and second-instar females of the same species in the pygidial appendages. However, not all homomorphic second-instar males burrow. Heteromorphic forms of the second-instar male have been observed in seven species among the examined Diaspidini, and they are variable especially in the structure of the pygidial margin. Heteromorphism in the second-instar male could be due to atavism but, in their morphology, most of the heteromorphic forms observed in this study apparently reflect the change effected in the female in adaptation to burrowing.

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1. INTRODUCTION

The scale insect family Diaspididae is a large group of highly advanced forms in the superfamily Coccoidea. It is characterized, above all, by the formation of a 'scale' or a peculiar type of test, which covers each female and male. The test itself is made of both waxy secretions and anal excretions, but the exuvial casts of the first and second instars are incorporated into the female test and the cast of the first instar is attached to the male test. The female test is easily detachable from the insect body, and the male test also loosely covers the body. The main function of the test may be to create a microenvironment in the space it encloses. The male metamorphoses within the test through the second-instar nymph, prepupa, and pupa into the adult in a relatively short time, and the adult male is quite ephemeral after emerging from the test. The female lives much longer and, except in the pupillarial forms, continues to grow after moulting into the third instar or the adult stage, during which a greater part of the test is formed. The fully formed test of the female is thus much larger than that of the male and, in a great many species, also larger than the female body, and serves to cover deposited eggs and newly hatched nymphs. It is expected, therefore, that the persisting stage of the adult female is of central importance in the life history and evolution of this insect group. The pupillarial diaspidids adopt another mode of life: the second-instar female grows considerably, and the adult female stays within the large exuvial cast of that instar, does not grow, and lays eggs within the cast in a space produced as the ovipositing body shrinks. This mode of life, however, is of secondary significance in the evolution of the family, having appeared sporadically in various groups.

In the adult females and nymphal instars, some posterior segments of the abdomen are fused to form a pygidium, which, in most diaspidids, is equipped with various appendages on the margin—trullae (lobes), pectinae (plates), which may be glanduliferous or not, gland spines, and pore prominences. These appendages occur singly or in combination, and are various in number, size, and shape. Their functions are still not well known, but these structures probably originated and have evolved in association with test formation, primarily in the adult female. In fact, the adult females of the pupillarial diaspidids are no longer engaged in test formation, and their pygidial appendages are modified, deformed, reduced, or completely obsolete. Certain taxa (Odonaspidini, Smilacicolini, and some genera belonging to other tribes) inhabiting concealed sites on the plant body (e.g., spaces beneath stipules, leaf-sheaths, etc.) do form tests, but the adult females have either lost marginal appendages completely or nearly so. Apparently the marginal appendages are useless for test formation in such confined spaces.

Female tests are sometimes partly or entirely covered with a very thin epidermal layer of the host plant, though they are still visible on the surface of the plant body. In a good many species, the trullae are strongly sclerotized, broad, blade-like processes. Such trullae seem to be the only processes that can be used like a knife in peeling the upper layer of the plant epidermis when the insect body makes an oscillatory or rotative movement in forming the test. In other cases, the insects burrow so deeply into the epidermis of the bark or leaves, or under the dense cover of trichomes on the lower surface of the leaves, that their tests are concealed from view (unless the the epidermal layer covering the test is thin and translucent). The occurrence of a burrowing insect may be suggested by a slight swelling of the plant surface and, when the insect burrows on the lower surface of the leaf, also by a small discoloured spot on the upper surface corresponding to the feeding site. So far as is known, this burrowing mode of life is rather unusual, occurring sporadically in limited groups of the family. In my preliminary approach to the function of the trullae, I examined several species that burrow under the tomentose or scaly cover of the leaves (Takagi, 1990: Fig. 1.1.2.1.11). These species belong to different genera, but they are similar in having serrate and prominent trullae, which suggest a circular saw. Thus, they indicate the role of the trullae as a sawing implement during burrowing. In the present study, I have examined further examples of burrowing diaspidids on purpose to see how their structure has been modified in association with burrowing. Another species occurring among the dense erect hairs on the twigs of the host plant is also included. Its habit may not exactly correspond to burrowing, but it possesses serrate trullae as in most of the burrowing forms observed in this study.

Authors have not been unanimous in the higher classification of the Diaspididae. In my previous paper (Takagi, 2002), I summarized my view about major groups of diaspidids based on the pygidial appendages. I recognized two subfamilies, the Diaspidinae and the Aspidiotinae, for the forms with appendages and, in each subfamily, three major levels, Level I–III, in the evolution of appendages. Level III comprises advanced forms in each subfamily. These forms, making up the bulk of the family, differ from the more primitive forms belonging to Level I and II in making oscillatory or rotative movements when forming their tests, especially at the adult female stage. Because burrowing requires a considerable amount of movement, it is expected that the burrowing mode of life arises among the forms of Level III.

2. DESCRIPTIONS

In the following descriptions, the diagnostic characters of the new genera and species are given mainly or exclusively on the basis of the adult females. Nymphal forms are not formally described, but are illustrated especially for the type species of some new genera. The terms 'trullae' and 'pectinae' are used in place of 'lobes' and 'plates' of other authors, because the meanings of the latter two terms are too broad and general to designate particular features. The term 'megaducts' is used in describing lepidosaphidines [2.10]. The term 'nymph' is adopted instead of 'larva' in accordance with some recent authors in Coccoidea. The abbreviations 'abd I–IX' stand for the first to ninth abdominal segments.

Depositories of the holotypes. FRIM: Entomology Unit, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia; UPLB: Museum of Natural History, University of the Philippines at Los Baños, Laguna, the Philippines; SEHU: Systematic Entomology Laboratory, Graduate School of Agriculture, Hokkaidô University, Sapporo, Japan.

2.1. *Damaia*, gen. nov.

Type species. *Damaia swintoniae*, sp. nov.

The adult female (Fig. 1) is diagnosed by the presence of a broadly flat frontal margin, slender dorsal ducts, three pairs of well-developed trullae, and narrowly rectangular gland spines between the trullae. These gland spines are quite unique, being of the same thickness throughout, with the apex truncated. The lateral trullae are bilobulate, with the outer lobule much smaller than the inner lobule. The median trullae and the inner lobules of the lateral trullae are dentate and nearly of the same size, and each of them is provided with a pair of slender scleroses arising from the basal corners. There are three long ducts, filiform or nearly so, arising from the margin on each side of the pygidium, thus representing marginal macroducts. Other dorsal ducts are small and slender, scattered rather than arranged in segmental rows. There are some small ducts of the usual two-barred type laterally on the thorax and the base of the abdomen. The pygidium is delimited by the intersegmental furrow between abd IV and V on the dorsal surface, but on the margin it appears to be defined by the notch between abd III and IV.

The first-instar nymph has a single terminal antennal seta, no strong ventral seta on the tarsus, and no ventral submedian setae on the prepygidial abdomen (Fig. 3). The second-instar male exhibits a heteromorphic character pattern (Fig. 2). These nymphal stages show that the genus definitely belongs to the tribe Diaspidini. However, they also display characters unusual in the tribe. The first instar has many eminent tubercles along the body margin. The second-instar male possesses narrowly rectangular gland spines. These gland spines are similar to those occurring between the trullae on the adult female, but they are different from the latter in having the associated duct remarkably enlarged. In addition, they occur not only on the pygidium but also on the prepygidial abdomen. The second-instar male is also remarkable in having many well-developed pectinae. In this character it reminds me of the second-instar male of *Nikkoaspis berincangensis* Takagi. In the female characters, however, *Damaia* has no relationship to *Nikkoaspis,* which belongs to the subtribe Kuwanaspidina, tribe Diaspidini. So far as I am aware, the new genus has no closely related forms in the Diaspidini. Based on the general character pattern of the second-instar male, and especially on its modified macroducts, the genus may tentatively be referred to the subtribe Chionaspidina.

Hypaspidiotus jordani (Kuwana), a member of the subfamily Aspidiotinae, is very similar to *Damaia swintoniae* in having three pairs of well-developed dentate trullae. It burrows under the vestiture on the lower surface of the leaves of *Castanopsis cuspidata* in Japan. Though belonging to the different subfamilies, these two species may represent a particular type of the pygidial fringe adapted to burrowing.

2.1.1. *Damaia swintoniae*, sp. nov. (Figs 1–3)

Material examined. Collected at Santubong (Damai Beach), Kuching District, Sarawak (Borneo Is.), Malaysia, on *Swintonia glauca* (Anacardiaceae), Oct. 1991 [material 91ML-232, -247, -277]. Females and males occurring on the lower surface of the leaves. Females burrowing under a thin epidermal layer of the leaf; tests visible through the epidermal layer, elongate, moderately expanded posteriorly, and dark brown. Males not burrowing; tests white, felted, and tricarinate. The description of the adult female is based on 27 specimens.

Holotype. Adult female, mounted from 91ML-247; deposited in FRIM.

Diagnosis (adult female: Fig. 1). Body elongate, broadly flat on the frontal margin, gradually broadening towards abd III, then narrowing on the pygidium; metathorax and abd I–III weakly lobed laterally; pygidium nearly obdeltate in outline. Prepygidial derm membranous; dorsal surface of the pygidium broadly sclerotic, with the intersegmental furrow between abd V and VI modified to form transverse slender scleroses across the sub-basal area; ventral surface of the pygidium sclerotized over a large apical area. Antennae situated on the frontal margin, separated from each other by a space as wide as the frame of the mouth-parts, each with a curved seta. Anterior spiracles each with 1 trilocular disc pore, at times with 2. Perivulvar disc pores in 5 groups, 2–5 in the median group, 4–7 in each anterolateral, and 3 or 4 in each posterolateral group. Anus small, much closer to the base than to the apex of the pygidium. Trullae well represented in 3 pairs; median trullae roughly dentate, separated from each other by a narrow space; second and third trullae bilobulate, the inner lobule similar to the median trulla in shape and size, the outer lobule very small and conical; median trullae and the inner lobules of the lateral trullae each basally with a pair of slender scleroses arising at the basal corners and converging anteriorly; a sclerotized patch of derm also associated with the base of each trulla. A strongly sclerotized marginal process present on the posterior angle of abd V, much smaller than the median to third trullae, angular, and often irregularly notched, followed by another process tending to be smaller and less sclerotized. Small macroducts scattered laterally on the metathorax and abd I, at times also on the mesothorax and abd II, few on each segment; other dorsal ducts slender, scattered rather than arranged on abd I–VI; 3 long slender ducts arising from the margin on each side of the pygidium, probably belonging to abd V–VII, the mesal two longer than the lateralmost and often filiform. Gland spines occurring on the abdominal segments marginally: 1–3 on each of abd I and II (usually 2 or 3 on I and 1 or 2 on II) and 1 on each of III–VIII and also between the median trullae (abd IX), those occurring on VII–IX peculiar in shape, being narrowly rectangular, with the apex truncated and as broad as the base.

Second-instar male (Fig. 2) heteromorphic, with narrowly rectangular gland spines and many well-developed pectinae [2.1; 3.4]. First-instar nymph (Fig. 3) with prominent tubercles on the body margin and strong marginal setae on the head and thorax but, in other features, characterized as in many other Diaspidini [2.1].

Remarks. The mesal two pairs of slender marginal ducts of the pygidium appear to arise at the inner bases of the second and third trullae, but it is not easy to observe their orifices. (The orifice of the lateralmost marginal duct is sclerotized and easily observable.) The narrow-rectangular gland spines occurring between the trullae are membranous and also difficult to observe even on well-stained specimens.

2.2. *Semonggokia*, gen. nov.

Type species. *Semonggokia xylopiae*, sp. nov.

The body of the full-grown adult female (Figs 4 and 5) is sclerotized throughout, with distinct intersegmental furrows. The pygidium is well defined by the intersegmental furrow between abd IV and V on the dorsal surface but, on the margin, the posterior half of abd IV including the marginal macroduct forms part of the pygidium. This genus is apparently referable to the tribe Diaspidini, but no macroducts of the type usual in the tribe have been found. Instead, slender dorsal ducts, a little larger than the ventral microducts, are present on the prepygidial segments. There are single slender dorsal ducts arising from the pygidial margin, representing marginal ducts. Three pairs of trullae are well developed but, in spite of this, the lateral trullae show no trace of outer lobules, which may be obsolete. The median trullae are set close together, but are not zygotic, and there are no setae between them. The median and lateral trullae have a long slanting outer margin, which is minutely serrate. A pore prominence is situated just mesad of the third trulla, and it is also serrate. The margin of abd V is sclerotized and minutely serrate for most part, and abd IV is also serrate or dentate on the posterolateral angle. The pygidial margin, thus, is largely composed of serrations, which are interrupted by relatively narrow spaces each bearing a small gland spine.

This genus is similar to *Mauritiaspis* Mamet described from Mauritius, and especially to *M. malloti* Mamet, the type species of *Mauritiasps*, in possessing minutely serrate trullae and pygidial margin. On *Semonggokia*, however, the second and third trullae are unilobed, the outer lobules being considered to be obsolete, whereas on *Mauritiaspis* both of these trullae are bilobulate. On *Semonggokia*, the antennae are unisetose, whereas on *Mauritiaspis* they are multisetose, with four or five stout setae. In diaspidids, in general, such a difference in the antennae suggests a remote relationship and, therefore, the resemblance between the two genera may be due to convergence in association with their cryptic modes of life. *Semonggokia* burrows into the epidermis of the leaves, whereas *Mauritiaspis* induces a leaf gall.

This genus, therefore, may have no closely related forms. It is referable to the subtribe Chionaspidina, because the second-instar male possesses modified ducts of the type common to many species of that subtribe (Fig. 6).

2.2.1. *Semonggokia xylopiae*, sp. nov. (Figs 4–6)

Material examined. Collected at Semonggok, Kuching District, Sarawak (Borneo Is.), Malaysia, on *Xylopia ferruginea* var. *oxyantha* (Annonaceae), Oct. 1991 [material 91ML-23]. Femlaes occurring on the lower surface of the leaves, burrowing into the epidermis. The presence of a burrowing female is suggested by a slight swelling of the epidermis. Males occur on the upper surface of the leaves, sitting in the sunken midrib, and sometimes also on the lower surface; tests white, with or without an amorphous mass of fluffy wax. The description of the adult female is based on 30 specimens.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Figs 4 and 5, A). At full growth, body narrowly obovoid, sclerotic throughout, with the free segments demarcated by strongly sclerotized intersegmental furrows; dorsally the meso- and metathorax and abd I–IV subequal in size and shape, similar in the arrangement of the ducts and the pattern of sclerotization, and little or only gently lobed laterally; pygidium nearly obdeltate, a little roundish marginally. Dorsal derm with particularly sclerotized patches on the cephaloprothorax and pygidium, and submarginally on the meso- and metathorax and abd I–V; intersegmental furrow between abd V and VI forming sub-basal scleroses on the pygidium. Antennae situated on the sclerotized frontal margin, separated from each other by a space as wide as the frame of the mouth-parts, each with a short seta. Anterior spiracles each with a small group of trilocular disc pores [see Remarks]. Perivulvar disc pores in 5 groups, 3–10 in the median group (mean 4.9, sample size 30), 10–18 in each anterolateral (mean 13.8, sample size 60), and 11–23 in each posterolateral group (mean 14.9, sample size 60). Anus small, somewhat nearer to the base than to the apex of the pygidium, nearly superimposed on the vulva. Median trullae set close together, but not united, with the outer margin much longer than the inner, slanting and minutely serrate. Second trullae each represented by a unilobed serrate process similar to the median trulla in shape but smaller. Third trullae each represented by a minutely serrate broad process, accompanied with a serrate pore prominence mesally. Each trulla with a pair of slender scleroses arising at the basal corners and converging anteriorly. Margin of abd V sclerotized and minutely serrate for most part, the serrate margin being divided halfway by a notch. Abd IV with a wide serrate or dentate process at the posterolateral angle. Marginal ducts slender: 1 arising at the mesal base of the second trulla, with no pore prominence; 1 associated with a pore prominence mesally to the third trulla; 1 in the posterolateral angle of abd V and IV each; a few similar ducts scattered submarginally in the basal corner of the pygidium. Slender dorsal ducts, a little smaller than the marginal ducts, scattered rather than arranged across the submedian and submarginal areas on the meso- and metathorax and abd I–IV. Gland spines absent in the prepygidial region and between the median trullae; 4 small gland spines on each side of the pygidium, belonging to abd V–VIII, each situated in a non-serrate space on the margin.

Second-instar female (Fig. 5, B) with 3 pairs of well-developed serrate trullae and slender marginal macroducts as in the adult female. Second-instar male (Fig. 6) heteromorphic, with many pectina-like processes and a good number of modified ducts along the pygidial margin [3.4].

Remarks. It was not easy to count spiracular disc pores owing to the presence of a sclerotized fold of derm surrounding them. The largest number of pores counted was seven. The second and third trullae are unilobed despite this species undoubtedly belonging to the Diaspidinae. The view adopted here is that their outer lobules are not fused with the inner but are obsolete. This supposition is based on the relative positions of the lateral trullae to the marginal setae of abd VI and VII and also on the presence of slender scleroses arising from the inner and outer bases of each trulla.

2.3. *Chionandaspis*, gen. nov.

Type species. *Chionandaspis ramicola*, sp. nov. The type species occurs on the twigs of the host plant. Two other species associated with the leaves of their host plants are referred to the genus.

The adult females of this genus (Figs 7, 10, and 12) are very similar to *Andaspis* MacGillivray, tribe Lepidosaphidini, in the configuration of the pygidial apex [for the state in *Andaspis*, see 2.11]. The median trullae are set close together but not united, with the outer margin much longer, slanting, and serrate. The second trullae are much smaller than the median trullae, with the inner lobule alone well represented; the third trullae are obsolete. There is a small, slender sclerosis shaped like an inverted U between the inner bases of the median trullae. Each median trulla bears a pair of well-developed scleroses arising from the inner and outer basal corners, and these scleroses are reniform, clavate, or mushroom-shaped. The second trullae also bear a pair of well-developed scleroses or a short sclerosis basally. The marginal macroducts of the pygidium are slender; similar ducts occur along the posterior borders of abd III and IV. Gland spines occur on the apices of the lateral lobes of some prepygidial segments and on the margin of the pygidium except between the median trullae. The pygidium is delimited by the intersegmental furrow between abd IV and V on the dorsal surface but, on the margin, it is defined by the notch between abd III and IV.

The first instar nymph of the type species (Fig. 9) has a single terminal antennal seta, no prominent ventral seta on the tarsus, and no submedian ventral setae on the prepygidial abdomen. The second instar males of the type species (Fig. 8) and *Chionandaspis foliicola* (Fig. 11) exhibit heteromorphic character patterns with modified ducts of the type usually observed in Chionaspidina. Based on these nymphal forms, this genus is referable to the tribe Diaspidini and probably to the subtribe Chionaspidina.

Some pygidial characters of this genus are similar to those of *Mimusaspis* Mamet occurring in Mauritius. The resemblance is especially remarkable between *M. mimusopis* Mamet, the type species of *Mimusaspis*, and the two leaf-associated species of *Chionandaspis*, *C. foliicola* and *C. palawanensis*, all of which have a peculiar pygidium produced so abruptly in the apical area as to appear excavated subapically. *Mimusaspis* differs from *Chionandaspis* especially in having multisetose antennae, non-serrate median trullae (based on the figures accompanying Mamet's descriptions), and a very long clavate sclerosis arising from the middle base of each median trulla. Furthermore, species of *Mimusaspis* apparently do not burrow. Originally, the type species of *Mimusaspis* was described as a member of *Lepidosaphes* and the genus was supposed to be somewhat related to *Andaspis*, but the descriptions and figures of the adult females of both the type species and another species (*M. badulae* Mamet) (Mamet, 1939; 1942; 1943) afford no good evidence that the genus belongs to the tribe Lepidosaphidini.

2.3.1. *Chionandaspis ramicola*, sp. nov. (Figs 7–9)

Material examined. Collected at Santubong (Damai Beach), Kuching District, Sarawak (Borneo Is.), Malaysia, on *Swintonia glauca* (Anacardiaceae), Oct. 1991 [material 91ML-52]. Females burrowing into the epidermis of the twigs. Males occurring mainly on the upper surface of the leaves; a few tests were found on the lower surface of the leaves and on the twigs; tests white, made of fluffy wax. The description of the adult female is based on 30 specimens.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Fig. 7). Body elongate, stout; cephaloprothorax with a pair of small marginal protuberances a little anterior to the anterior spiracles; meso- and metathorax and abd I–III lobed laterally, especially metathorax and abd I and II strongly produced to form digitiform processes; pygidium broad, obdeltate. Prepygidial derm membranous; a submarginal boss present dorsally on abd I. Dorsal intersegmental furrow between abd V and VI forming slender transverse scleroses across the sub-basal area of the pygidium; ventral surface of pygidium sclerotized towards the apex. Antennae on or within the frontal margin, separated from each other by a space much narrower than the frame of the mouth-parts, each with a short seta. Anterior spiracles each with 3–8 trilocular disc pores forming a compact arched group. Perivulvar disc pores in 5 groups, 2–5 (usually 4) in the median group, 11–22 in each anterolateral (mean 15.7, sample size 60), and 13–22 in each posterolateral group (mean 17.2, sample size 60), the last group being an irregularly double or sometimes partly triple longitudinal row. Anus small, posterior to the level of the vulva. Median trullae set close together, but not united, with a small sclerosis shaped like an inverted U between the inner bases, with no setae or gland spines between them; with the outer margin much longer than the inner margin, slanting, and serrate; each with a reniform sclerosis connected to the inner basal corner through a slender stalk, and with a mushroom-shaped sclerosis, also slender-stalked, arising from the outer basal corner. Second trullae with the inner lobule much smaller than the median trulla, oblong, sclerotized, notched apically, and with the outer lobule represented by a small membranous conical process; inner lobule with a slender-stalked, mushroom-shaped sclerosis arising from the inner basal corner and a rod-like sclerosis arising from the outer corner. Third and fourth trullae represented by sclerotized serrations of the pygidial margin. Macroducts slender, but not filiform; marginal ducts on abd II–VIII: 1 on II, opening in a small sclerotized tubercle at the apex of the lateral lobe; 2 on each of III–VII, the posterior or mesal duct on each segment associated with a sclerotized pore prominence; 1 on VIII, associated with a small pointed membranous prominence united with the gland spine occurring just laterally to the median trulla; submarginal ducts on abd III–V: 3–6 on III in a short row, 1 or 2 (usually 1) on each of IV and V. Gland spines occurring marginally on abd II–VIII: 3 or 4 on the apex of the lateral lobe of II, 3–5 on III, and 3 or 4 (usually 3) on IV; 1 on each of V–VIII; those on II–IV well developed, annulate on the basal half.

Second-instar male (Fig. 8) heteromorphic; pygidium with a pair of broad membranous processes apically, fringed with spinous processes or serrations [2.3; 3.4]. First-instar nymph (Fig. 9) with main features as in many other Diaspidini [2.3].

2.3.2. *Chionandaspis foliicola*, sp. nov. (Figs 10 and 11)

Material examined. Collected at Santubong (Damai Beach), Kuching District, Sarawak (Borneo Is.), Malaysia, on *Swintonia glauca* (Anacardiaceae), Oct. 1991 [material 91ML-277]. Females occurring on the upper surface of the leaves, burrowing under a thin epidermal layer; tests thin and white, looking pale brownish through the epidermal layer. Males occurring on the lower surface of the leaves; tests white, made of fluffy wax. The material includes *Damaia swintoniae* [2.1.1], of which the females and males occur on the lower surface of the leaves together with males of *Chionandaspis foliicola*. Description of the adult female is based on 30 specimens.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Fig. 10). Body elongate; meso- and metathoarx and abd I–III lobed laterally, metathorax and abd I and II being especially strongly produced; pygidium obdeltate, produced apically so abruptly as to appear excavated subapically. Prepygidial derm membranous; a submarginal dorsal boss present on abd I; ventral surface of the pygidium sclerotized in a narrow area anterior to the median trullae. Antennae situated on or just within the frontal margin, separated from each other by a space as wide as the frame of the mouth-parts, each with a short seta. Anterior spiracles each with 1–3 (usually 2) trilocular disc pores. Perivulvar disc pores in 5 groups, each of the antero- and posterolateral groups forming an elongate, single or double, or partly triple, row; 2–5 (usually 4) in the median group, 7–12 in each anterolateral (mean 9.8, sample size 60), and 9–18 in each posterolateral group (mean 14.0, sample size 60). Anus small, as large as a perivulvar disc pore, situated much posteriorly to the level of the vulva. Median trullae set close together, but not united, with a very short inner margin and a long outer margin, which is oblique, nearly straight, and minutely serrate; the space between their inner bases with a slender sclerosis bifurcate in the posterior third; each median trulla with a pair of rod-like scleroses, the outer sclerosis tending to be clavate. Second trullae represented by the inner lobule alone, small but sclerotized, basally with a short sclerosis. Abd V and VI with the margin narrowly sclerotized and often bearing a few denticles. Marginal macroducts of the pygidium very long, but not filiform, 1 between the median and second trullae, opening in a small membranous pore prominence, which is united with the gland spine occurring just laterally to the median trulla; 2 on each of abd V and VI, the inner duct on each segment associated with a slight pore prominence. Long dorsal macroducts, somewhat shorter than the marginal macroducts, occurring on abd III and IV along the posterior borders of the segments: 5–10 (usually 8) forming a submarginal row and 3–5 (usually 4) forming a submedian row on III; 2–8 (mean 5.7, sample size 60) in a submarginal row on IV. A group of microducts submedially on the ventral surface of the supposed abd IV. Small ducts occurring on the apex of the lateral lobes of the meso- and metathorax and abd I and II: 3–7 on the mesothorax, 3–5 on each of the metathorax and abd I, and 1–3 on II. Gland spines occurring on the meso- and metathorax and abd I–VIII: 1–3 small gland spines on the mesothorax within the apex of the lateral lobe; occurring marginally on more posterior segments, 2–5 on the metathorax, 3–5 on each of abd I and II, 2–5 on III, 1 or 2 on IV, and 1 on each of V–VIII.

Second-instar male (Fig. 11) heteromorphic, differing from that of *Chionandaspis ramicola* (Fig. 8) mainly in having more ducts on the dorsal surface along the pygidial margin [2.3; 3.4].

Remarks. *Chionandaspis foliicola* differs remarkably from *Chionandaspis ramicola* in the shape of the pygidium, which is excavated subapically, but it does resemble the latter species in the details of the pygidial apex and the dorsal macroducts. These species are also very similar in the second-instar males (Figs 8 and 11). They were collected at the same locality on the same plant species, the females occurring on the leaves and twigs, respectively. This fact could suggest the possibility that they are ecophenotypic forms of the same species. However, the second-instar males of the two forms do not exactly agree in the distribution pattern of ducts along the abdominal margin despite their common association with the leaves. I therefore have no doubt that *C. foliicola* is a distinct species.

2.3.3. *Chionandaspis palawanensis*, sp. nov. (Fig. 12)

Material examined. Collected at Brooke's Point (Maasin Forest), Palawan, the Philippines, on *Antiaris toxicaria* (Moraceae), Aug. 1993 [material 93PL-138]. Females occurring on the lower surface of the leaves, mostly on the midrib, burrowing under a thin translucent epidermal layer. No male tests were found. It seems that the material, when collected, included no living insect. More than ten specimens of the adult female have been mounted from the material, but none of them is in good condition. Two of them, though not entirely favourable for study and illustration, have been selected for preparing the description and figure.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 12). Very similar to *Chionandaspis foliicola*, but distinguishable by the following characters: anus distinctly larger than a perivulvar disc pore, and situated at the level of the vulva; submedian microducts occurring on the ventral surface of abd IV enlarged, somewhat smaller than the dorsal macroducts of the segment. The following characters should also be given on the basis of some specimens—anterior spiracular disc pores: 2 or 3; perivulvar disc pores: 4 or 5 in the median group, 10–13 in each anterolateral, and 12–15 in each posterolateral group; dorsal macroducts: 7–9 submarginals and 6–8 submedians on abd III, and 3 or 4 submarginals on IV; enlarged submedian microducts on the ventral surface of abd IV: 7–11.

Remarks. I have been puzzled how to treat this form, which is very close to *Chionandaspis foliicola*. However, it differs noticeably from the latter in the larger size of the anus, which is situated about the centre of the pygidium. Because, in diaspidid species in general, the size and position of the anus are fairly stable, I am much inclined to the view that this form represents a distinct species. Furthermore, *C. palawanensis* occurs on the lower surface of the leaves, whereas *C. foliicola* was found on the upper surface.

2.4. *Pinangaspis*, gen. nov.

Type species. *Pinangaspis uniclavata*, sp. nov.

This genus is referable to the subtribe Chionaspidina, tribe Diaspidini, based on the second-instar male (Fig. 14), which has modified ducts of the type usually observed in that subtribe. However, the adult female is so greatly modified that the relationship of the genus to other Chionaspidina is uncertain. The median trullae are set close together and parallel, and their inner bases are united by a robust mushroom-shaped sclerosis. The second and third trullae are well developed but unilobed, with no scleroses on their bases. The dorsal surface is devoid of the usual macroducts. Instead, there are small two-barred lateral ducts in the prepygidial region, groups of filiform submarginal ducts on some posterior abdominal segments, and single filiform marginal ducts on the pygidium. Tubercular gland spines occur mainly on the lateral lobes of the free abdominal segments, each with a long, filamentous apical extension. The pygidium is delimited by the intersegmental furrow between abd IV and V on the dorsal surface, but on the margin it appears to include part of abd IV.

2.4.1. *Pinangaspis uniclavata*, sp. nov. (Figs 13 and 14)

Material examined. Collected at Bukit Cendana, Pulau Pinang [Penang Is.], Malaya, Malaysia, on *Fissistigma* sp. (Annonaceae), Nov. 1991 [material 91ML-496]. Females and males occurring on the lower surface of the leaves. Females burrowing, the tests appearing dark brown through the epidermis. Males not burrowing; tests white, obscurely tricarinate. Some 10 specimens of the adult female have been examined.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Fig. 13). Body broadly fusiform; free segments gently lobed laterally; pygidium obdeltate. Prepygidial derm membranous. Pygidium broadly sclerotic on the dorsal surface, the dorsal intersegmental furrow between abd V and VI forming a linear sclerosis across the sub-basal area; ventral surface widely sclerotized towards the apex. Antennae situated on or just within the frontal margin, separated from each other by a space narrower than the frame of the mouth-parts, each with a long seta. Anterior spiracles each with 1 or 2 trilocular disc pores, at times with none. Perivulvar disc pores few, 1–5 irregularly spaced in a transverse row at the level of the anus. Anus sub-basal. Median trullae set close together, the inner bases united by a robust mushroom-shaped sclerosis; each trulla nearly triangular, blunt apically, usually notched once on the inner side and once or twice on the outer, basally with a pair of short scleroses. Second trullae with the inner lobule alone developed, much smaller than the median trulla, conical, and sclerotized. Third trullae each represented by a sclerotized process, which is larger than the second trulla, rounded apically, and notched once on the slanting outer margin. Marginal macroducts represented by 2 long filiform ducts on each side of the pygidium, occurring at the inner bases of the second and third trullae. Similar dorsal ducts occur in the posterolateral corners of abd III–V: 1–5 on III, 6–9 on IV in a loose cluster, and 3–5 on V in an oblique row. Small lateral ducts on abd I–III, variable in number but generally few. Tubercular gland spines, each with a long filamentous apical extension, occurring laterally on the metathorax and abd I–V: 1 on the metathorax, about 1–5 on each of I and II, usually 3 on each of III and IV, and 1 on V. Three marginal gland spines on each side of the pygidium: 1 laterally to each trulla.

Second-instar male (Fig. 14) heteromorphic, with poorly developed marginal processes on the pygidium [2.4; 3.4].

2.5. *Pinnaspis* Cockerell

This genus belongs to the subtribe Chionaspidina, tribe Diaspidini. Nearly 40 species have been known in this genus, mostly occurring in tropical to warm-temperate Asia. However, some difficulties lie in identifying several species, which may include other species (Williams and Watson, 1988). Some species may occasionally occur in bark crevices but, so far as I am aware, the known species of the genus are not cryptic in habit. The females of the two species described below burrow under the leaf tomentum, and possess enlarged and finely serrate median trullae. On one of them all the marginal macroducts occurring on the pygidium are single. In other features these species are very similar to other species of *Pinnaspis*, and there seems to be no good reason to exclude them from the genus.

According to the description, *Pinnaspis megaloba* Takahashi possesses relatively large median trullae for a member of the genus, but it does not burrow. It is peculiar in the shape of the median trullae and in having eight groups of perivulvar disc pores. In my view, it should be placed in another genus.

2.5.1. *Pinnaspis serrulata*, sp. nov. (Figs 15 and 16)

Material examined. Collected at Mariveles, Bataan, Luzón, the Philippines, on *Pterospermum celebicum* (Sterculiaceae), Aug. 1994 [material 94PL-108]. Females and males occur on the lower surface of the leaves. Females burrowing under the tomentum, the presence of a female being suggested by a slight swelling on the tomentum; tests white. Males occurring on the surface of the tomentum; tests white, tricarinate. The description of the adult female is based on 35 specimens.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 15). Body elongate, somewhat fusiform, at times (when the female has failed to copulate?) becoming very long owing to the elongation of the meso- and metathorax; free abdominal segments weakly lobed laterally; pygidium obdeltate. Prepygidial derm membranous; abd I with a submarginal dorsal boss; pygidium sclerotic on the dorsal surface, with a pair of slender scleroses (preanal scleroses) in the median subbasal area, the ventral surface sclerotized towards the apex. Antennae separated from each other by a space a little narrower than the frame of the mouth-parts, each with a long seta. Anterior spiracles each with 1–5 (usually 2 or 3) trilocular disc pores; posterior spiracle usually with 1 disc pore, rarely with 2 or none. Perivulvar disc pores in 5 groups: 1–4 (usually 2 or 3) in the median group, 2–8 in each anterolateral (mean 5.5, sample size 70), and 2–9 in each posterolateral group (mean 6.3, sample size 70). Anus situated anteriorly to the centre of the pygidium. Median trullae relatively large, closely appressed together along their entire mesal margins, confluent through an elongate sclerosis arising at their inner bases, roundish on their free margins, which are minutely serrate. Second trullae with the inner and outer lobules each represented by a very small sclerotized process. Marginal macroducts: 1 mesally to the second trulla (on abd VII), opening in a membranous pore prominence; 2 on VI, the inner one associated with a sclerotized pore prominence; 2 on V, the inner one associated with a sclerotized pore prominence, the outer tending to be removed from the margin; IV with 1 or 2 macroducts in the posterolateral corner of the segment. Lateral macroducts present in prepygidial abdominal segments: 0–3 (usually 1 or 2) on abd I; 0–2 (usually 1 or 2) on II; usually 2 or 3 on III, one of them occurring in the posterolateral corner of the segment and distinctly larger than the other lateral macroducts. Marginal gland spines well represented on the pygidium, 1 on each of abd V–VIII, the one occurring on VIII (just laterally to the median trulla) smaller and united with the pore prominence belonging to VII. Lateral gland spines present on abd II–IV, diminishing in size anteriorly: 1 or 2 on abd II, usually 2 (rarely 1) on III, and 2 (at times 3) on IV.

Second-instar male (Fig. 16) peculiar in having a series of prominent angular lobes along the pygidial margin [3.4].

2.5.2. *Pinnaspis simplior*, sp. nov. (Fig. 17)

Material examined. Collected at Banao, Guinobatan, Albay, Luzón, the Philippines, on *Pterospermum celebicum* (Sterculiaceae), Nov. 1992 [material 92PL-37]. Females occurring on the lower surface of the leaves, burrowing under the tomentum, the presence of a female being suggested by a slight swelling on the tomentum; tests white. No male tests found on the leaves. The description of the adult female is based on 30 specimens.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 17). Similar to *Pinnaspis serrulata* [2.5.1] especially in having enlarged serrate median trullae, but differing in having a single marginal macroduct on each of abd V and VI as well as on abd VII. Anterior spiracles each with 1–3 (usually 1 or 2) trilocular disc pores; posterior spiracles without disc pore. Perivulvar disc pores: 4 (at times 2 or 3) in the median group, 5–9 in each anterolateral (mean 7.3, sample size 60), and 6–11 in each posterolateral group (mean 7.7, sample size 60). Preanal scleroses absent. Median trullae larger and their free margins more roundish than in *P. serrulata*. Abd IV with 2 or 3 macroducts in the posterolateral corner, one of them being situated on the margin. Lateral macroducts on abd I–III: a few very small ducts on I, hardly distinguishable from microducts, which are sometimes present on the segment; 2 or 3 on II; usually 3 on III, one of them situated on the posterior border of the segment and larger than the other lateral macroducts. Abd II without gland spines on the lateral lobe; III often with 1; IV with 2 (at times 1 or 3). In other characters, nearly as on *P. serrulata*.

Remarks. On this species, all the marginal macroducts of the pygidium are single. As compared with *Pinnaspis serrulata*, however, there is no other particular character worthy of generic separation [also see 3.1]. Two further adult female specimens of *Pinnaspis* were collected at Sepilok, Sabah, Malaysia, on *Pterospermum* sp. in association with *Bayuraspis javanensis* (=*Metandaspis javanensis* Williams) [for the latter species, see 2.14.1]. They are very similar to the specimens from Albay. They are, however, not good in condition, and are not definitely identifiable with *Pinnaspis simplior*.

2.6. *Mayonia*, gen. nov.

Type species. *Mayonia callicarpae*, sp. nov.

This genus is referable to the tribe Diaspidini and the subtribe Fioriniina, which should include not only *Fiorinia* Targioni-Tozzetti and other pupillarial genera but also many non-pupillarial ones. The non-pupillarial *Pseudaulacaspis* MacGillivray, for example, may afford the biological nucleus for the concept of the subtribe, in which the pupillarial genera should represent modified forms. In this subtribe the adult female possesses a pair of well-developed setae between the median trullae and the heteromorphic second instar male is usually provided with glanduliferous craters (communal pores of ducts). The new genus is close to *Pseudaulacaspis* and may be regarded as a peculiar form of the latter. It is, however, distinguishable from *Pseudaulacaspis* by the combination of the following characters in the adult female (Fig. 18): presence of a small pyriform sclerosis at the inner base of the second trulla; the median trullae are elongate and serrate; the second trullae are extremely reduced; there are no submedian macroducts. The body is fusiform, with the pygidium delimited by the intersegmental furrow between abd IV and V on the dorsal surface. So far as represented in the collection at hand, *Pseudaulacaspis* seems to be one of the largest genera in the family, including a number of undescribed species occurring in tropical Asia. Because the boundaries of *Pseudaulacaspis* are still not clear, the erection of *Mayonia* is rather tentative. *Rutherfordia* MacGillivray is another genus close to *Pseudaulacaspis*. *Mayonia* and *Rutherfordia* are both diagnosed by having a small sclerosis on the inner base of the second trulla. *Rutherfordia* is peculiar in having a pair of enlarged ducts at the posterior end of the body in the first-instar nymph, whereas such ducts are absent in *Mayonia callicarpae* (based on exuvial casts).

2.6.1. *Mayonia callicarpae*, sp. nov. (Figs 18, A–C and 19)

Material examined. Collected at the foot of Volcano Mayon, at an altitude of 850m, Albay, Luzón, the Philippines, on *Callicarpa* sp. (Verbenaceae), Nov. 1992 [material 92PL-49]. Females and males occur on the lower surface of the leaves, both burrowing under the tomentum; tests elongate, thin, and white, those of the male much narrower. The description of the adult female is based on 30 specimens.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 18, A–C). Body moderately elongate, fusiform; metathorax and free abdominal segments gently lobed laterally; pygidium roundish marginally. Prepygidial derm membranous; abd I with a rather large submarginal dorsal boss; pygidium sclerotic dorsally, the ventral surface sclerotized towards the apex. Antennae situated within the frontal margin, separated from each other by a space narrower than the frame of the mouth-parts, each with a long seta. Anterior spiracles each with a loose cluster of 2–10 trilocular disc pores (mean 5.0, sample size 57). Perivulvar disc pores in 5 groups: 4–7 in the median group (mean 6.0, sample size 30), 7–15 in each anterolateral (mean 11.0, sample size 60), and 6–15 in each posterolateral group (mean 10.3, sample size 60). Anus situated about the centre of the pygidium, at the level of the vulva. Median trullae elongate, separated from each other by a narrow space, parallel to each other, their inner bases connected with each other through a strongly curved sclerosis; each trulla about 1.5 times as long as wide, nearly symmetrical, serrate on both sides, rounded apically. Second trullae reduced to very small pointed processes representing the inner and outer lobules, with a small pyriform sclerosis at the inner base of the inner lobule. Third trullae each represented by a marginal prominence. Marginal macroducts: 1 mesally to the second trulla (on abd VII), 2 on each of abd V and VI, the inner one associated with a pore prominence sclerotized on the margin, the prominence on abd VI being especially strongly sclerotized. Submarginal macroducts as large as the marginal macroducts, forming segmental rows on abd III–V: 4–10 (usually 5–7) on abd III, the outermost one situated on the margin; 4–10 (usually 6 or 7) on IV, the outermost one or two on the margin; 1–5 (usually 2 or 3) on V just anteriorly to the marginal macroducts. Submedian macroducts absent [see Remarks]. Much smaller lateral macroducts on abd I–III: 1–4 (usually 2 or 3) on I, 2–6 (usually 3–5) on II, and 2–4 (usually 3) on III. Marginal gland spines single on abd V–VIII, well developed except on VIII; 1–4 (usually 2 or 3) gland spines on the lateral lobe of abd III and 1–3 (usually 2) on the margin of IV also well represented; a few small gland spines on the lateral lobe of abd I and II each, at times none on I, and 1 or 2 very small ones occasionally present on the lateral lobe of the metathorax.

Second-instar male (Fig. 19) homomorphic, with the median trullae elongate and serrate as in the adult female (Fig. 18, A and C) and the second-instar female (Fig. 18, D) [3.4].

Remarks. The adult females have no submedian macroducts except a single specimen, which is provided with one submedian macroduct on each of abd III and IV on the left side of the body and two on abd V on the other side. Based on the limited number of the specimens examined, it is not possible to decide whether the occurrence of submedian macroducts is a normal variation or not.

2.7. *Bayokaspis*, gen. nov.

Type species. *Bayokaspis luzonensis*, sp. nov.

This genus belongs to the subtribe Fioriniina [for the subtribe, see 2.6]. Like *Fiorinia* Targioni-Tozzetti, it is pupillarial, the adult female being retained within the heavily sclerotized exuvial cast of the second instar and much simplified in external features. Compared with *F. fioriniae* (Targioni-Tozzetti), the type species of *Fiorinia*, it is characterized in the adult female (Fig. 20) by the following characters: the median trullae are not zygotic; the lateral trullae are completely obsolete; the marginal macroducts are much reduced in size; there are many small gland tubercles along the prepygidial margin; and there are no gland spines on the pygidial margin. The median trullae are parallel, rounded, and serrate. The pygidium is delimited on the dorsal surface by the intersegmental furrow between abd IV and V, and on the margin by the notch between these segments. In the adult and second-instar female stages, this genus is very similar to the new genus *Kulatinganaspis* described below, from which, however, it differs remarkably in the first instar [2.8].

2.7.1. *Bayokaspis luzonensis*, sp. nov. (Figs 20–22)

Material examined. Collected in Luzón, the Philippines, on *Pterospermum diversifolium* (Sterculiaceae; local name: Bayok): at Puerto Azul (Paniman Beach), Ternate, Cavite, Dec. 1992 [material 92PL-104]; at Bagac (2 sites: an inland site and Montemar Beach), Bataan, Aug. 1994 [94PL-90, -145]. Occurring on the lower surface of the leaves. Females burrowing under the tomentum. Male tests on the surface of the tomentum, white, felted, and not carinate. About 35 specimens (about 20 from Puerto Azul and 15 from Bagac) of the adult female have been examined.

Holotype. Adult female mounted from 94PL-90; deposited in UPLB.

Diagnosis (adult female: Fig. 20, A–D). Body elliptic; abd IV gently lobed laterally; pygidium produced, obdeltate. Prepygidial derm membranous; segmentation indistinct, the intersegmental furrows being obscure except those between abd III and IV and between IV and V. Dorsal surface of pygidium sclerotic, the ventral surface sclerotized towards the apex but not strongly. Antennae situated within the frontal margin, separated from each other by a space about twice as wide as one of their tubercles, each with a short seta. Anterior spiracles each with 1–3 trilocular disc pores. Perivulvar disc pores: 2–5 (usually 3 or 4) medians in a single transverse row; 4–8 (usually 5–7) in each anterolateral and 5–11 (usually 6–8) in each posterolateral group, forming single or irregularly double longitudinal rows. Anus situated anteriorly to the centre of the pygidium, but at the level of the vulva. Median trullae prominent, parallel, separated from each other by a space much narrower than one trulla, with a pair of short setae between; without a distinct sclerosis connecting their bases; each trulla symmetrical, as long as wide, rounded, minutely serrate on the entire margin. Lateral trullae absent, the margin of abd VII gently lobed instead. Three single marginal macroducts on each side of the pygidium, belonging to abd V–VII, a little larger than the ventral microducts (which are scattered along the margin), associated with no pore prominence; other dorsal ducts absent. Many small conical gland spines (often partly reduced to mere microducts) present on the meso- and metathorax and the base of the abdomen along the margin (10–45 on each side), forming a continuous or interrupted row; similar gland spines (1–13) often present on the head margin laterally to the antenna. No marginal gland spines present on the pygidium.

Second-instar female (Fig. 20, E) differs from the adult female in the median trullae nearly triangular and in having marginal gland spines. Second-instar male (Fig. 21) heteromorphic, with a pair of glanduliferous craters, but also with the median trullae similar to those in the second-instar female [3.4]. First-instar nymph (Fig. 21) with 5 antennal segments as in many Diaspidini [2.8].

Remarks. In the specimens from Bagac (both sites), the gland spines occurring along the body margin are more numerous than in those from Puerto Azul; Bagac material with 3–13 on each side of the head and about 19–45 in the row running along each margin on the meso- and metathorax and abd I. In the specimens from Puerto Azul, only a few gland spines (1–4 on each side) are occasionally present on the head and about 10–20 occur in the row ending on abd I, usually with an isolated gland spine on abd II.

2.8. *Kulatinganaspis*, gen. nov.

Type species. *Kulatinganaspis quezonensis*, sp. nov.

This genus is pupillarial, belonging to the subtribe Fioriniina [for the subtribe, see 2.6], and is very similar to *Bayokaspis* [2.7] in the adult and second-instar female stages. In the adult female, it differs from *Bayokaspis* in having no gland spines in the prepygidial region and in lacking submedian dorsal setae on abd VI and VII. (*Kulatinganaspis* has submedian dorsal setae on the prepygidial segments and at times also on abd V, whereas *Bayokaspis* is provided with them on abd II–VII.) The median trullae are a little divergent, and each of them is nearly triangular, rounded apically, and minutely serrate on the entire margin. The pygidium is delimited on the dorsal surface by the intersegmental furrow between abd IV and V, but there is no intersegmental notch on the margin. These characters may appear too subtle to recognize *Kulatinganaspis* as a distinct genus. However, in the first instar, *Kulatinganaspis* differs from *Bayokaspis* in many characters, of which some are as follows (compare Figs 22 and 25) [characters on *Bayokaspis* in brackets]: 1) the body is unusually elongate [moderately elongate]; 2) a tubercle is present on the frontal margin between the antennae, bearing a pair of setae [such a tubercle is absent]; 3) the antennae are six-segmented [five-segmented]; 4) the head is devoid of enlarged dorsal ducts [the head has a pair of enlarged dorsal ducts]; 5) the thorax is devoid of submedian dorsal ducts [the thorax has three pairs of submedian dorsal ducts]; 6) the pygidium is devoid of dorsal ducts [the pygidium has a pair of ducts posteriorly to the anus]; and 7) there are no gland spines on the body margin [well-developed gland spines are present around the thorax and abdomen]. Our knowledge of first instar diaspidids is still not sufficient to evaluate their characters taxonomically. However, the characters mentioned above, when combined, seem to indicate that these genera are not only distinct but also remotely related. I, therefore, adopt the view that the close similarity between the adult females is due to convergence, at least to some extent. In both genera, the females burrow under the tomentum of *Pterospermum* leaves and, because they are pupillarial, they do this in the second instar only. In fact, due to the shape of the median trullae, they are more closely similar in the second instar than in the adult stage (compare Figs 20 and 23), which fact may support the supposed convergence in association with burrowing.

2.8.1. *Kulatinganaspis quezonensis*, sp. nov. (Figs 23–25)

Material examined. Collected at Santa Lucia, at the foot of Mt. Banahao, Quezon, Luzón, the Philippines, on *Pterospermum obliquum* (Sterculiaceae; local name: Kulatingan), Dec. 1992 [material 92PL-92]. Females and males occurring on the lower surface of the leaves, burrowing under the tomentum. Second-instar exuvial casts of the female with the dorsum heavily sclerotized and black. Male tests white, with the caudal end exposed from the tomentum. About 20 specimens of the adult female have been examined.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 23, A–D). Body elongate, with the lateral margins nearly parallel; pygidium broadly obdeltate. Prepygidial derm membranous; pygidium largely sclerotic dorsally, the ventral surface sclerotized towards the apex. Antennae situated within the frontal margin, separated from each other by a space narrower than the frame of the mouth-parts; at times with a small tubercle between them. Anterior spiracles each with a group of 4–10 trilocular disc pores divided into several subgroups. Perivulvar disc pores: 5–8 in the median group, 7–13 in each anterolateral and also in each posterolateral group. Anus situated about the centre of the pygidium. Median trullae prominent, a little divergent, separated from each other by a space about half as wide as one of them, with a pair of short setae between; without a distinct sclerosis connecting them; each trulla nearly triangular, rounded apically, a little asymmetrical, with the inner margin longer than the outer; minutely serrate along the entire margin. Lateral trullae absent, the margin of abd VII gently lobed instead. Dorsal macroducts reduced in size, nearly as small as the ventral microducts; marginal macroducts occurring on abd V–VII, usually 1 on V and 2 on each of VI and VII, somewhat removed from the margin, with the orifice surrounded by a sclerotized rim; lateral macroducts on abd III and IV and often also on II: 0 or 1 on II, 1–4 (usually 2 or 3) on III, and 2–4 (usually 3) on IV; 1 submedian duct usually present on each of abd IV and V. Gland spines absent except for an occasional small one on the margin of abd V. Marginal setae of the pygidium short, most not produced beyond the margin.

Second-instar female (Fig. 23, E) similar to that of *Bayuraspis luzonensis* (Fig. 20, E), with the median trullae nearly triangular as in the latter [2.8]. Second-instar male (Fig. 24) homomorphic, very similar to the adult and second-instar females in the shape of the median trullae. First-instar nymph (Fig. 25) characterized, above all, by the body extraordinarily elongate, the antennae with 6 segments, and the presence of an interantennal tubercle [2.8].

2.9. *Singapuraspis*, gen. nov.

Type species. *Singapuraspis lasianthi*, sp. nov.

This genus is a non-pupillarial form referable to the subtribe Fioriniina [for the subtribe, see 2.6]. The adult female is diagnosed, above all, by the absence of differentiated marginal macroducts and the presence of segmental clusters of dorsal macroducts on the marginal to submarginal area of the pygidium. In these characters, *Singapuraspis* is similar to *Rolaspis* Hall and some other genera. The new genus is distinguishable from them by the following combination of characters: the median trullae are not zygotic in spite of the presence of a sclerosis between them; the pygidial margin laterally to the median trulla is rugged, with a continuous series of conical or tubercular processes, among which the lateral trullae are not distinguishable in shape; there are no gland spines on the pygidial margin, nor in the prepygidial region; and the dorsal surface of the pygidium is reticulate over a large central area. The pygidium is well defined on the dorsal surface by the intersegmental furrow between abd IV and V, and on the margin by the notch between them.

2.9.1. *Singapuraspis lasianthi*, sp. nov. (Figs 26–29)

Material examined. Collected at Bukit Timah, Singapore, on *Lasianthus maingayi* (Rubiaceae), July 1992 [material 92SP-29]. Females and males occurring among the dense erect hairs covering the nodes of the twigs. Males also occur on other parts of the twigs and along the midrib on the lower surface of the leaves, these parts being densely covered with shorter hairs. Female tests deeply inserted and held erect among the dense hairs, long elliptic, with both dorsal and ventral portions well formed and gently swollen; blackish brown. Male tests also inserted among the hairs, white, and not carinate. The description of the adult female is based on about 20 specimens.

Holotype. Adult female, deposited in SEHU.

Diagnosis (adult female: Figs 26 and 27). Body oblong to broad obovate, with the free segments gently lobed laterally; pygidium broad, roundish on the margin. At full growth, the derm sclerotic throughout, with the intersegmental furrows heavily sclerotized; pygidium reticulate over a large central area of the dorsal surface, wrinkled longitudinally on other parts. Antennae situated within the frontal margin, separated from each other by a space nearly as broad as the frame of the mouth-parts, each with a short curved seta. Anterior spiracles each with a loose cluster of 20–56 trilocular disc pores; posterior spiracles each with 9–23 disc pores in a single or partly irregularly double, at times triple, transverse row. Perivulvar disc pores absent. Anus situated anteriorly to the centre of the pygidium. Median trullae set close together, with a pair of setae and a sclerosis between, not united through the sclerosis; each trulla broadly rounded and serrate along the entire margin. Abd VI and VII rugged marginally, having a continuous series of conical or tubercular processes, among which the lateral trullae are not distinguishable in shape. Dorsal macroducts largely confined to the pygidium and to the marginal to submarginal area, those occurring on the margin not distinguishable in size; 1 or 2 in the posterolateral corner of abd IV; 7–20 on V, usually forming 2 rows united on the margin; 8–18 on VI, usually some of them in a separate group anterior to the others; 1–3 on VII, marginal. Microducts abundant along the body margin in the prepygidial region; also scattered between the margin and the spiracles, and abundant submarginally on the ventral surface of the pygidium, forming segmental rows. Gland spines absent.

Second-instar female (Fig. 28) with each median trulla asymmetrical, laterally followed by angular processes occurring nearly along the entire pygidial margin; gland spines absent. Second-instar male (Fig. 29) similar to the second-instar female in the pygidial appendages, but the median trullae with a rather deep incision, thus appearing bilobulate.

Remarks. *Singapuraspis lasianthi* may not be a 'burrowing' form in the strict sense of the word, occurring among the dense erect hairs on the host plant. It is included here, because it has elaborately serrate median trullae, as in most of the other species described in this paper [3.2].

2.10. *Lepidosaphes* Shimer

This genus, as understood in a broad sense in accordance with Williams and Watson (1988) and Danzig (1993), covers the 11 genera recognized as distinct by Borchsenius (1963; 1978). In this sense, the genus comprises more than one hundred known species, and there may be many others mainly in Asia. Some of the known species are cryptic in habit, occurring beneath plant parts such as stipules and bark flakes but most, if not all, do not burrow into the bark or leaf epidermis or under the leaf vestiture. The three species described below burrow under the vestiture on the lower surface of the leaves, at least as the female. One species is very close to those referred by Borchsenius to his genus *Paralepidosaphes*, but the relationships of the other two species are not exactly knowable in the present state of our knowledge of Asian species.

In the following descriptions, the pygidium is understood as follows: it is delimited by the intersegmental furrow between abd V and VI on the median area of the dorsal surface, but the constriction separating the pygidium from the prepygidial region on the margin lies midway on abd IV, the marginal macroduct of abd IV being included within the pygidium.

Lepidosaphes and other lepidosaphidine genera have large marginal macroducts on the pygidium, of which the orifices are elongate oval, with the longitudinal axis held perpendicular to the pygidial margin, and surrounded by a thick sclerotized rim. These macroducts are called 'mégapores' by French authors, and may be termed 'megaducts' in accordance with the well-established terms 'macroducts' and 'microducts' (to which the terms 'macropores' and 'micropores' in French correspond). However, they are not invariable. In *Lepidosaphes crotonifolii*, sp. nov., the lateral four of the marginal macroducts on each side of the pygidium have a slender rim around the orifice [2.10.1], and in *Lepidosaphes clerodendri* and *Andaspis glutae*, spp. nov., the lateralmost is reduced to a much smaller duct [2.10.2; 2.11.1]. In *Hexandaspis bataanensis*, sp. nov., the marginal macroducts are good megaducts, but occur only in three pairs [2.12.1]. The presence or absence of megaducts has been adopted in dividing lepidosaphidines into subtribes by some authors, but I have grave doubts as to the taxonomic value of this feature at the subtribal level [2.13; 2.14].

2.10.1. *Lepidosaphes crotonifolii*, sp. nov. (Figs 30 and 31)

Material examined. Collected at Bukit Cendana, Pulau Pinang [Penang Is.], Malaya, Malaysia, on *Croton argyratus* (Euphorbiaceae), Oct. 1991 [material 91ML-457]. Females and males occurring on the lower surface of the leaves, burrowing under the dense cover of peltate scales, their presence being suggested by slight swellings on the cover; tests thin, pale in colour. Some specimens of the adult female were mounted, but not all of them are in good condition. The description below is based mainly on 5 specimens.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Fig. 30). Body rather slender, with abd I strongly lobed laterally; pygidium broad obdeltate, slightly roundish on the margin; prepygidial derm membranous; ventral surface of the pygidium with 2 pairs of sclerotized areas arising from the bases of the median and second trullae, and with 2 pairs of slender sclerotic patches more laterally. No dorsal bosses present. Antennae situated between the frontal margin and the mouth-parts, separated from each other by a space as wide as the frame of the mouth-parts, each with 2 curved setae, of which one is smaller than the other. Anterior spiracles each with 1–3 trilocular disc pores. Perivulvar disc pores in 5 groups: 2 or 3 in the median group, 5–7 in each anterolateral, and 3 or 4 in each posterolateral group. Anus situated near the base of the pygidium. Median trullae separated from each other by a space much narrower than one trulla; each trulla as long as wide, nearly symmetrical, roughly dentate. Second trullae with the inner lobule smaller than the median trulla, and the outer lobule smaller than the inner, but well represented, both lobules roughly dentate. Megaducts numbering 6 on each side of the pygidium; 1 between the median and second trullae (on abd VII), with no pore prominence; 2 on abd VI, the inner one with no pore prominence, the outer opening at the base of a roughly dentate, sclerotized, slight marginal prominence; 2 on abd V, each associated with a sclerotized low marginal prominence; 1 in the posterolateral corner of abd IV; mesal two of these ducts with a thickly rimmed orifice, but the lateral four with the rim around the orifice slender and weak, tending to be distorted in slide-mounted specimens. Dorsal and lateral macroducts much smaller than the megaducts, but not particularly reduced in size. Lateral macroducts on the meso- and metathorax and abd I: 1–7 in the posterolateral corner of the mesothorax; 28–40 on the metathorax between the lateral margin and the posterior spiracle; 13–17 on abd I on the anterior half of the lateral lobe. Submarginal dorsal macroducts on abd II–IV, at times 1 on the posterior border of abd I: 6–9 in an infrasegmental cluster and 1 or 2 on the posterior border on II; 4–8 in an infrasegmental cluster and 1 or 2 along the posterior border on III, and at times another in the anterolateral corner; 2–5 in an infrasegmental cluster and 1 or 2 along the posterior border on IV, and usually with another in the anterolateral corner. Submedian dorsal macroducts on abd III–VI, forming oblique segmental rows: 3–7 on III, 5–9 on IV, 2–5 on V, and 2 or 3 on VI. Small dorsal ducts occurring submarginally on abd VII and VIII: 1 or 2 on VII (in front of the second trulla), and 1 on VIII (in front of the median trulla). Small conical gland spines occurring on abd I, forming a transverse row across the ventral surface of the lateral lobe; marginal gland spines on the succeeding segments, 1 on II at the apex of the lateral lobe, 2 on each of III–VIII and between the median trullae, those occurring between the median trullae and between the median and second trullae not surpassing the length of the trullae. A lateral spur present between abd I and II.

Remarks. This species is well characterized by abd I being strongly lobed and the median and second trullae dentate. It reminds me of *Lepidosaphes abdominalis* Takagi, in which, however, not only abd I but also the other free segments of the abdomen are strongly lobed. In Borchsenius' classification, *L. crotonifolii* may belong to *Mytilaspis*, whereas *L. abdominalis* is referable to *Lepidosaphes*.

2.10.2. *Lepidosaphes clerodendri*, sp. nov. (Figs 32 and 33)

Material examined. Collected at Anak Chelong, Perlis, Malaya, Malaysia, on *Clerodendron villosum* (Verbenaceae), Nov. 1991 [material 91ML-407]. Females occurring on the lower surface of the leaves on the sides of the veins, which are densely hairy; tests visible *in situ*, but apparently burrowing under the hairs, dull brown, the dorsal surface coarse with growing lines. Males present on the upper surface of the leaves; tests brown. The following description is based on more than 10 mounted specimens, of which only a few are in good condition.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Figs 32 and 33). Body rather robust, fusiform, with the free segments moderately lobed laterally, and with the pygidium broad obdeltate, slightly rounded marginally. Prepygidial derm membranous; dorsal surface of the pygidium sclerotic on a broad median area, the ventral surface with 2 pairs of sclerotized areas arising from the bases of the median and second trullae and with a pair of slender sclerotic patches laterally to them. No dorsal bosses present. Antennae situated between the frontal margin and the mouth-parts, separated from each other by a space narrower than the frame of the mouth-parts, each with 3 or 4 setae, which are usually subequal in size. Anterior spiracles each with 3–5 trilocular disc pores. Perivulvar disc pores in 5 groups: 9–14 in the median group, 11–20 in each anterolateral, and 7–19 in each posterolateral group. Anus situated near the base of the pygidium. Median trullae prominent, a little divergent, separated from each other by a space nearly half as wide as one of them, the pygidial margin between them recessed rather deeply; each trulla nearly symmetrical, roundish, irregularly dentate over a broad apical margin. Second trullae much smaller than the median trullae, yet well represented; inner lobule roundish apically, with a notch subapically on the outer slanting margin; outer lobule much narrower. Megaducts numbering 5 on each side of the pygidium: 1 between the median and second trullae (on abd VII), with no pore prominence; 2 on abd VI, the inner one with no pore prominence, the outer associated with sclerotized marginal serrations; 2 on V, the inner one associated with a sclerotized angular pore prominence, the outer with sclerotized marginal serrations. A slender duct (diminished megaduct) present at the posterolateral corner of abd IV, with a small orifice opening in a sclerotized angular prominence. Lateral and dorsal macroducts small and slender, but distinctly larger than the ventral microducts. Lateral macroducts strewn on the meso- and metathorax and abd I. Submarginal dorsal macroducts forming a loose infrasegmental cluster on each of abd I–IV; segmental rows of dorsal macroducts also present on these segments, confined to the submarginal area on I, tending to extend mesally on the succeeding segments, forming a nearly continuous row across the submarginal and submedian areas on IV; abd V with 3–9 ducts forming an infrasegmental cluster submarginally and 10–22 ducts forming a nearly continuous segmental row across the submarginal and submedian areas; in a similar manner abd VI with 1–7 ducts in an infrasegmental row and 11–20 ducts in a segmental row; 1 macroduct, a little larger than the neighbouring dorsal ducts, present in front of the megaduct of abd VII. Ventral microducts in 3 longitudinal submarginal rows on each side of the pygidium. Marginal gland spines of the pygidium slender, 2 between the median trullae (on abd IX) and 2 on each of abd V–VIII; similar gland spines present on more anterior segments, 2–7 on abd III and 2–5 on IV; abd III sometimes also with a few conical gland spines within the margin. Conical gland spines also present on the anterior segments: 0–3 on the lateral side of the head, 1 or 2 on the prothorax posteriorly to the anterior spiracle, 1–5 on the mesothorax, 1–6 on the metathorax posterolaterally to the posterior spiracle, 1–8 on abd I in a transverse row on the lateral lobe, and 3–7 on II within or on the margin. Three lateral tubercles present on each side of the prepygidial abdomen, each with a slender duct.

Remarks. This species is diagnosed in having the median trullae dentate over a broad apical margin and the margin between them recessed to form an apical incision on the pygidium. The combination of some other characters suggests that it falls in *Pistaciaspis* in Borchsenius' classification but, in the present state of our knowledge, it is not certain that this species is really related to the *Pistacia*-associated species occurring in Central Asia and Southwest Asia.

2.10.3. *Lepidosaphes yakusimana*, sp. nov. (Figs 34 and 35)

Takagi, 1990: 16 (Fig. 1.1.2.11, F) [*Lepidosaphes* sp., 'Japan, on *Rhododendron*'; median and second trullae of the adult female figured].

Material examined. Collected on Yaku-Sima, an island near the southern end of Kyûsyû, Japan, at altitudes of 1400–1900m, on *Rhododendron yakusimanum* (Ericaceae), April 1975 (M. Haruki leg.), June 1980 (M. Suwa leg.), and Oct. 1982 (M. Miyazaki leg.). Females and males occurring on the lower surface of the leaves, burrowing under the dense tomentum; tests dark chestnut brown. The description below are based on 30 specimens of the adult female mounted from the material collected in 1982.

Holotype. Adult female collected in 1982; deposited in SEHU.

Diagnosis (adult female: Figs 34 and 35). Body fusiform, with the free segments moderately lobed laterally; pygidium broad, roundish along the margin. Prepygidial derm membranous; head with or without conical processes, which, when present, are rather numerous and scattered along the frontal margin, mostly on the ventral surface; ventral surface of the pygidium with 2 pairs of sclerotized areas arising from the bases of the median and second trullae and with another pair laterally. No dorsal bosses present. Antennae situated between the frontal margin and the mouth-parts, separated from each other by a space narrower than the frame of the mouth-parts, each with 2 or 3 setae usually unequal in size. Anterior spiracles each with 9–19 trilocular disc pores (mean 12.5, sample size 60), sometimes 1–4 of them being separated from the others, forming a small cluster anteromesad of the main cluster. Perivulvar disc pores in 5 groups: 6–12 in the median group (mean 8.0, sample size 30), 8–17 in each anterolateral (mean 12.0, sample size 60), and 4–17 in each posterolateral group (mean 11.0, sample size 60). Anus situated near the base of the pygidium. Median trullae separated from each other by a space much narrower than one of them, broader than long, roundish or obtusely angulate apically, minutely serrate. Second trullae with the inner lobule smaller than the median trulla, but well represented, broad, serrate except on the mesal and lateral margins or notched subapically on the slanting outer margin; outer lobule much narrower than the inner. Megaducts numbering 6 on each side of the pygidium: 1 between the median and second trullae (on abd VII), opening in a membranous pore prominence; 2 on abd VI, the inner one with no pore prominence, the outer associated with sclerotized irregular marginal serrations; 2 on V, the inner one associated with a sclerotized angular pore prominence, the outer with sclerotized marginal serrations; 1 on IV, opening in an angular pore prominence. A small duct present at the base of the dorsal marginal seta of abd VII. Other dorsal ducts minute, similar in size to the ventral microducts; sparsely scattered in the lateral and submarginal areas and arranged in submedian segmental rows on abd I–V; few in the thoracic region; 7–13 on abd VI, most of them forming a segmental row across the submedian and submarginal areas; 3–6 (usually 4) on VII, forming a shorter row. Abundant ventral microducts scattered on the prosoma and across the metathorax; abd II with no ventral microducts on the lateral lobe; each of abd III–VI with a submarginal row of ventral microducts. Conical gland spines on abd I, numbering 7–15 on one side, all or most of them being situated on the lateral lobe and often a few situated more interiorly. Slender gland spines on the lateral lobes of abd II–IV: 4–7 on II, 3 or 4 (usually 4) on III, and 2–4 (usually 3 or 4) on IV; 2 marginal gland spines on each of abd V–VIII and between the median trullae (on abd IX). Three lateral spurs present on each side of the prepygidial abdomen, each with a duct. A sclerotized patch of derm usually present in the posterolateral corner of the metathorax, often bearing 1 or 2 spinous processes.

Remarks. This species belongs to *Paralepidosaphes* in Borchsenius' classification, and may be distinguishable from the other species of that group by the following combination of characters: the median trullae are serrate; the prepygidial submedian dorsal ducts are not enlarged, and each row is disconnected from the submarginal dorsal ducts, which are quite few; a sclerotized patch of derm is present in the posterolateral corner of the metathorax, often with a few spinous processes.

2.11. *Andaspis* MacGillivray

The genus *Andaspis*, as understood in a broad sense in accordance with Tang (1986), Matile-Ferrero (1988), and Williams and Watson (1988), includes the three genera erected by Borchsenius (1967). About 40 species are known in *Andaspis*, but several species, especially those described from South Africa, may not be referable to this genus. Most species are distributed in tropical to warm-temperate Asia and Australia. This genus is apparently very close to *Lepidosaphes* Shimer, but most species are bark-burrowing. *Andaspis*, as compared with *Lepidosaphes*, is especially characteristic in the shape of the median trullae. These trullae are large and set close together, typically with the mesal margins short, straight and parallel, then diverging to the apices, which are blunt or rounded, and with the outer margins much longer, straight or nearly so, oblique, and serrate. In many species, the median trullae are equipped with a prominent sclerosis arising from the middle of the base or with a pair of scleroses arising from the basal corners. These characters of the median trullae are apparently associated with burrowing. In other features the species of the genus vary in parallel with the variation in *Lepidosaphes* to some extent. The composition of the pygidium is also interpretable as in *Lepidosaphes* [2.10].

Andaspis, as understood in this paper, may be a good taxon, but I do not adopt the view that *Andaspis* and some other lepidosaphidine genera having the median trullae shaped as in *Andaspis* constitute a distinct higher taxon, the subtribe Andaspidina. *Hexandaspis*, gen. nov., for example, is somewhat similar to *Andaspis* in the shape of the median trullae, but is peculiar in other characters and may not necessarily be closely related [2.12]. Furthermore, median trullae similar to those of *Andaspis* also occur in Diaspidini [2.2 and 2.3].

2.11.1. *Andaspis glutae*, sp. nov. (Figs 36 and 37)

Material examined. Collected at Bukit Timah, Singapore, on *Gluta wallichii* (Anacardiaceae), July 1992 [material 92SP-7]. Females burrowing into the epidermis of the branches; some tests were nearly exposed but closely stuck on the bark. Male tests also present on the branches but not burrowing. Tests of both sexes blackish brown. The description below is based on 30 specimens of the adult female.

Holotype. Adult female, deposited in SEHU.

Diagnosis (adult female: Figs 36 and 37). Body fusiform, broadest across abd II and III, or (when overgrown?) elongate, with the metathorax and abd I–IV subequal in width; pygidium obdeltate. Prepygidial derm remaining membranous, but intersegmental furrows tending to be sclerotized at full growth; dorsal surface of the pygidium sclerotic, the ventral surface with 2 pairs of sclerotized areas arising from the bases of the median and second trullae and with a pair of oblique sclerotic patches laterally to them. Six submarginal dorsal bosses present on each side of the abdomen, belonging to abd I–VI. Antennae situated in front of the mouth-parts, separated from each other by a space narrower than the frame of the mouth-parts, each with 2 setae, of which one is robust and the other much smaller. Anterior spiracles each with 2–4 trilocular disc pores, one of them being often displaced mesad or anteromesad. Perivulvar disc pores in 5 groups: 1–7 in the median group (mean 4.4, sample size 30), forming a single transverse row, 4–8 in each anterolateral (mean 6.1, sample size 60), and 4–13 in each posterolateral group (mean 7.6, sample size 60). A few disc pores also present on the preceding segment, similar to those in the perivulvar groups, numbering 1–6 (mean 3.2, sample size 30), arranged in a single transverse row in the median area (on 2 specimens 1 or 2 additional disc pores present in the submedian area on one side only). Anus situated near the base of the pygidium. Median trullae separated from each other by a narrow space, with the outer margin much longer than the inner margin, slanting, and serrate; each trulla with a long blunt sclerosis arising from the middle of the base. Second trullae well developed; inner lobule serrate on the oblique outer margin, the outer represented by a much smaller, conical process. Megaducts numbering 5 on each side of the pygidium: 1 between the median and second trullae (on abd VII), with no pore prominence; 2 on abd VI, associated with a serrate marginal prominence; 2 on V, the inner one opening in an angular sclerotized pore prominence, the outer associated with sclerotized marginal serrations. A slender duct (diminished megaduct) present on abd IV, with a much smaller orifice opening in the sclerotized posterolateral angle of the segment. Another slender duct present in front of the megaduct of abd VII. Other dorsal ducts very small, nearly as small as the ventral microducts, scattered laterally on the meso- and metathorax and abd I–V and arranged in segmental rows on these abdominal segments, the rows on abd III–V extending to the submedian area; about 20–34 arranged in a perpendicular row on abd VI across the submedian and submarginal areas. Ventral microducts abundant on the meso- and metathorax and abd I in the lateral to submarginal area, occurring also posteriorly to the posterior spiracles and between them. Gland spines on abd II–VII: 3 or 4 on the lateral lobe of II, short and robust except 1 or 2 on the margin; 2 slender marginal gland spines on each of III–VII; 1 or 2 tubercular gland spines at times occurring on the lateral lobe of abd I. No gland spines are discernible between the median trullae nor between the median and second trullae, but there arise from each of these spaces 2 slender ducts that should be associated with gland spines. No lateral tubercles or spurs present.

Remarks. This species may be related to *Andaspis dasi* described by Williams (1963) from West Bengal, India. According to Williams (1980) and Williams and Watson (1988), *A. dasi* is a variable species, identical with *Andaspis numerata* described by Brimblecombe (1959) from Queensland, Australia, and distributed in a broad region including Pacific islands, occurring on various plants. Compared with the descriptions of *A. dasi*, *A. glutae* is distinguishable from *A. dasi* or *A. numerata* by the following characters: each antenna has two setae; abdominal disc pores are present on the last prepygidial segment in addition to the perivulvar groups; the marginal macroduct occurring in the posterolateral corner of abd IV is slender; abd VI is provided with more numerous dorsal ducts, which form a longer row across the submedian and submarginal areas.

2.11.2. *Andaspis makilingensis*, sp. nov. (Figs 38 and 39)

Material examined. Collected at Mud Spring, Mt. Makiling, Los Baños, Laguna, Luzón, the Philippines, on an undetermined plant of the family Rubiaceae, Aug. 1994 [material 94PL-3]. Females and males occurring on the bark. Females burrowing into the epidermis; tests slender, dark brown or nearly black. Male tests dark brown. The description below is based on 30 specimens of adult females.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Figs 38 and 39). Body at full growth with the lateral sides of the prepygidial region nearly parallel; mesothorax elongate; metathorax and free abdominal segments gently lobed laterally; pygidium obdeltate. Prepygidial derm membranous; united head and prothorax densely granulate laterally; pygidium somewhat sclerotic on the dorsal surface, the ventral surface with 2 pairs of longitudinal sclerotized areas arising from the bases of the median and second trullae, and more laterally with 3 pairs of sclerotic patches submarginally. Dorsal submarginal bosses present on the abdomen, variable in number, always present on abd I, II, IV and VI, present or absent on III and V; a small boss sometimes discernible in the supposed prothoracic region. Antennae situated between the frontal margin and the mouth-parts, separated from each other by a space nearly as wide as the frame of the mouth-parts, each with 2 setae unequal in size and often also with 1 much smaller seta. Anterior spiracles each usually with 2 trilocular disc pores separated horizontally from each other by a space; at times 2 or 3 disc pores at the outer position, and rarely no disc pore at the inner position. Perivulvar disc pores in 5 groups: 2–4 in the median group (4 in 22 out of 30 samples), forming a single transverse row; 3–8 in each anterolateral (6 in 46 out of 60 samples), and 4–6 in each posterolateral group (4 in 57 out of 60 samples). Anus situated near the base of the pygidium. Median trullae somewhat broader than long, with the outer margin much longer than the inner, slanting, and dentate; separated from each other by a narrow space; each trulla with an ill-defined sclerosis arising from the middle of the base. Second trullae with the inner lobule much smaller than the median trulla, notched or dentate on the sloping outer margin, and with the outer lobule represented by a small conical process. Megaducts numbering 6 on each side of the pygidium: 1 mesad of the second trulla (on abd VII), with no pore prominence; 2 on each of VI and V, associated with sclerotized marginal dentations or serrations; 1 in the posterolateral angle of IV. A slender duct present just anteriorly to the megaduct of abd VII. Dorsal and lateral ducts small and slender, yet distinctly larger than the ventral microducts of the pygidium. Dorsal ducts scattered laterally in the posterolateral corner of the mesothorax, on the metathorax, and on the free abdominal segments, and arranged segmentally on abd II–V; abd VI with 5–8 ducts forming a submedian row. Ventral ducts abundant laterally on the meso- and metathorax and abd I; microducts scattered in a band across the metathorax. Tubercular gland spines on abd I, 5–13 forming a row across the lateral lobe; 2–6 conical gland spines on the posterolateral corner of abd II; 2 slender gland spines occurring marginally on each of the succeeding segments, those occurring between the median trullae and between the median and second trullae being very small. Three inconspicuous lateral tubercles present on each side of the prepygidial abdomen, often merged into the body margin, each with a duct.

Remarks. This species may be related to species referred by Borchsenius (1967) to his genus *Raoaspis*. It appears to be especially close to *Andaspis indica* (=*Raoaspis indica*), but may differ from the latter in lacking gland spines on the metathorax, in having fewer gland spines on abd I–III, in having a band of microducts between the posterior spiracles, and in the median trullae being dentate rather than minutely serrate. *Raoaspis indica* was described by Borchsenius (1967) as occurring on *Quercus* in India. According to Danzig (1968), however, it was collected not in India but at Kunming, Yunnan, China. In fact, Tang (1986) described *A. indica* on the basis of the specimens collected in Yunnan on an undetermined plant.

2.11.3. *Andaspis conocarpi*, sp. nov. (Fig. 40)

Material examined. Collected at Bukit Larut [Maxwell Hill], at an altitude of 1100m, Perak, Malaya, Malaysia, on *Lithocarpus conocarpus* (Fagaceae), Oct. 1986 [material 86ML-155]. Females occurring on the lower surface of the leaves, burrowing under the hairy cover; found mainly on the side of lateral veins. No male tests were found. About 12 specimens of the adult female have been mounted from the material, but not all of them are in good condition.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Fig. 40). Body gradually broadening towards the base of the abdomen, then narrowing towards the pygidium, which ends with an obtuse apex; metathorax and abd I–IV lobed laterally. Prepygidial derm membranous; dorsal surface of the pygidium finely and densely striate longitudinally, with the intersegmental furrow between abd V and VI sclerotized in the submedian to submarginal area; the ventral surface with 2 pairs of elongate triangular sclerotized areas arising from the bases of the median and second trullae and with a pair of long, oblique, slightly curved sclerotic patches laterally to them. Antennae situated in front of the mouth-parts, separated from each other by a space a little narrower than the frame of the mouth-parts, each with a straight or a little curved fleshy seta. Anterior spiracles usually with no disc pores (one of the specimens examined with 1 trilocular disc pore in front of the left spiracle). Perivulvar disc pores in 5 groups: 2–4 in the median group, 6 or 7 in each anterolateral, and 4 in each posterolateral group. Anus close to the base of the pygidium. Median trullae separated from each other by a space about one-third as wide as one trulla, roundish, serrate, with the outer margin longer than the inner margin; each trulla with a pair of slender scleroses arising from the basal corners and converging anteriorly. Second trullae with the inner lobule well developed, serrate on the oblique margin, and provided with a slender sclerosis arising from the inner base; outer lobule represented by a small triangular process. Megaducts numbering 6 on each side of the pygidium: 1 between the median and second trullae (on abd VII), opening in a membranous pore prominence; 2 on abd VI, the outer associated with slightly developed marginal serrations; 2 on V; and 1 in the posterolateral corner of IV. A much smaller dorsal macroduct present at the base of the marginal seta of abd VII. Other macroducts also small; about 10–20 scattered laterally on the mesothorax, some of them being very small; about 15–25 on the metathorax laterally on both surfaces, on the ventral surface extending to the posterior spiracle and often including very small ducts; 10–14 scattered on the lateral lobe of abd I, most of them situated dorsally; 7–10 on the lateral lobe of II, all dorsal; 5–8 submarginally on the dorsal surface of III, 2 or 3 of them being situated on the posterior border of the segment; 1 or 2 submarginally on the dorsal surface of IV near the anterior border of the segment; submedian dorsal macroducts present on III–VI: 2–4 on each of III and IV, 2 or 3 on V, and 1 on VI. Ventral microducts few on the pygidium. Tubercular gland spines occurring on abd I–IV: 4–6 ventrally on the lateral lobe of I, 2–4 on II just within the margin, 2 or 3 on III and 1 or 2 (usually 2) on IV marginally. A very small marginal gland spine present on abd V near the marginal macroduct of IV, and also on VI near the marginal macroducts of V. Other marginal gland spines larger: 2 laterally to the second trulla; 2 between the median and second trullae, associated with the pore prominence; and 2 between the median trullae, united together at their inner bases.

Remarks. This species is very close to *Andaspis crawii* (Cockerell), which, occurring on *Castanopsis* species in Japan and Taiwan, burrows under the vestiture on the lower surface of the leaves. *A. conocarpi* differs from the latter (represented by the Japanese form) mainly in the following characters [characters on *A. crawii* in brackets]: 1) the megaducts number six on each side of the pygidium [the megaducts number five, being single on abd IV, V, and VII and paired on VI]; 2) a dorsal duct is present just in front of the marginal seta of abd VII [no dorsal duct is present in front of the marginal seta of abd VII]; 3) a submedian dorsal macroduct is present on abd VI, being situated mesad of the submedian seta of the segment [no submedian dorsal macroduct is present on abd VI]; 4) a number of ventral ducts are present laterally on the mesothorax [lateral ducts are absent on the mesothorax except for a few occasional ducts]; 5) the inner lobule of the second trulla is remarkably developed, with a long slanting outer margin, and the outer lobule is represented by a very small conical process [the inner lobule is stub-like in shape and the outer lobule relatively well developed]; 6) no microducts are present within the frontal margin [some ventral microducts are present within the frontal margin]; 7) each antennal tubercle bears a single seta, which is fleshy and straight or only a little curved [each antennal tubercle bears one or two slender setae]; and 8) no disc pores are usually associated with the anterior spiracles [one or two disc pores are associated with each anterior spiracle]. In most of these characters, *A. conocarpi* is primitive in comparison with *A. crawii*, whereas it is more derivative in 5) and 7).

In Taiwan, *Andaspis crawii* is represented by two forms. One form is not different from the Japanese form, having a few submedian dorsal macroducts on each of abd III-V. The other form has more submedian macroducts, which may occur also on abd II and VI (Takagi, 1970).

2.12. *Hexandaspis*, gen. nov.

Type species. *Hexandaspis bataanensis*, sp. nov.

This genus is referable to the subtribe Lepidosaphidina, tribe Lepidosaphidini. The adult female (Figs 41 and 42) is diagnosed, above all, in having three pairs of extraordinarily developed trullae. The median trullae are quite large and elaborately serrate along their entire margin, and are asymmetrically conical, with the outer margin longer than the inner margin. The second and third trullae are also enlarged, less produced than the median trullae, but are very broad and serrate. These lateral trullae are unilobed, but the second trullae show a trace of division into the inner and outer lobules. The posterior half of the pygidial margin is thus largely composed of serrations, which are interrupted by the spaces bearing gland spines between the trullae. The megaducts are reduced to three on each side of the pygidium: all of them are single, occurring on abd V-VII. In spite of this reduction in number the megaducts show no trace of reduction in size, and the rims of their orifices are thick and heavily sclerotized. The other dorsal ducts are slender and mostly arranged along the posterior borders of abdominal segments. The pygidium is delimited by the intersegmental furrow between abd V and VI on the dorsal surface, but on the margin it appears to be defined by the notch between abd IV and V.

This genus is somewhat similar to *Andaspis* MacGillivray in the shape of the median trullae [for the state in *Andaspis*, see 2.11], but is peculiar in the enlarged trullae and especially in the broad unilobed second and third trullae. It may be related to *Andaspis*, but it is also possible that the similarity is due to convergence. In any case, as compared with *Andaspis*, *Hexandaspis* apparently represents a distinct type adapted to the burrowing mode of life. *Hexandaspis* is also very similar to *Bayuraspis*, gen. nov., in the enlarged and serrate trullae, but the similarity again could be due to convergence [2.14]. *Hexandaspis* is diagnosed by having three pairs of single megaducts on the pygidium, whereas *Pallulaspis* Ferris, another lepidosaphidine genus, has four pairs of single megaducts. These two genera are quite different in other features, showing that single megaducts can appear in parallel in different lineages. In *Hexandaspis bataanensis*, however, the reduction in number of megaducts is probably associated with burrowing [for the occurrence of well-developed single marginal macroducts on the pygidium in another burrowing species, see 2.5.2], whereas *P. ephedrae* Ferris, the type species of *Pallulaspis*, does not burrow.

2.12.1. *Hexandaspis bataanensis*, sp. nov. (Figs 41–43)

Material examined. Collected at Bagac (two sites: an inland site and Montemar Beach), Bataan, Luzón, the Philippines, on *Pterospermum diversifolium* (Sterculiaceae), Aug. 1994 [material 94PL-90, -145]. Females and males occurring on the lower surface of the leaves, burrowing under the dense tomentum. Females occurring on the midrib and thick lateral veins; tests elongate, moderately convex dorsally, and light to blackish brown; male tests occurring on the blade, occasionally on veins, greyish brown. The following description of the adult female is based on 15 specimens mounted from 94PL-90 and 30 specimens from 94PL-145.

Holotype. Adult female mounted from Montemar Beach, 94PL-145; deposited in UPLB.

Diagnosis (adult female: Figs 41 and 42). Body elongate; at full growth, very long owing to the elongation of the mesothorax, with the lateral sides nearly parallel and with the free segments only gently lobed laterally; pygidium obdeltate, little roundish along the margin. Prepygidial derm membranous; dorsal surface of the pygidium broadly sclerotized, the ventral surface with 2 pairs of sclerotized areas arising from the median and second trullae and 3 pairs of sclerotic patches more laterally. Submarginal dorsal bosses always present on abd I, II, IV, and VI, often occurring on III and sometimes on V; and a small boss usually present on VII, situated mesad of the marginal macroduct of VI, sometimes hardly discernible or apparently lacking. Antennae situated in front of the mouth-parts, separated from each other by a space a little narrower than the frame of the mouth-parts, each with 2 (rarely 1 or 3) slender setae. Anterior spiracles each with 1 or 2 (at times 3 and rarely 4) trilocular disc pores; when there are 2 or more disc pores, one of them is often removed mesally. Perivulvar disc pores in 5 groups: 2–5 (usually 3 or 4) in the median group, forming a single transverse row; 4–9 in each anterolateral (6 in 70 out of 90 samples), and 3–7 in each posterolateral group (4 in 86 out of 90 samples). Anus small, only a little larger than a perivulvar disc pore, situated near the base of the pygidium. Median trullae large and prominent, separated from each other by a space much narrower than one of them; each trulla nearly triangular, rounded apically, asymmetrical, with the outer margin much longer than the inner, elaborately serrate on the entire margin. Second trullae also well developed, but smaller and less prominent than the median trullae, each represented by a very broad serrate process, which has a slight notch near the outer extremity (thus suggesting that it is formed from the united inner and outer lobules). Third trullae similar to the second, but smaller and without notch. Megaducts well developed, with a thick rim around the orifice, numbering only 3 on each side of the pygidium, belonging to abd V–VII: 1 occurring in front of the space between the median and second trullae; 1 near the inner base of the third trulla; 1 on abd V in the posterolateral corner, which forms an angular prominence. A small duct present in front of the megaduct of abd VII. Other dorsal ducts all slender, being of microduct size, scattered submarginally on the metathorax and abd I–V and arranged in segmental rows on the abdomen as posteriorly as VI, but absent from the median and submedian areas of the basal 1 or 2 segments; dorsal ducts on VI arranged in a segmental row through the submedian and submarginal areas (except 1 or 2 occasionally isolated on the submarginal area) or, when fewer, arranged on the submedian area only (execpt 1 or 2 occasionally isolated on the submarginal area). Ventral ducts abundant on the mesothorax over a broad lateral area, and on the metathorax in a band running across the segment along the anterior border to the lateral margins; some ventral ducts present in the anterolateral corner of abd I. Tubercular gland spines occasionally present on the metathorax, numbering 1–3 and situated posterolaterally to the posterior spiracle; 4–12 on abd I, forming a transverse row submarginally; 2–5 on II on the lateral lobe. Slender marginal gland spines occurring on the succeeding abdominal segments: 1–4 (usually 2) on abd III, 1 or 2 (usually 2) on each of IV and V, 1 (rarely 2) on VI, and 2 on each of VII and VIII and between the median trullae (on IX), those occurring on VIII and IX small, not surpassing the median trullae.

First-instar nymph (Fig. 43) with main features characterized as in many Lepidosaphidini.

Remarks. In all the examined specimens from Montemar Beach, the dorsal ducts occurring on abd VI are numerous (14–23 on each side) and form a segmental row through the submedian and submarginal areas (Fig. 42). The 15 specimens from the inland site are more variable: four of them do not differ from the Montemar form (having 12–21 ducts on each side of the segment), whereas in the other 11 specimens, the ducts are fewer (6–10 on each side) and occur on the submedian area (Fig. 41) except one or two occasionally isolated on the submarginal area. In other characters, however, no serious differences have been found between the two forms.

2.13. *Santubongia*, gen. nov.

Type species. *Santubongia swintoniae*, sp. nov.

The type species has no differentiated marginal macroducts in the adult female (Figs 44 and 45) (and also in the second-instar female). The other features and the general morphological pattern of the first-instar nymph (Fig. 46) indicate that it belongs to the tribe Lepidosaphidini. In fact, in the adult female, the configuration of the pygidial apex is remarkably similar to that in *Neopinnaspis* McKenzie, which, in possessing megaducts, is definitely referable to the tribe Lepidosaphidini and the subtribe Lepidosaphidina. The median and second trullae are well developed, strongly sclerotized, and closely appressed together at the apex of the pygidium. There are no gland spines discernible between the median trullae, nor between the median and second trullae, in spite of the presence of well-developed slender gland spines on the pygidium laterally to these trullae and also on the prepygidial segments anteriorly as far as abd II. Apparently there is no space for gland spines between the trullae, which are so closely crowded. The trullae are crenate or nearly serrate. The dorsal ducts are slender, and arranged in well-defined segmental rows on the prepygidial segments anteriorly as far as the mesothorax. On the dorsal surface, the pygidium may be delimited by the intersegmental furrow between abd V and VI, though on the margin the pygidium may be defined by the notch between abd IV and V. The posterior border of abd VI is well marked by sclerotization, clearly demarcating the segment from abd VII throughout the submedian and submarginal areas. In *Neopinnaspis*, the segments posterior to abd V are completely fused, and the intersegmental furrow between abd VI and VII is obsolete, leaving a pair of scars laterally to the anus. This difference in the pattern of segmentation, in addition to the absence of megaducts, may justify the erection of the new genus *Santubongia*.

Santubongia swintoniae burrows into the bark epidermis, but species of *Neopinnaspis* do not, their tests being exposed on the surface of the plant. The close similarity of these two genera in the unusual configuration of the pygidial apex cannot be attributed to convergence due to similarity in habit, and may indicate a close phylogenetic relationship between *Santubongia* and *Neopinnaspis*. If this view is correct, *Santubongia* should belong to the subtribe Lepidosaphidina, in spite of the absence of megaducts.

2.13.1. *Santubongia swintoniae*, sp. nov. (Figs 44–46)

Material examined. Collected at Santubong (Damai Beach), Kuching District, Sarawak (Borneo Is.), Malaya, Malaysia, on *Swintonia glauca* (Anacardiaceae), Oct. 1991 [material 91ML-52]. Occurring on the bark in association with *Chionandaspis ramicola* [2.3.1]. The female burrows into the epidermis of the bark. The male is unknown. One specimen of the adult female with the exuvial casts and two specimens of the first-instar nymph have been mounted.

Holotype. Adult female, deposited in FRIM.

Diagnosis (adult female: Figs 44 and 45). Body elongate, fusiform, with the free segments slightly lobed laterally; pygidium obdeltate, roundish on the basal margin. Prepygidial derm membranous; dorsal surface of the pygidium sclerotic especially over a broad median area, the intersegmental furrow between abd V and VI thickly sclerotized, and the posterior border of VI also sclerotized in a nearly straight line across the submedian and submarginal areas; ventral surface of the pygidium apically with a sclerotized area forming 4 peaks associated with the median trullae. Submarginal dorsal bosses numbering 6 on each side, belonging to abd I–VI, fairly large and well sclerotized. Antennae situated in front of the mouth-parts, separated from each other by a space narrower than the frame of the mouth-parts, each with 2 setae, of which one is much smaller than the other. Anterior spiracles each with 2 trilocular disc pores. Perivulvar disc pores in 5 groups: 2 medians, 4 or 5 anterolaterals, and 4 or 6 posterolaterals. Anus situated near the border between abd V and VI. Two pairs of trullae well developed and heavily sclerotized. Median trullae appressed together along nearly their entire mesal margins, which are separated from each other by a slender space; apices set close together, rounded; outer margin oblique and roundish, notched 4 or 5 times, thus appearing crenate or nearly serrate; each trulla with a short, apically blunt sclerosis arising at the middle of the base. Second trullae immediately neighbouring the median trullae, well developed; inner lobule almost as large as the median trulla and similar in shape to the latter, notched several times or serrate on the outer margin; outer lobule represented by an angular process. Third and fourth trullae not recognizable; instead, posterolateral corners of abd V and VI angular, each followed by sclerotized marginal serrations. No differentiated marginal macroducts present on the pygidium. Dorsal ducts slender, mostly arranged in segmental rows across the body along the posterior borders of the meso- and metathorax and abd I–VI; numerous on V and VI; a group of about 6 ducts present on the base of the inner lobule of the second trulla, and a few ducts on the base of the median trulla. A number of ventral ducts strewn in a band across the mesothorax and also the metathorax; some present in the anterolateral corner of abd I. Small conical gland spines present submarginally on abd I in an irregular row, numbering 7 or so. Slender marginal gland spines occurring on abd II–VII, 2 on each segment. Three lateral spurs on each side of the prepygidial abdomen, broad basally, and pointed apically.

First-instar nymph (Fig. 46) with the terminal (sixth) antennal segment not annulate.

2.14. *Bayuraspis*, gen. nov.

Type species. *Metandaspis javanensis* Williams.

In describing *Metandaspis javanensis*, Williams (1963) pointed out the possibility that the species did not belong to *Metandaspis* Williams. According to him, the prominent median trullae and their peculiar paraphyses are important characters to exclude it from *Metandaspis*, of which the type is *Mytilaspis recurvata* Froggatt, an Australian species. *M. javanensis* burrows under the tomentum of *Pterospermum* leaves, whereas *M. recurvata* does not burrow, the 'Scales thickly covering the bark of the branches and twigs of the Black Wattle (*Acacia decurrens*)' (Froggatt, 1915). It is, therefore, also possible that the difference in the size of the median trullae may simply reflect the difference in habit.

Metandaspis javanensis does share some remarkable characters with *Metandaspis recurvata* in the adult female. Above all, both lack differentiated marginal macroducts and have scattered dorsal ducts on the pygidium. Nonetheless, there are some noteworthy differences. On *M. javanensis*, each median trulla is symmetrical, with the inner and outer margins equal in length, the second trullae are broad and unilobed, and the dorsal intersegmental furrow between abd V and VI is well marked throughout, attaining the marginal notch between the segments. These characters, in addition to the prominent size of the median trullae and their peculiar basal scleroses, may be sufficient to exclude this species from *Metandaspis*.

Bayuraspis javanensis is very similar to *Hexandaspis bataanensis*, sp. nov. [2.12.1], in having prominent median trullae and broad second trullae, both these trullae being elaborately serrate. On the other hand, *B. javanensis* differs from *H. bataanensis* in the symmetrical shape of each median trulla, the complete absence of the third trullae, the absence of megaducts, the presence of scattered dorsal ducts on the pygidium, and the complete demarcation of abd V from abd VI on the dorsal surface. Because both these species burrow under the tomentum of *Pterospermum* leaves, the possibility cannot be excluded that their similarity in the median and second trullae is due to convergence.

Bayuraspis may be referred to the lepidosaphidine subtribe Coccomytilina on account of the absence of megaducts, but I am not fully convinced that this character can be of taxonomic value at the subtribal level. *Mempelaspis* Takagi is a primitive lepidosaphidine referable to Level II in my classification scheme, possessing pectinae, and yet it is provided with good megaducts (Takagi, 2000). The absence of megaducts in some lepidosaphidines of Level III, therefore, could be due to their loss, which may have happened in different lineages in parallel [for a possible case, see 2.13]. If this view is correct, the validity of the subtribe Coccomytilina, based on the absence of megaducts alone, is open to doubt. For this reason *Bayuraspis* may tentatively be referred to the subtribe Lepidosaphidina.

2.14.1. *Bayuraspis javanensis*, comb. nov. (=*Metandaspis javanensis*) (Fig. 47)

Williams, 1963: 30 [*Metandaspis*; Java, on *Pterospermum javanicum*].

Takagi, 1992: 46, 59, 69, and 73 [*Metandaspis*; Sepilok, Sabah, on *Pterospermum* sp.; first-instar nymph (Fig. 10); pygidium (Fig. 26), perivulvar disc pore (Fig. 33), and spiracular disc pore (Fig. 34) of the adult female].

Material examined. Collected at Sepilok, Sandakan, Sabah (Borneo Is.), Malaysia, on *Pterospermum* sp. (Sterculiaceae; local name for *Pterospermum* spp.: Bayor or Bayur), Nov. 1988 [material 88ML-347]. Females occurring on the lower surface of the leaves, burrowing under the tomentum.

2.15. *Banahaoa*, gen. nov.

Type species *Banahaoa bayokana*, sp. nov.

This genus belongs to the subtribe Aspidiotina, tribe Aspidiotini, and may be related to *Hemiberlesia* Cockerell (s. lat., including *Abgrallaspis* Balachowsky). The boundaries of *Hemiberlesia* are still not clear to me, but the erection of *Banahaoa* is considered here to be justified by the following characters of the adult female (Fig. 48): the median trullae are appressed together along their entire mesal margins, with their inner bases situated posteriorly to their outer bases; absence of gland spines between the median trullae; absence of sclerotized processes representing lateral trullae; and the presence of thickened and lanceolate marginal setae on both surfaces of abd VII. Furthermore, on *Banahaoa*, the median trullae are serrate along a long slanting outer margin, and there are spiniform pectinae on abd VII and VIII only. The pygidium is delimited by the intersegmental furrow between abd III and IV on the dorsal surface, but on the margin it appears to be defined by the notch between abd II and III.

This genus is especially characterized by the occurrence of lanceolate marginal setae on the dorsal and ventral surfaces of abd VII. Several other aspidiotine genera, namely *Octaspidiotus* MacGillivray, *Acanthaspidiotus* Borchsenius and Williams, and *Oceanaspidiotus* Takagi, are also provided with lanceolate or thickened marginal setae on the pygidium, but these genera are more closely similar to *Aspidiotus* Bouché than to *Banahaoa*, especially in having well-developed pectinae on abd V–IX.

2.15.1. *Banahaoa bayokana*, sp. nov. (Fig. 48)

Material examined. Collected at Santa Lucia, at the foot of Mt. Banahao, Quezon, Luzón, the Philippines, on *Pterospermum celebicum* (Sterculiaceae; local name: Bayok-bayokan), Dec. 1992 [material 92PL-91]. Females and males occurring on the lower surface of the leaves, burrowing under the tomentum; females mainly on the midrib, and males on the blade. Tests thin and white. About 10 mounted specimens of the adult female are available, but none of them is in good condition. It seems that the material, when collected, bore dead insects only.

Holotype. Adult female, deposited in UPLB.

Diagnosis (adult female: Fig. 48). Body obpyriform; pygidium produced, roundish on the margin. Dorsal surface of the pygidium sclerotic, striate longitudinally, with a sclerotized patch laterobasally on each side; ventral surface with a sclerotized area apically, and with a pair of longitudinal sclerotized bands associated with the perivulvar disc pores. Antennae situated within the frontal margin, separated from each other by a space as wide as the frame of the mouth-parts, each with a long curved seta. Perivulvar disc pores in 4 groups: 6–12 in each anterolateral group, and 4–10 in each posterolateral group. Anus elliptical, shorter than the median trulla, separated from the bases of the median trullae by a space more than twice as long as its longitudinal diameter. Median trullae prominent, appressed together along their entire mesal margins, their inner bases situated much posteriorly than their outer bases; margin between apex and lateral margin sloping, roundish and serrate. No sclerotized lateral trullae. Pectinae spiniform, 2 just laterally to the median trulla on abd VIII and also on VII, shorter than the median trulla, pointed or shortly divided apically. Abd VI and VII occasionally with small, irregular, membranous processes on the margin, which probably represent reduced lateral trullae and pectinae. Dorsal and ventral marginal setae of abd VII thickened, lanceolate. Dorsal macroducts of the pygidium not filiform; marginal macroducts with the orifice surrounded by a thick sclerosis, 1 medially near the inner bases of the median trullae, 1 just laterally to the median trulla, 1 between the marginal setae of abd VI and VII, sometimes 1 present just mesally to the marginal seta of V; 5–12 submarginal macroducts in an irregularly double or triple oblique row arising near the outer base of the median trulla and running towards the laterobasal sclerotized patch of the pygidium. Microducts scattered along the body margin except on the dorsal surface of the pygidium.

2.16. *Cephalaspidiotus*, gen. nov.

Type species. *Cephalaspidiotus palaquii*, sp. nov.

This genus belongs to the tribe Aspidiotini, and is well characterized in the adult female (Fig. 49) by the body deeply constricted between the metathorax and abdomen, the head and thorax being fused to form an enormous mass. Other aspidiotines, especially those belonging to the subtribes Pseudaonidiina and Selenaspidina, also have a deeply constricted body, but in them the constriction occurs between the meso- and metathorax. In pygidial features, this genus is similar to *Aspidiotus* Bouché and many other genera of the subtribe Aspidiotina. In this subtribe, *Cephalaspidiotus* may be recognized by the perivulvar disc pores present only in one pair of lateral groups and the pectinae extraordinarily developed, as well as by the deeply constricted body and the enormous cephalothorax. The margin of the abdomen is notched only between abd II and III and, thus, the boundary of the pygidium appears to be between these segments. On the dorsal surface, however, the pygidium is delimited by the intersegmental furrow between abd IV and V.

2.16.1. *Cephalaspidiotus palaquii*, sp. nov. (Figs 49 and 50)

Material examined. Associated with *Palaquium* spp. (Sapotaceae) in Malaysia and Singapore. Collected at Taman Bako [Bako National Park], Sarawak (Borneo Is.), Malaysia, on *Palaquium* sp., Oct. 1991 [material 91ML-148]; at Bukit Timah, Singapore, on *Palaquium gutta*, July 1992 [92SP-32, -67]. Females occurring on the lower surface of the leaves, burrowing under the velvety cover of trichomes; burrow large, about 5mm in diameter at maximum, and externally recognizable by an obscure slight swelling on the velvety cover; test rudimentary and very thin (it is easily broken when the burrow is opened). Male tests occurring within the maternal burrow [3.3], oblong, thin, and white. The description of the adult female is based on 30 specimens from Taman Bako and another 30 from Bukit Timah, 92SP-32.

Holotype. Adult female mounted from 91ML-148; deposited in FRIM.

Diagnosis (adult female: Fig. 49). Body robust, deeply constricted between the metathorax and abd I. Head and thorax fused to form a conspicuous mass, which is transversely oblong, broader than the abdomen, and swollen laterally to form a low tubercle on each side; abd I and II forming together a round lobe laterally; pygidium swollen marginally on its base (abd III), rather rapidly narrowing posteriorly, and rounded along a broad apical margin. At maturity, the fused head and thorax become sclerotic, with some more heavily sclerotized patches on the dorsal surface; dorsal surface of the pygidium sclerotic, longitudinally striate, with sclerotized patches laterobasally; ventral surface with a pair of sclerotized bands arising from the bases of the median trullae and extending to the lateral ends of the vulva. Antennae situated between the frontal margin and the mouth-parts, separated from each other by a space nearly as wide as the frame of the mouth-parts, each with a single seta. Perivulvar disc pores in a single pair of oblong clusters situated laterally to the vulva, sometimes with 1 or a few pores isolated anteriorly to the cluster; 12–20 on each side on the specimens mounted from 91ML-148 (mean 15.6, sample size 60), 9–19 on the specimens from 92SP-32 (mean 16.3, sample size 60). Anus oblong, as long as the median trulla, situated halfway between the centre and apex of the pygidium. Vulva appearing to be short-operculate. Median trullae well developed, separated from each other by a narrow space, each trulla nearly symmetrical, a little longer than wide, gently narrowing apicad, truncated apically, with a distinct notch subapically on each side; a robust sclerosis present on the inner base, much shorter than the trulla. Lateral trullae not discernible as such. Pectinae occurring along a broad apical margin of the pygidium: 2 between the median trullae, not surpassing the trullae, slender, divided apically; 2 just laterally to the median trulla, also slender, followed by a very slender spiniform process (modified second trulla?) overlapping with the dorsal marginal seta of abd VII; laterally to the spiniform process, a number of well-developed pectinae present as far as the dorsal marginal seta of abd IV, well fimbriated on the lateral side. The pectinae occurring laterally to the median trulla are not always exactly countable, because some are split to varying degrees: about 14–18 (usually 16) on the specimens from 91ML-148, and about 16–20 on the specimens from 92SP-32. Dorsal ducts not filiform, most of them forming 3 single or irregularly double or triple longitudinal rows, which may become partly mixed, on each side towards the apex of the pygidium: 19–34 on the specimens from 91ML-148 (mean 25.0, sample size 60), 16–26 on the specimens from 92SP-32 (mean 21.4, sample size 60); 1 marginal macroduct present between the bases of the median trullae. Minute ducts sparsely scattered submarginally on the cephalothorax, and a few dorsally on the prepygidial abdomen.

First-instar female and male (Fig. 50) differing greatly in the length of the legs [3.3].

Remarks. The specimens collected in Taman Bako, Sarawak, and those from Bukit Timah, Singapore, agree well in the number of perivulvar disc pores. On the other hand, they show some differences in the numbers of dorsal macroducts and pectinae. However, as stated in the description above, the pectinae are occasionally split to varying degrees, which may have affected the count. No further difference has been found to suggest that the two forms belong to different species.

2.17. *Morganella* Cockerell

The type species, *Morganella longispina* (Morgan), is widely distributed in the tropical, subtropical and warm-temperate regions of the world, occurring on trees of various families. Other species, five from Africa and one from North America, were referred to the genus by authors. However, in these species, the pectinae are modified into spiniform, blade-like, or only slightly fimbriate processes. In contrast, *M. longispina* is characterized by the well-developed pectinae, most of which are fimbriate not only on their lateral sides but also on their mesal. The species described below displays these characters to a more marked degree. The discovery of the new species, which is undoubtedly congeneric with *M. longispina*, requires critical re-examinations on the generic positions of the African and North American species previously referred to *Morganella*. Chou (1985) proposed the new genus *Sudanaspis* for *Morganella vuilleti* [written '*vuilletti*' by him; =*Aspidiotus* (*Hemiberlesia*) *Vuilleti* Marchal] originally described from Senegal, but he gave no account of the other African and the North American species.

2.17.1. *Morganella polyctena*, sp. nov. (Fig. 51)

Specimens examined. Collected at Bagac (two sites: an inland site and Montemar Beach), Bataan, Luzón, the Philippines, on *Pterospermum diversifolium* (Sterculiaceae), Aug. 1994 [material 94PL-90, -145]. Females and males occurring on the lower surface of the leaves, burrowing under the tomentum. Female tests hard, nearly round, highly convex dorsally, and black, with the posterior end produced and curved up to be exposed from the tomentum when fully formed. Male tests smaller and elongate, with the posterior end curved up, thus exposed. About 17 specimens of the adult female, mostly mounted from the material collected at the inland site, 94PL-90, have been examined and compared with specimens of *Morganella longispina* collected in Japan.

Holotype . Adult female mounted from 94PL-90; deposited in UPLB.

Diagnosis (adult female: Fig. 51). Very similar to *Morganella longispina*, differing mainly in the following characters [characters on *M. longispina* in brackets]: 1) dorsal surface of the pygidium thickly strewn with variously shaped sclerotized dots and lines over a broad central area [dorsal surface of the pygidium longitudinally striate except on a narrow central area, which is reticulate]; 2) anus elliptic or amygdaloid, as long as the median trulla or nearly so, separated from the bases of the median trullae by a space shorter than its length [anus subcircular to elliptic, about half as long as the median trulla, separated from the bases of the median trullae by a space longer than its longitudinal diameter]; 3) each median trulla with 2 notches subapically on the lateral side [each median trulla notched only once subapically on the lateral side]; 4) pectinae numbering 16–19 on each side of the pygidium, conspicuously fimbriate on both their mesal and lateral sides except several ones occurring just laterally to the median trulla, the lateralmost one or two being thickened [pectinae numbering 13 or 14 on each side of the pygidium, less conspicuously fimbriate especially on their mesal side, the lateralmost one or two being not especially thickened]; and 5) marginal setae of abd IV and V and usually also of III extraordinarily developed on both surfaces, much surpassing pectinae in length and flagelliform (marginal setae of VI elongate, but not surpassing pectinae in length, tapering apically; those of VII nearly as long as the neighbouring pectinae, spiniform) [marginal setae of abd IV–VI (not III–V) extraordinarily long and flaggelliform]. The two species also differ in the length of the antennal setae: on *M. polyctena*, each antennal tubercle bears a nearly straight or curved seta at most about 25µm long (sometimes accompanied by a shorter one), whereas on *M. longispina*, the antennal seta reaches about 40µm and is often strongly curved. Furthermore, *M. polyctena* was collected from the leaves of the host plant, whereas *M. longispina* occurs on the twigs and branches of various plants, no record of its association with the leaves having been made in spite of its wide distribution.

2.18. *Kochummenaspis*, gen. nov.

Type species. *Kochummenaspis filiorum*, sp. nov.

This genus is so peculiar in the characters of the adult female (Figs 52 and 53) that it is not easy to find a relationship to other forms. The body is tripartite, being distinctly constricted between the meso- and metathorax and also between the metathorax and the abdomen. The apex of pygidium is produced to form a narrow obdeltate area, set with elongate, elaborately serrate median trullae on the entire lateral margins, thus forming a prominent, conical, serriferous process. The lateral trullae are well represented in three pairs and unilobed. There are well-developed glanduliferous spiniform processes on the pygidial margin, and some of them are expanded and dentate on the lateral base. The pygidium is devoid of macroducts except for a few long filiform ducts arising marginally or submarginally. There are, however, small ducts of the two-barred type in the prepygidial region. The second-instar male (Fig. 54) possesses macroducts of the two-barred type on both the pygidium and the prepygidial region. In this latter instar, the macroducts are not diminished in size, and those on the dorsal surface of the pygidium are thickly rimmed around their orifices.

The lateral trullae show no trace of division into lobules. Based on this character, *Kochummenaspis* is referable to the subfamily Aspidiotinae, and, therefore, the glanduliferous marginal processes of the pygidium, which appear to be gland spines, should be modified pectinae. The genus belongs neither to the Thysanaspidini nor to the Leucaspidini because, in these tribes, the pectinae are not glanduliferous. The presence of well-developed trullae and pectinae in the adult female excludes it from the Smilacicolini and the Odonaspidini. It has long filiform ducts, as in many species of the tribe Aspidiotini, but it should be excluded from that tribe, too, because of the two-barred ducts, which are well represented in the second-instar male. After all, *Kochummenaspis* should belong to the tribe Parlatoriini unless it represents a new tribe. Even if it really belongs to the Parlatoriini, it is so aberrant that its relation to other forms of the tribe is utterly unknown.

It is too premature to make a generalization on the character patterns of diaspidid higher taxa based on the first instar. The first-instar female and male of *Kochummenaspis filiorum* (Figs 55 and 56) are apparently modified in certain features. But, based on the present knowledge, they do not positively contradict the view that the genus is referable to the Parlatoriini.

I gratefully dedicate this genus to the late Mr Kizhakkedathu Mathai Kochummen (1931–1999), Botanist in 1957–1986 at the Forest Research Institute of Malaysia. (The plant genus *Kochummenia* Wong, 1984, Rubiaceae, is also named after him.)

2.18.1. *Kochummenaspis filiorum*, sp. nov. (Figs 52–64)

Material examined. Collected in Malaya, Malaysia, on *Schoutenia accrescens* (Tiliaceae): at Bukit Bauk, Terengganu, July 1990 [material 90ML-223, -242]; at Hutan Simpan Beserah [Beserah Forest Reserve], Kuantan, Pahang, Aug. 1990 [90ML-503]; at Bukit Cendana, Pulau Pinang [Penang Is.], Nov. 1991 [91ML-455]. Females occurring on the lower surface of the leaves, burrowing under the tomentum; burrow large, attaining about 5mm in diameter (Fig. 58); tests vestigial (Fig. 59) [3.3]. Males occurring in the maternal burrow [3.3]; tests, when fully formed, about 0.8–1.0mm long and 0.3mm wide, white, and smooth dorsally (Fig. 58). A number of adult females have been mounted, but observations of some details are based on a limited number of teneral adult females.

Holotype. Adult female mounted from 91ML-455; deposited in FRIM.

Diagnosis (adult female: Figs 52, 53, 57, and 58). Body at full growth oblong, sclerotic throughout, divided into 3 parts by marginal constrictions and intersegmental furrows: prosoma (fused head and pro- and mesothorax), metathorax, and abdomen; prosoma as broad as or broader than the metathorax, nearly oblong transversely, broadly tuberculate at each anterolateral corner; metathorax gently lobed laterally; abdomen without distinct intersegmental notches, a little broadening on the base, then gradually narrowing towards the apex of the pygidium. Pygidium slightly roundish along the margin; dorsal surface remarkably reticulate over a broad area, longitudinally striate submarginally; ventral surface roughly and strongly striate longitudinally over the posterior half, with scaly processes on a broad median area of the anterior half. Antennae, on the full-grown body, situated on the frontal margin, separated from each other by a space as wide as the frame of the mouthparts, each bearing a curved seta. Anterior spiracles becoming further apart from the mouthparts as the body grows, each with 1 or 2 quinquelocular disc pores, sometimes with none; each disc pore situated in the bottom of a short duct-like invagination of the derm; posterior spiracles usually with no disc pore, rarely with 1 also invaginated. Perivulvar disc pores absent. Anus situated about the centre of the pygidium. Vulva opening in a transverse slit running nearly across the pygidium and dividing the ventral surface of the pygidium into the anterior and posterior halves. Apex of the pygidium produced in a narrow obdeltate shape, set with elongate median trullae on the entire lateral margins, together forming a prominent conical process, with the outer bases sunken into the pygidium. Median trullae with the apices rounded and separated from each other by a narrow space, which is occupied by a pair of small spinous processes, and with a long outer margin, which is oblique, straight and elaborately serrate, ending with a short basal margin. Lateral trullae represented by 3 pairs of unilobed processes subequal in size and shape, broad and dentate. There are well-developed spinous glanduliferous processes on the pygidial margin: 2 between the median and second trullae; 2 between the second and third trullae, the inner one with the lateral base expanded and dentate; 2 or 3 between the third and fourth trullae, the inner one or, when 3 in this space, inner two expanded and dentate on the lateral base; 1 or 2 laterally to the fourth trulla, expanded and dentate on the lateral base. Three very long filiform ducts present marginally on each side of the pygidium: 1 arising from a sharp process situated between the median and second trullae, 1 from an angular process mesally to the second, and 1 from a small angular process mesally to the fourth; also 1 or 2 filiform ducts occurring submarginally on abd V. Small 2-barred ducts scattered along the margin of the prepygidial region. On full-grown specimens, the pygidium has a thickly sclerotized band arising at the base of the median trulla, extending laterally along the bases of the lateral trullae and glanduliferous processes, but interrupted at several places. In teneral specimens, a strong, curved sclerotized band is discernible only around the base of each median trulla, although there is a very small sclerosis near the margin between the second and third trullae.

Second-instar male (Fig. 54) with the median trullae shaped nearly as in the adult female, the second trullae represented by a pair of small, serrate processes, and 2 spiniform pectinae between the median and second trullae; no further lateral trullae present. First-instar female (Fig. 55) and male (Fig. 56) differing greatly in the size of the legs and also in the size and shape of the trullae situated near the pygidial apex [3.3].

3. DISCUSSIONS

In the present study, 25 diaspidid species belonging to 18 genera are dealt with, and 24 species and 14 genera are described as new. They are here referred to the tribes Diaspidini and Lepidosaphidini, subfamily Diaspidinae, and the tribes Aspidiotini and Parlatoriini, subfamily Aspidiotinae. These four tribes are ranked at Level III in my scheme (Takagi, 2002), which arranged the major groups of the Diaspididae on the basis of the pygidial appendages. In four of the 25 species, the females occur on the twigs or branches of the host plants and burrow into the bark epidermis. Another species included in the present study lives among the dense erect hairs on the twigs. All the remaining species are associated with the leaves, and the females burrow either into the epidermis on the upper or lower leaf surface or, in most species, under the dense cover of trichomes on the lower surface. The presence of the male has been ascertained in 20 species. In some species, the males apparently burrow. In two species, the males occur only in the maternal burrows [3.3]. It seems that the insects start to burrow into the plant epidermis or beneath the leaf vestiture after moulting into the second instar, because the exuvial casts of the first instar are usually left on the outside of the burrows. The burrowing second-instar nymphs of both sexes are similar to the conspecific adult females, especially in the pygidial appendages.

Eight diaspidid species belonging to seven genera, three tribes, and two subfamilies have been available from *Pterospermum* spp., mostly from Luzón, the Philippines. Four species belonging to three genera and two tribes of the subfamily Diaspidinae have been collected on *Swintonia glauca* at one and the same locality in Sarawak, Borneo. The leaves of the *Pterospermum* species have a tomentose cover on the lower surface, and the females of all the eight diaspidid species burrow under this tomentum. *Swintonia glauca* has no tomentum, the leaves being glabrous on both surfaces. In two of the four diaspidid species associated with this plant, the females burrow into the epidermis on the upper or lower leaf surface whereas, in the other two species, the females live in the bark epidermis. There is, therefore, nothing common to *Pterospermum* and *Swintonia* with regard to the burrowing habits of these diaspidids. However, it may reasonably be expected that further burrowing forms will be discovered from these plants. *Pterospermum* is especially worthy of attention. This plant genus comprises about 20 species distributed in tropical Asia, and their leaves are densely covered with trichomes on the lower surface.

3.1. Evolution of pygidial appendages

The genus *Ulucoccus* Takagi, for which the subfamily Ulucoccinae was erected (Takagi, 2002), is a very primitive diaspidid, having no well-formed pygidial appendages apart from minute gland spines. It is referred to Level 0 in my scheme of classification based on the evolution of pygidial appendages, and approximately may represent a remote ancestral form of some diaspidids, if not of all the extant taxa of the family. Non-glanduliferous pectinae appear in Level I taxa: the subtribe Protodiaspidina, tribe Diaspidini, possesses pectinae in combination with well-developed pygidial gland spines, and the tribe Thysanaspidini, subfamily Aspidiotinae, has well-developed pectinae alone on the pygidium. Non-glanduliferous pectinae are also well represented in the Level II taxa of the Diaspidinae and Aspidiotinae. Fimbriate processes similar to these pectinae occur in the family Conchaspididae, an isolated group of Coccoidea, and are well developed in *Fagisuga* Lindinger and *Asceloconchaspis* Williams. Scanning electron microscopy has shown that fimbriate processes occur also in *Conchaspis* Cockerell. Though these processes are much reduced in size, they persist in five species of the genus from eastern Asia, which represent three species groups (Takagi, 1992; 1997). The fimbriate processes of conchaspidids occur dorsally on the apex of the abdomen, where the anus is situated, and 'are assumed to perform an important function at the excretion of the anal substance, which is used for constructing the test' (Takagi, 1997). In the Diaspididae, the pectinae are extensions from the ventral surface of the pygidium, whereas the anus is situated on the dorsal surface. The diaspidid pectinae are not homologous with the conchaspidid fimbriate processes, and may not necessarily perform the same function as in the Conchaspididae.

Level III taxa of the Diaspidinae have no pectinae, but are generally provided with marginal pore prominences and marginal serrations, which may have replaced pectinae in the course of their evolution. The Level III taxa of the Aspidiotinae generally do have pectinae, but these are glanduliferous and may approach the pygidial gland spines of the Diaspidinae in function. It may be assumed that the non-glanduliferous pectinae are not essential to test formation, having disappeared in the Level III taxa, which represent a greater part of the family. It is not clear what function, then, they perform in the diaspidids of Level I and II. Because pygidial gland spines and glanduliferous pectinae are wax-secreting organs, they must have some function in test formation. However, they are occasionally lost in various taxa, suggesting that their function in test formation is subsidiary. From this viewpoint, it appears paradoxical that well-developed glanduliferous pectinae occur in *Cephalaspidiotus palaquii* and *Kochummenaspis filiorum*, which form rudimentary tests in the burrows [3.3].

In the diaspidids of Level II, some pectinae are sclerotized and modified in shape to form trullae at the supposed posterolateral corners of pygidium-composing segments. In the subfamily Aspidiotinae, the tribe Leucaspidini represents Level II. The females of all known species of this tribe are pupillarial, so that they are no longer engaged in test formation in the adult stage. In the subfamily Diaspidinae, the subtribe Kuwanaspidina, tribe Diaspidini, and the subtribe Mempelaspidina, tribe Lepidosaphidini, are referable to this level, having non-glanduliferous pectinae. (The subtribe Mempelaspidina has, in addition, glanduliferous pectinae of a peculiar type, which is assumed to have originated from the union of a gland spine and a non-glanduliferous pectina.) I have presented the view (Takagi, 1999; 2000) that, in these subtribes, the trullae perform a claw-like function when the female insect moves backwards to form the test and moves forwards whilst depositing eggs in the completed elongate test. The diaspidids belonging to Level III are principally provided with well-developed trullae, which are, in general, broad and robust. Their female tests are sometimes covered with a thin upper layer of the plant epidermis. The trullae have acquired a new function in those diaspidids, serving now as a cutting implement probably to clear the plant surface at the site for test formation, and they occasionally peel the plant epidermis when the insect body makes an oscillatory or rotative movement whilst forming the test. This could explain how burrowing forms arose among Level III diaspidids.

3.2. Morphological modifications in the adult females

The two burrowing species of *Pinnaspis* [2.5.1; 2.5.2] differ from the other congeneric species in having enlarged and minutely serrate median trullae. Moreover, in one of them (*P. simplior*), all the marginal macroducts of the pygidium are single. The three burrowing species of *Lepidosaphes* [2.10.1; 2.10.2; 2.10.3] differ from the non-burrowing species of the genus in having dentate or serrate trullae. In one of them (*L. crotonifolii*), the lateral four of the marginal macroducts on each side of the pygidium have the rim around the orifice attenuated and, in slide-mounted specimens, often distorted. In another species (*L. clerodendri*), the lateralmost of the marginal macroducts is much smaller than the others (which are good megaducts). In short, these macroducts exhibit a tendency towards reduction in number, size, or shape. In these species, the modified trullae and the reductive marginal macroducts are apparently associated with the burrowing habit. The dentate or serrate trullae are expected to saw the plant tissue when the insect moves during burrowing, while the marginal and other dorsal ducts are considered to be reduced in function in the burrowing mode of life, in which the test may be less beneficial to the insect. However, the number of the marginal macroducts is not stable even in the non-burrowing species of *Pinnaspis* and *Lepidosaphes*, and the serrate or dentate trullae alone do not suffice to exclude the burrowing species from these genera.

The three new species of *Andaspis* [2.11.1; 2.11.2; 2.11.3] are not particularly different from other congeneric species, which principally burrow into the epidermis of the bark. However, *A. conocarpi* and its close relative *A. crawii* are rather peculiar in the genus in having roundish median trullae. Both these species occur on the leaves and burrow under the cover of trichomes on the lower surface.

Morganella polyctena [2.17.1] is very similar to *Morganella longispina*, a non-burrowing species, from which it differs mainly in having more pectinae. It is not self-evident what significance this character has for the burrowing habit of *M. polyctena*.

Because the 14 new genera are based exclusively on burrowing species, it is impossible to trace modifications of features in these species on the basis of comparisons with non-burrowing congeners. Most of the species have serrate or dentate trullae, which are diverse in shape. It should be noted, however, that the three species of *Chionandaspis* [2.3.1; 2.3.2; 2.3.3], of which one species (*C. ramicola*) occurs on the bark and the other two (*C. foliicola* and *C. palawanensis*) are associated with the leaves, show no appreciable difference in the shape of the median trullae in spite of their different burrowing sites. Instead, the leaf-associated species are peculiarly characterized by the pygidium being abruptly produced apically. *Mayonia callicarpae* [2.6.1] and *Kochummenaspis filiorum* [2.18.1] should also be mentioned, because they have unusually elongate median trullae, which suggest the blade of a hand-saw. Such trullae may require a reciprocating movement in the direction parallel to the serrate margin to fulfil their role as a saw. On the other hand, *Pinangaspis uniclavata* [2.4.1] and *Cephalaspidiotus palaquii* [2.16.1] do not appear to have been modified in the shape of the median trullae, which are simply notched as usual in non-burrowing diaspidids. These species, together with *Morganella polyctena*, form exceptions to the general tendency of burrowing forms to have serrate or dentate trullae.

Singapuraspis lasianthi [2.9.1] occurs among the dense erect hairs on the twigs, and may not 'burrow' in the strict sense of the word. Nevertheless, this species is similar to most of the others described here in having serrate median trullae, suggesting a similar use of the trullae. *Amphisoma erectum* Takagi and *Galeomytilus obesus* Takagi, both associated with another plant (*Colona serratifolia*), also occur among the dense erect hairs on the twigs, but they have another adaptation, with the pygidial appendages nearly obsolete (Takagi, 1995).

The dorsal ducts tend to be few and small or very slender on the species of the four new genera [2.1; 2.2; 2.3; 2.4] belonging to the subtribe Chionaspidina, tribe Diaspidini, and *Kochummenaspis filiorum* [2.18.1], which is referred to the Parlatoriini. This is also the case with *Bayokaspis luzonensis* [2.7.1] and *Kulatinganaspis quezonensis* [2.8.1], which belong to the subtribe Fioriniina, tribe Diaspidini. It should be emphasized that these two species have very small marginal ducts on the pygidium in the second-instar female, too, which is the only stage to burrow among the female instars in these pupillarial species. In the tribes Diaspidini and Parlatoriini, the dorsal macroducts of the two-barred type are usually broad and fairly large and, no doubt, the slender dorsal ducts in these burrowing forms are diminished macroducts. In the other new genera, too, the dorsal ducts may have been reduced in either size or number in association with burrowing, although there is no good evidence for this assumption.

No general tendency in the development of the pygidial gland spines in the adult females has been found on the 11 new genera belonging to the Diaspidinae (Diaspidini and Lepidosaphidini): on the species of five genera [2.2; 2.7; 2.8; 2.9; 2.14] these gland spines are much reduced in size or lost, but not on the others. *Cephalaspidiotus palaquii* [2.16.1], which belongs to the tribe Aspidiotini, subfamily Aspidiotinae, possesses well-developed pectinae comparable to those of *Morganella polyctena* [2.17.1], another burrowing aspidiotine. In *Kochummenaspis filiorum* [2.18.1], which is here referred to the tribe Parlatoriini, subfamily Aspidiotinae, the pectinae are modified in shape but are well developed in size [for a possible explanation, see 3.3].

The cursory review above shows that the morphological traits in the burrowing adult females are not uniform. Indeed the trullae, especially the median pair, are saw-toothed on most species, which is easily explainable, but even this tendency is not without exception. It seems certain that, in the exceptional species, the trullae are still used like a knife to form a burrow under the leaf tomentum. In this regard, *Cephalaspidiotus palaquii* [2.16.1] is especially noteworthy. It shows no evident modifications to the trullae, pectinae, or dorsal macroducts in association with burrowing, in spite of the fact that it forms a large familial burrow [3.3]. The bipartite body of this species with its enlarged cephalothorax may be the only evident modification, because the occurrence of a deep constriction between the metathorax and abdomen is unusual (in contrast with the occurrence of a constriction between the meso- and metathorax, which is not infrequent). *Kochummenaspis filiorum* [2.18.1] has a tripartite body, constricted between the meso- and metathorax and also between the metathorax and the abdomen. It agrees with *C. palaquii* in forming a large familial burrow [3.3]. Their constricted bodies may move in some peculiar manner.

3.3. Familial burrows

The females of *Cephalaspidiotus palaquii* [2.16.1] and *Kochummenaspis filiorum* [2.18.1] form extraordinarily large burrows, in which males stay, grow, form their tests, and metamorphose into the adult stage. The burrow attains about 3–5mm across, and each may be large enough to accommodate a good number of male tests. However, it seems that the number of male offspring produced by one adult female is generally few in these species.

The largest number of male tests observed in one maternal burrow was ten in *C. palaquii* and seven in *K. filiorum*. Furthermore, not all the examined burrows harboured male tests. Winged adult males were obtained from a few burrows of *C. palaquii*.

I have failed to find male tests outside the burrows in *Cephalaspidiotus palaquii* and *Kochummenaspis filiorum*. In both species, the first-instar males are remarkably different from the first-instar females in having much shorter legs (Figs 50, 55, and 56). These short legs support the view that the males occur exclusively within the maternal burrows. (The first-instar male of *K. filiorum* is provided with well-developed caudal setae. On the other hand, in the first instar of *C. palaquii*, the caudal setae in the male are much shorter than those in the female, as might be expected on the assumption that the caudal setae are useful for dispersal by wind.) A similar case of sexual dimorphism in the first instar is known in *Conchaspis socialis* Green (Conchaspididae), which forms a familial test (Takagi, 1997). In *K. filiorum*, the first-instar male and female noticeably differ also in the shape of the trullae situated near the apex of the pygidium. These trullae are short and serrate in the male (Fig. 56), whereas in the female they are prominent and so deeply incised as to be bilobulate, somewhat like the jaws of an open wrench or of a pair of pliers (Fig. 55). The second-instar male is similar to the adult female (and also to the second-instar female) in having elongate and serrate median trullae (Fig. 54). Because the male stays within the maternal burrow during the immature stages, the serrate trullae in the nymphal stages are useless and may simply reflect the state in the adult female. On the other hand, the trullae in the first-instar female are not only remarkable in size but also quite unique in shape, and must have some function. The first-instar female does not burrow after settling on a new site, the exuvial cast being left on the surface of the tomentum after the moult to the second instar, in which the female starts to burrow under the tomentum. Apparently the trullae in the first-instar female are not used for burrowing. To proceed further on the role of the trullae in this stage may be to commit a mere speculation, but it would not be unreasonable to make an analogy between the trullae and an open wrench or a pair of pliers. Using this analogy, the trullae are incised so deeply that their lobules or jaws may be long enough to seize several slender terminal hairs of tomentum-composing trichomes between them. If the analogy is not misleading, the trullae should be useful for anchoring the insect body to the flossy surface of the tomentum. (I observed some ten exuvial casts of the firstr-instar female *in situ* on the tomentum, using a scanning electron microscope. The casts were embedded in the surface of the tomentum, with the margin, especially of the abdomen, covered with terminal hairs of trichomes protruding from around. The posterior end of the abdomen was thus concealed from view, and I failed to see how the trullae were held on the tomentum.)

The familial (or, to be more exact, matrifilial) burrows suggest that *Cephalaspidiotus palaquii* and *Kochummenaspis filiorum* should be advanced burrowing forms. Curiously enough, *C. palaquii* is very similar to certain non-burrowing Aspidiotina in its pygidial characters and may have changed little from its non-burrowing ancestor except for the bipartite body [3.2]. On the other hand, *K. filiorum* is an unusual form of uncertain relationship. Whether it belongs to the tribe Parlatoriini or not, the species apparently has undergone a great change in its morphology in association with the evolution of its burrowing habit. The two species, however, do agree in maintaining well-developed glanduliferous pectinae (which are well fimbriate in *C. palaquii*, while shaped like gland spines in *K. filiorum*). The second-instar female and male are also provided with well-developed pectinae in *C. palaquii*, whereas they possess only a few spiniform pectinae in *K. filiorum* [the second-instar male of this species: Fig. 54].

The female test of *Cephalaspidiotus palaquii* is very thin and fragile, and that of *Kochummenaspis filiorum* is hardly recognizable. Burrows of *K. filiorum* have been observed by scanning electron microscopy (Figs 58–64). The burrow is formed under the tomentum, which is composed of interwoven stalked-stellate trichomes, and its ceiling is made of trichomes cut off at their bases. The central area of the ceiling is covered with the exuvial cast of the second instar and a thin film surrounding the cast, both appearing to be adhered to the surface of the ceiling, which, otherwise, is exposed (Fig. 59). At higher magnifications (Figs 60–62), the film proves to be composed of wax filaments, which are divisible into two main types in thickness, suggesting that they originate from different secretory organs. The glanduliferous pectinae and the long filiform dorsal ducts arising from the pygidial margin may be the main organs secreting these wax filaments. The pectinae may be responsible for the fine filaments, which are crossed to form a loose net, and this net intermingles with another loose net composed of the thick filaments probably secreted by the filiform marginal ducts. If this interpretation is correct, we find an explanation for the well-developed pectinae in the adult female that are maintained in contrast with the reductive ducts. The test is poorly formed owing to the reductive dorsal ducts. However, this vestigial test may still be useful for strengthening the ceiling of the burrow, and the role of the pectinae is now less subsidiary in forming it. Little wax is found on the floor of the burrow, where bases of trichomes cut off are exposed and clearly visible (Fig. 63). These bases show a smooth cut (Fig. 64), which the insect must have made by the use of the median trullae. The straight serrate margin of the median trulla in the adult female is about twice as long as the diameter of the base of a trichome and, thus, it is apparently long enough to saw the trichome.

3.4. Second-instar males

I hold the view that the pygidial appendages evolved primarily in the adult female associated with test formation, and that they are also manifested in the nymphal stages in a more or less modified state. So far as the pygidial appendages are concerned, the second-instar female is very similar to the conspecific adult female (except for pupillarial forms, in which the pygidial appendages in the adult female tend to be modified and reduced), whereas the second-instar male may be similar (homomorphic) or quite dissimilar (heteromorphic) to the adult and second-instar females of the same species. Furthermore, in the Diaspidini, the heteromorphic second-instar males are generally provided with modified ducts on the margin of the abdomen. Homomorphic and heteromorphic forms of the second-instar male may occur in species that are very closely similar in the adult females, which suggest that the species should be very closely related unless convergence is involved. The change from one form to the other in the second-instar male, therefore, can be abrupt. In my supposition, the manifestation of a heteromorphic phenotype is due to an atavistic mechanism, reflecting the character pattern of a remote ancestor. However, homomorphism and heteromorphism are not always discrete, and there occur heteromorphic forms that approach the conspecific female patterns in various degrees (see below).

Burrowing starts in the second instar, and in the male this instar is the only stage that can burrow. So far as observed, the burrowing second-instar males are homomorphic, but not all homomorphic second-instar males burrow.

Heteromorphism prevails especially in the tribe Diaspidini. In the present study 12 species belong to the tribe, and the second-instar males of ten species have been available and examined. Of these, the second-instar males of only *Mayonia callicarpae* (Fig. 19), *Kulatinganaspis quezonensis* (Fig. 24), and *Singapuraspis lasianthi* (Fig. 29) are homomorphic; the males of the former two species burrow under the leaf tomentum and the male of the last lives among the dense erect hairs on the twigs and leaves. The second-instar males of the other seven species are heteromorphic, but they are various in the structure of the pygidial margin. The second-instar male of *Pinangaspis uniclavata* (Fig. 14) has poorly developed processes on the pygidial margin as in many other Chionaspidina. This type of heteromorphic form probably approaches the supposed *Ulucoccus*-like ancestor [3.1] to a considerable degree.

Of the remaining six species, the second-instar males of *Damaia swintoniae* (Fig. 2), *Semonggokia xylopiae* (Fig. 6), and two species of *Chionandaspis* (Fig. 8 and Fig. 11) are not the same in their morphological details, but they are similar in having a pair of prominent and dentate or serrate processes, which are membranous or not strongly sclerotized, at the apex of the pygidium. These processes apparently correspond to the dentate or serrate median trullae in the adult females. The second-instar males of *D. swintoniae* and *S. xylopiae* are provided with remarkable pectinae or pectina-like processes on the pygidial margin, which also correspond to the well-developed lateral trullae in the adult females (because the trullae and the pectinae are homologous [3.1]). It should be emphasized that all these pygidial processes in the second-instar males exhibit new characters (in terms of shape, number, or sclerotization) as compared with the appendages in the adult females they correspond to. The second-instar male of *Bayokaspis luzonensis* (Fig. 21) is heteromorphic in possessing glanduliferous craters (communal pores of ducts), which are characteristic of the heteromorphic second-instar males of other Fioriniina and also of Kuwanaspidina. Nevertheless, it has good median trullae, which are similar to those in the second-instar female, the only burrowing stage in this pupillarial species, rather than to those in the adult female. These cases suggest that the phenotypic manifestation in the heteromorphic second-instar male is influenced to a varying degree by the genetic change effected in the burrowing female.

The second-instar male of *Pinnaspis serrulata* (Fig. 16) affords another case. It is provided with modified macroducts of the type common to the heteromorphic second-instar males of many Chionaspidina. Yet it bears no resemblance to the latter in having a continuous series of prominent angular lobes along the pygidial margin, and does not resemble the adult female either, there being no evident correspondence between their pygidial appendages.

The heteromorphic second-instar males of the Diaspidini form the test around the growing body, which makes no particular movement. This is well shown by the tricarinate type of test, in which the three carinae run undisturbed along the length of the dorsal surface. Various pygidial processes in heteromorphic forms, such as observed in the present study, apparently have no adaptive significance for test formation. Basically atavistic, but produced under the influence of the genetic change effected in the evolving female, and yet relatively free from adaptive constraint, heteromorphic forms may change dramatically, sometimes resulting in novel phenotypes, as well exemplified by *Pinnaspis serrulata*. Thus, heteromorphism may bring hidden phenotypic potential into view.

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CORRECTIONS

TAKAGI, S., 2002. One new subfamily and two new tribes of the Diaspididae (Homoptera: Coccoidea). *Ins. matsum. n. s.* 59: 55–100, 2 tables, 26 figs.

p. 57, line 9 from bottom: for 'THREE' read 'TWO'

p. 71, line 2 from top: for 'angiospermes' read 'angiosperms'

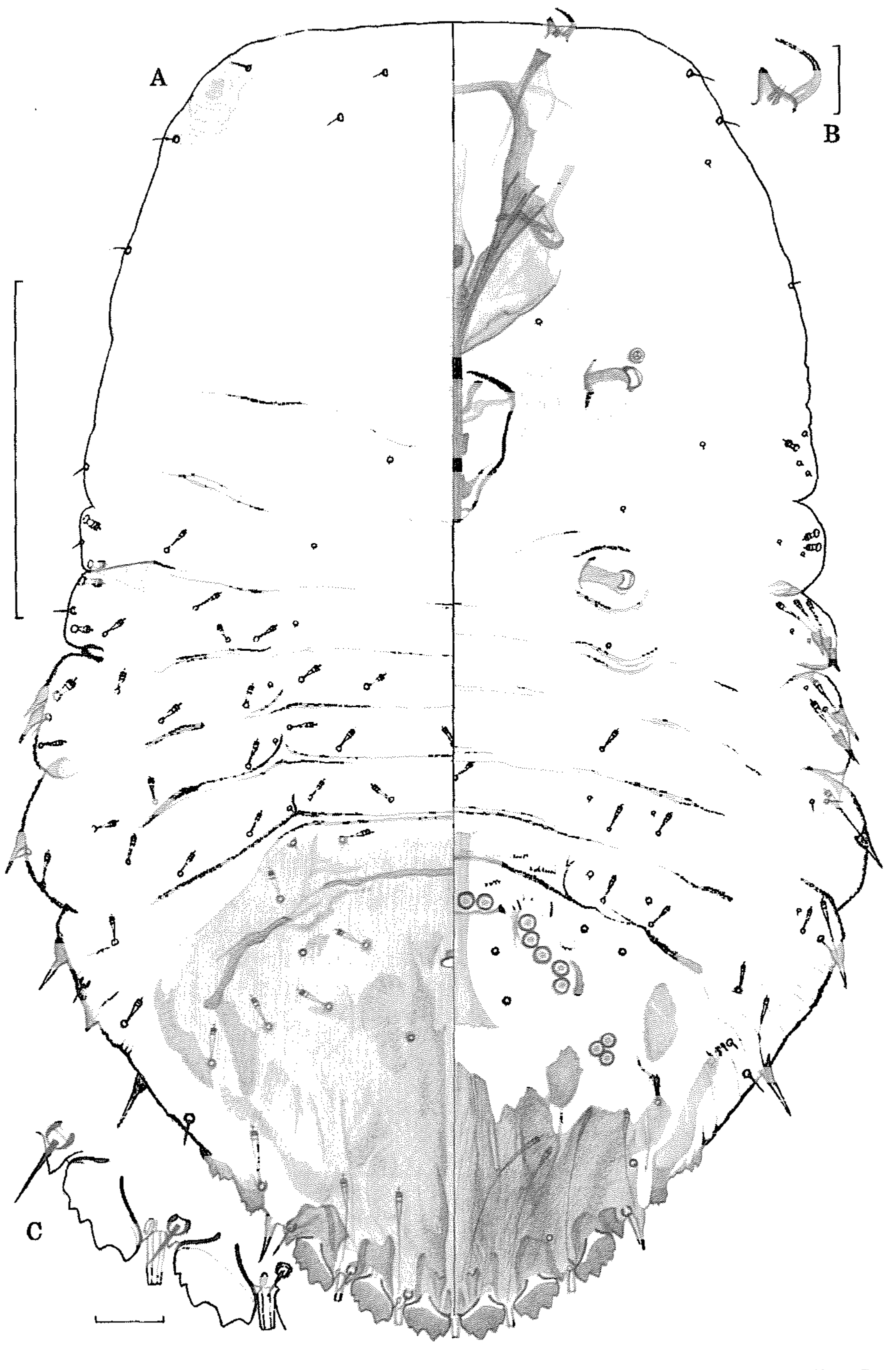

Fig. 1. *Damaia swintoniae*: adult female [91ML-247]. B: antenna; C: second and third trullae. Scales: A, 100µm; B and C, 10µm.

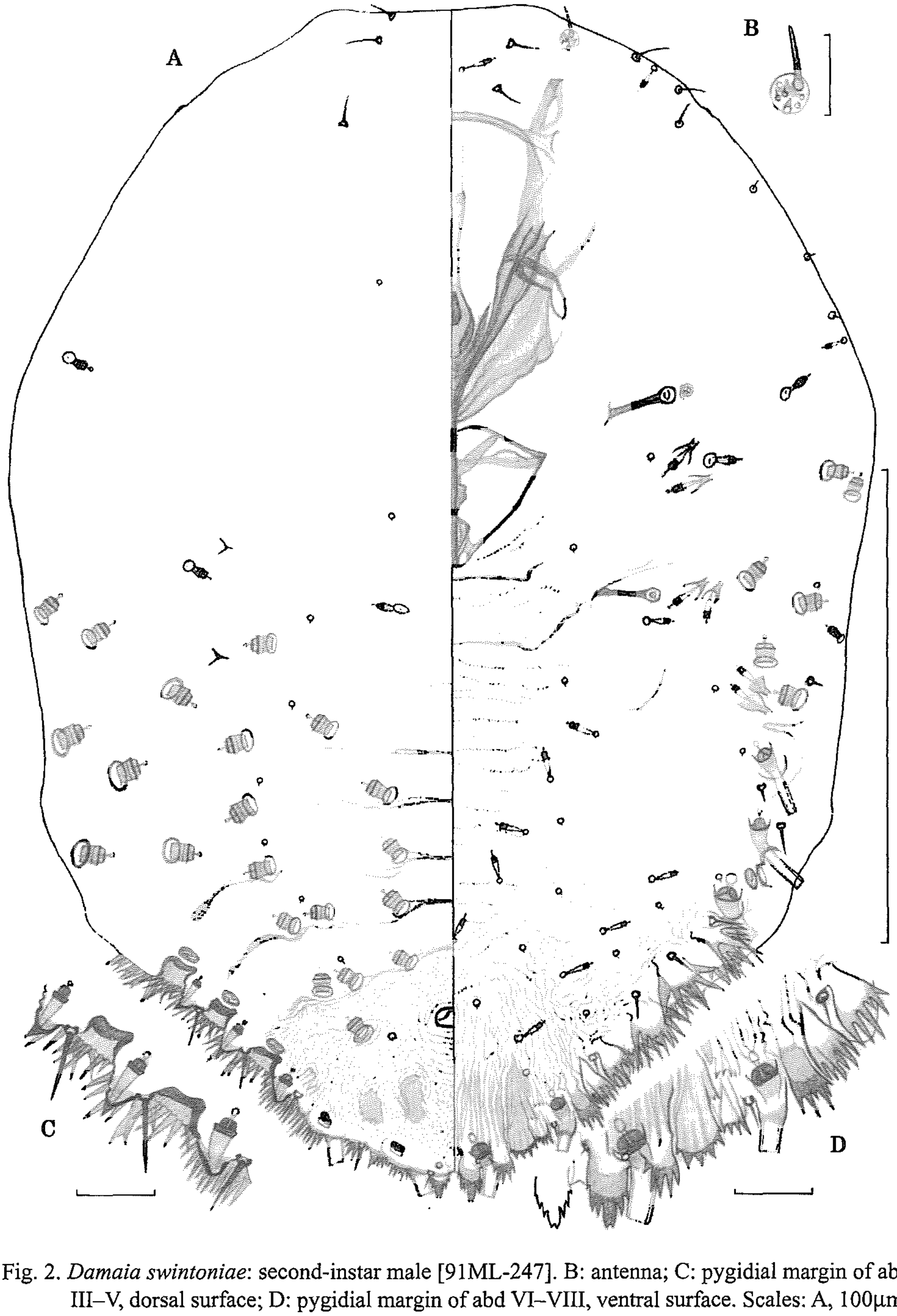

Fig. 2. *Damaia swintoniae*: second-instar male [91ML-247]. B: antenna; C: pygidial margin of abd III–V, dorsal surface; D: pygidial margin of abd VI–VIII, ventral surface. Scales: A, 100μm; B–D, 10μm.

Fig. 3. *Damaia swintoniae*: first-instar nymph [91ML-247]. B: antenna; C: caudal seta. Scale (for A–C): 100µm.

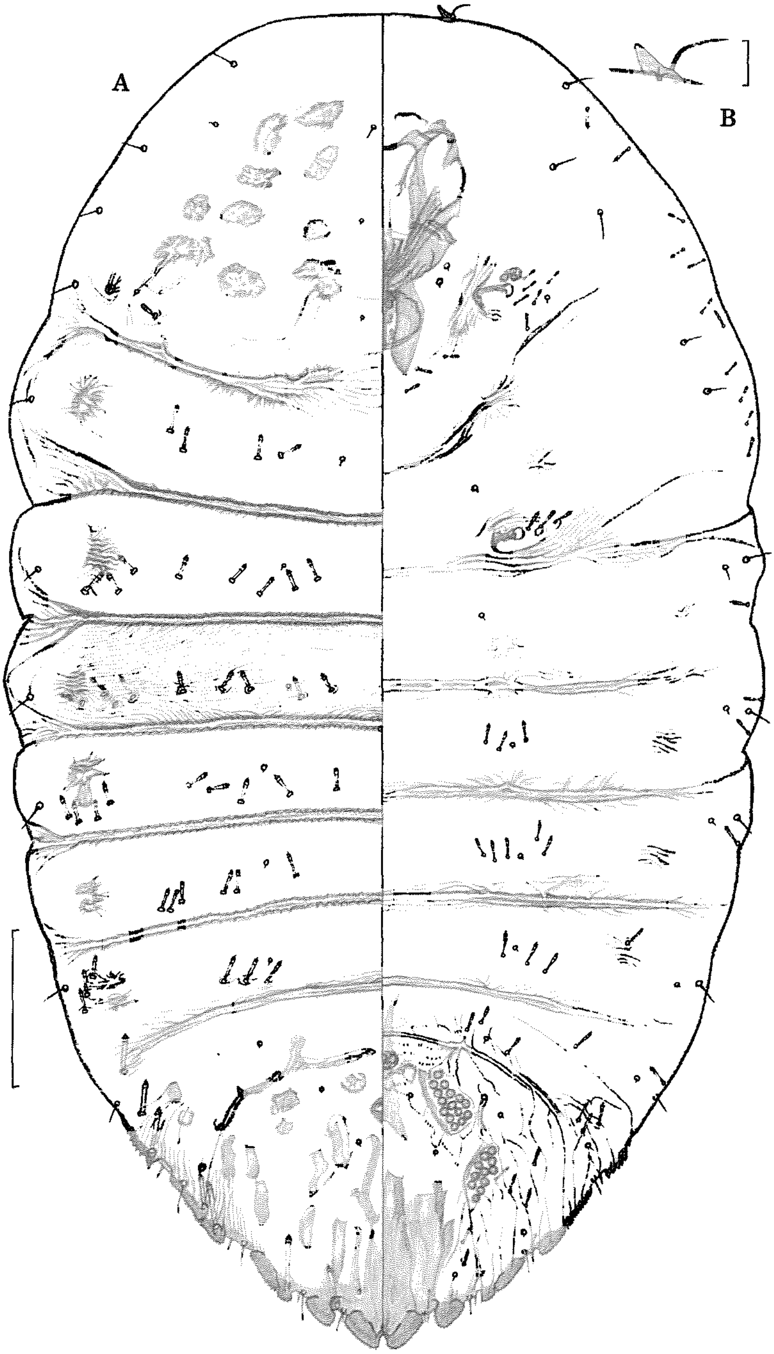

Fig. 4. *Semonggokia xylopiae*: adult female. B: antenna. Scales: A, 100µm; B, 10µm.

Fig. 5. *Semonggokia xylopiae*. A: adult female, pygidium; B: exuvial cast of the second-instar female, pygidial margin. Scales: 10μm.

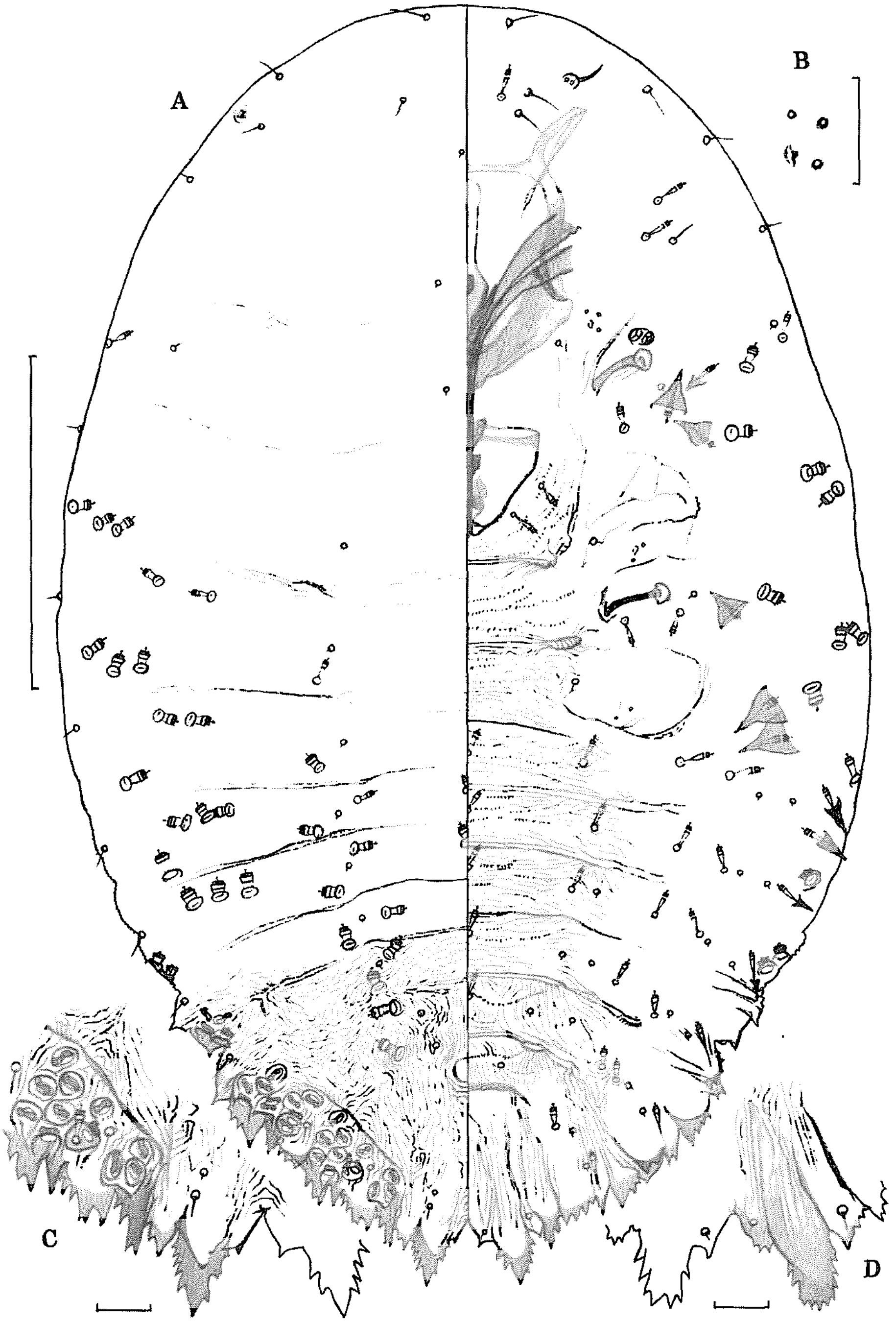

Fig. 6. *Semonggokia xylopiae*: second-instar male. B: rudiments of the fore leg; C: apex of the pygidium, dorsal surface; D: apical processes of the pygidium in another specimen, ventral surface. Scales: A, 100μm; B–D, 10μm.

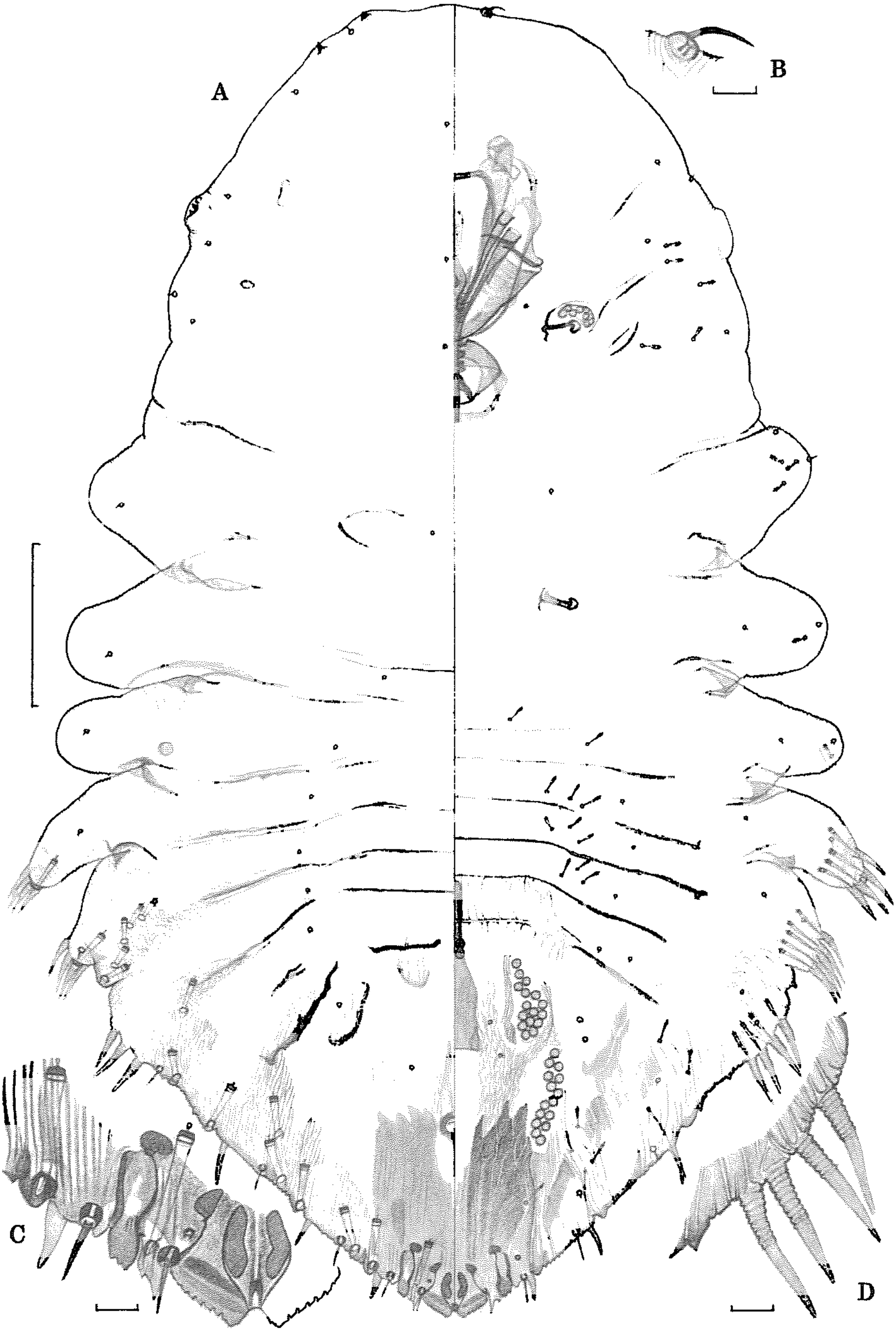

Fig. 7. *Chionandaspis ramicola*: adult female. B: antenna; C: apex of the pygidium, dorsal surface; D: marginal gland spines on abd IV. Scales: A, 100μm; B–D, 10μm.

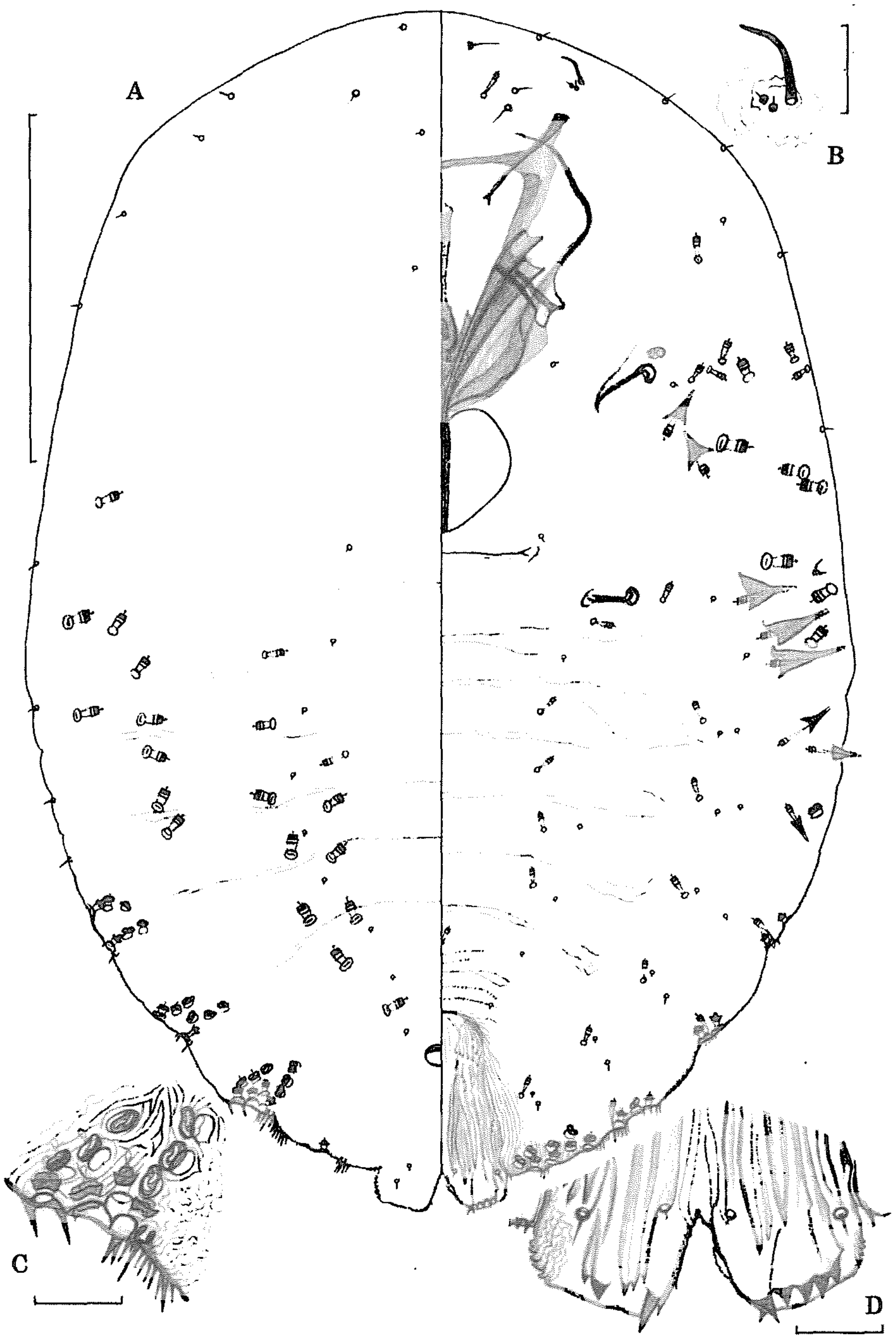

Fig. 8. *Chionandaspis ramicola*: second-instar male. B: antenna; C: dorsal ducts on the margin of abd VI; D: apical processes of the pygidium, ventral surface. Scales: A, 100µm; B–D, 10µm.

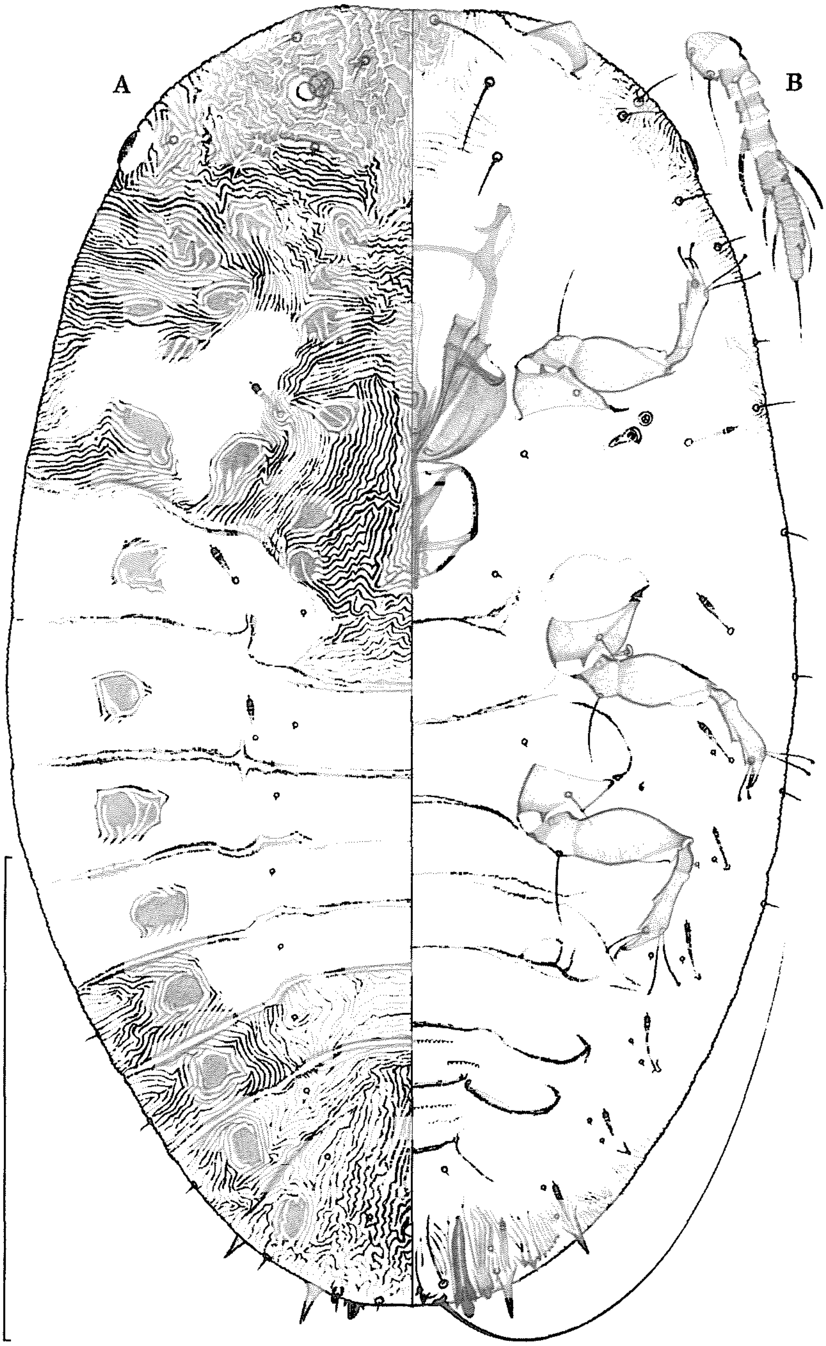

Fig. 9. *Chionandaspis ramicola*: first-instar nymph. B: antenna (figured from another specimen). Scales: A, 100µm; B, 10µm.

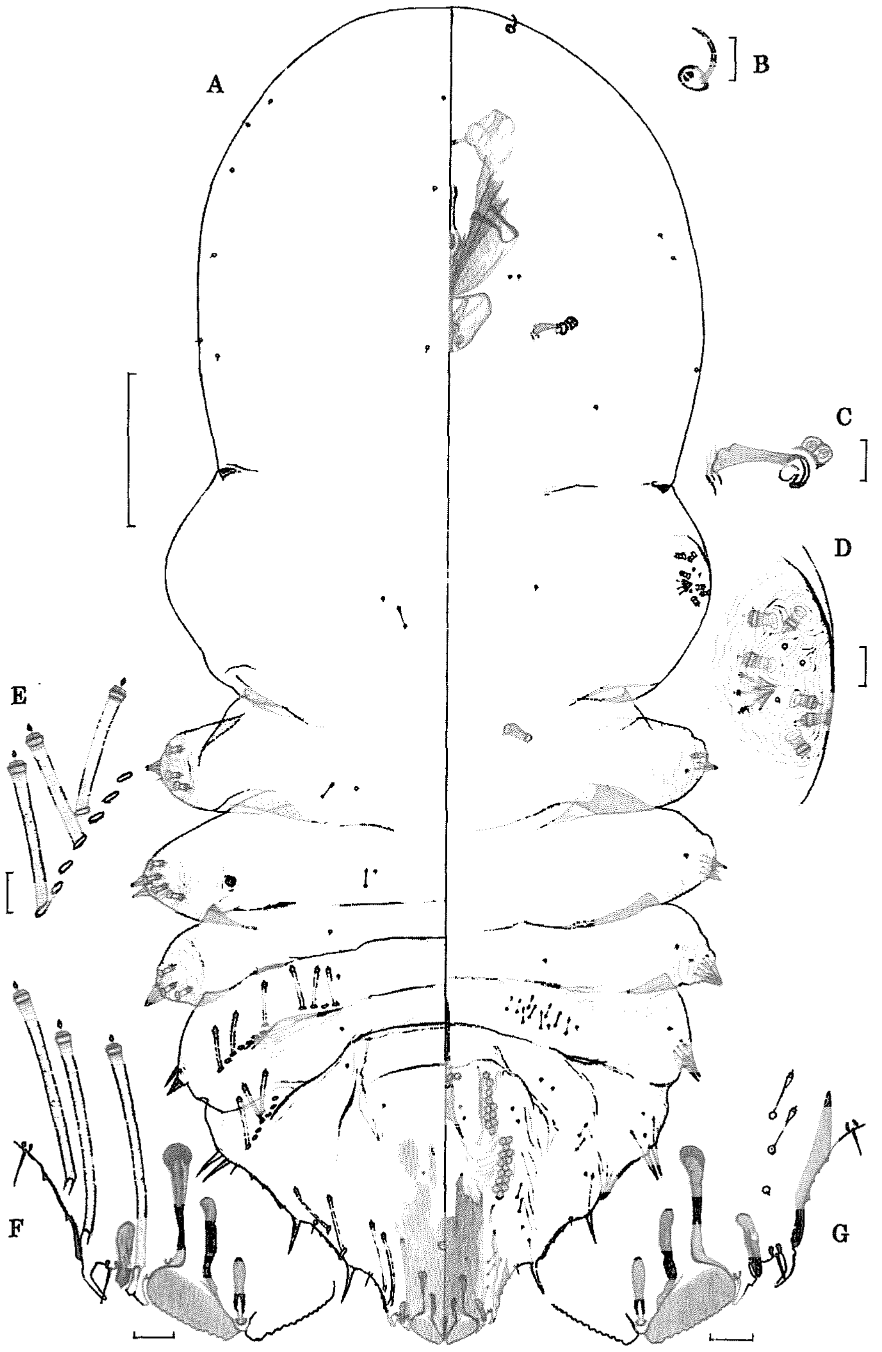

Fig. 10. *Chionandaspis foliicola*: adult female. B: antenna; C: anterior spiracle; D: lateral lobe of the mesothorax; E: submarginal dorsal ducts on abd IV; F: apex of the pygidium, dorsal surface; G: apex of the pygidium, ventral surface. Scales: A, 100µm; B–G, 10µm.

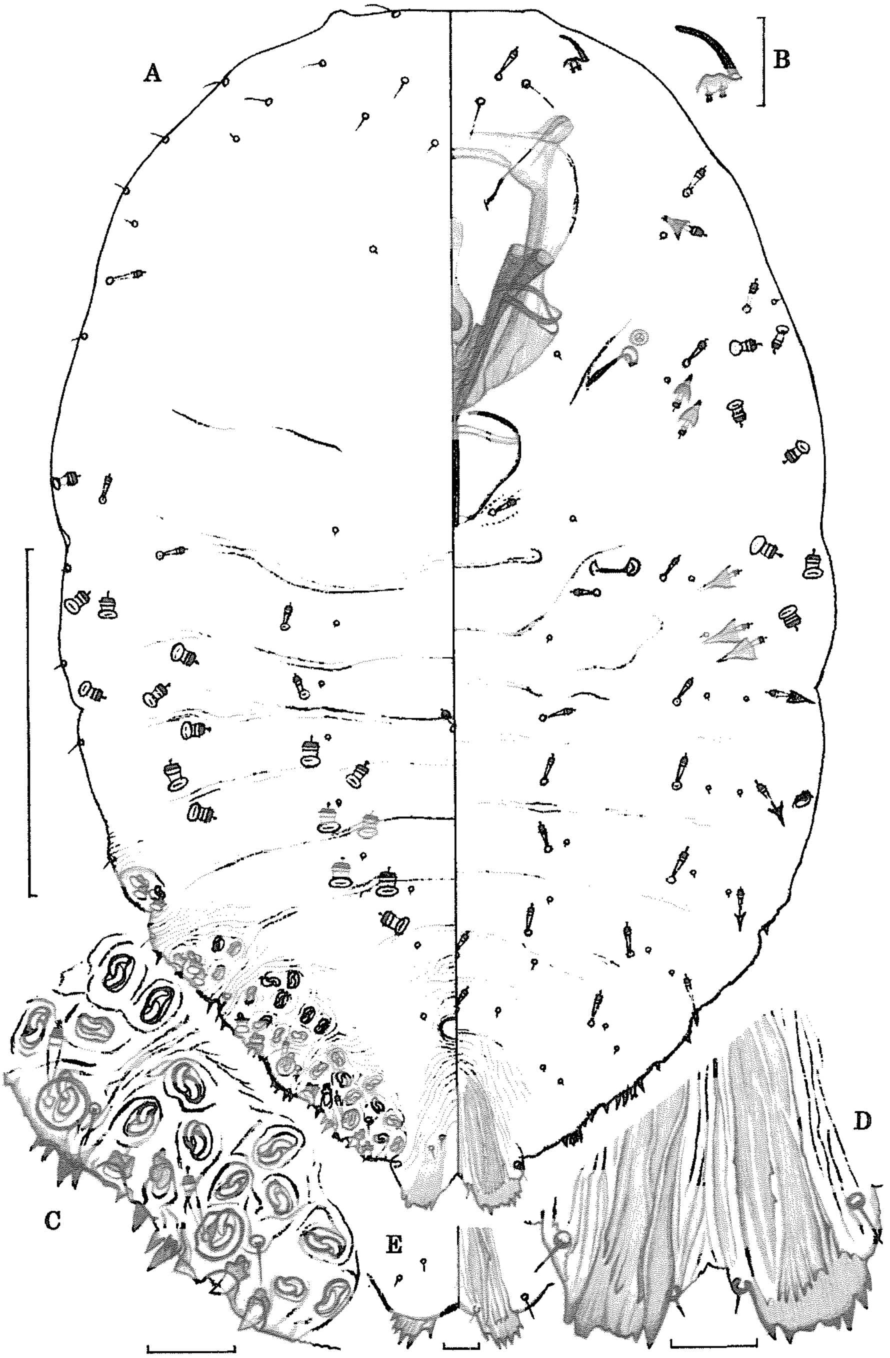

Fig. 11. *Chionandaspis foliicola*: second-instar male. B: antenna; C: dorsal ducts on the margin of abd VI and VII; D: apical processes of the pygidium, ventral surface; E: apical processes of the pygidium in another specimen. Scales: A, 100µm; B–E, 10µm.

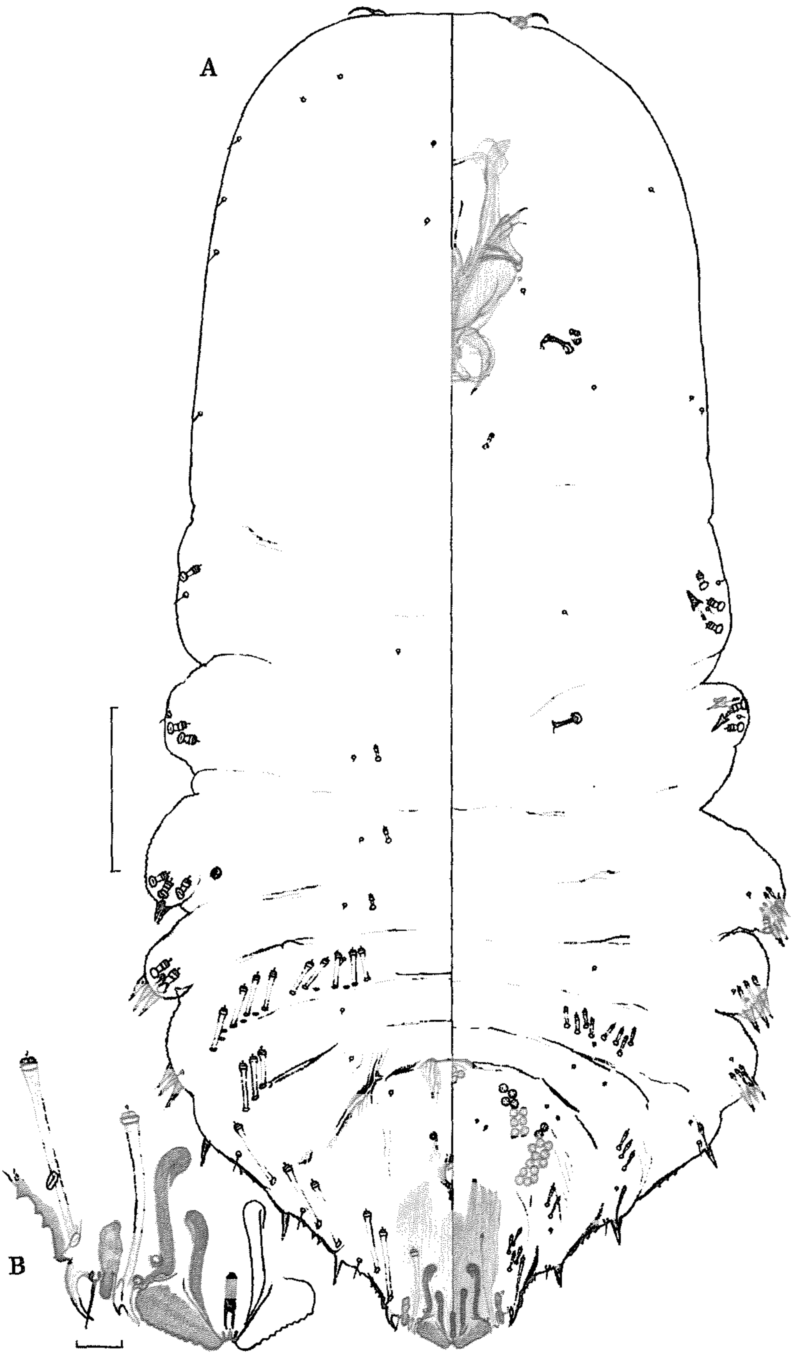

Fig. 12. *Chionandaspis palawanensis*: adult female. B: apex of the pygidium, dorsal surface. Scales: A, 100μm; B, 10μm.

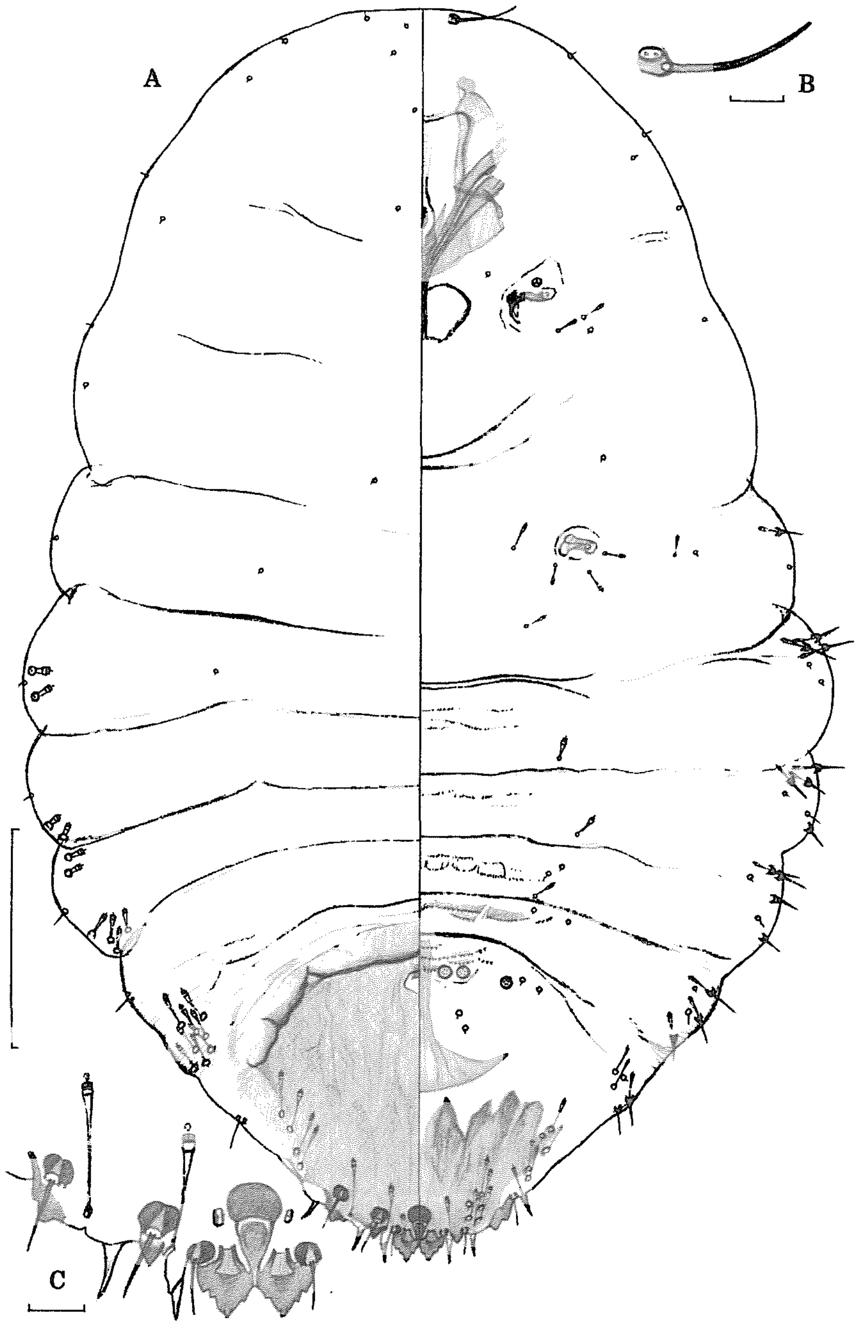

Fig. 13. *Pinangaspis uniclavata*: adult female. B: antenna; C: apex of the pygidium, dorsal surface. Scales: A, 100µm; B and C, 10µm.

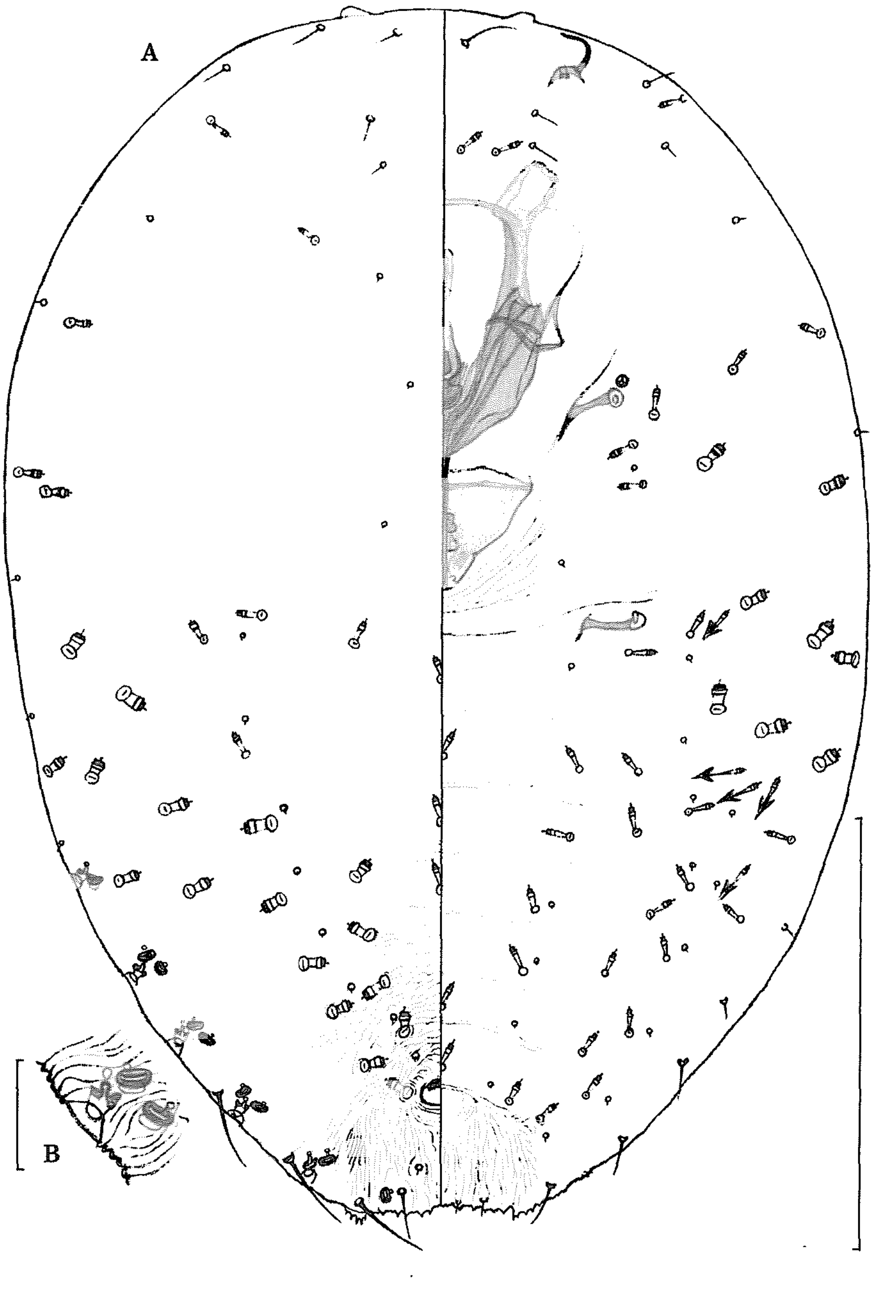

Fig. 14. *Pinangaspis uniclavata*: second-instar male. B: dorsal ducts on the margin of abd IV. Scales: A, 100μm; B, 10μm.

Fig. 15. *Pinnaspis serrulata*: adult female. B: antenna; C: anterior spiracle; D: posterior spiracle; E: pygidium; F: median trullae. Scales: A, 100μm; B–F, 10μm.

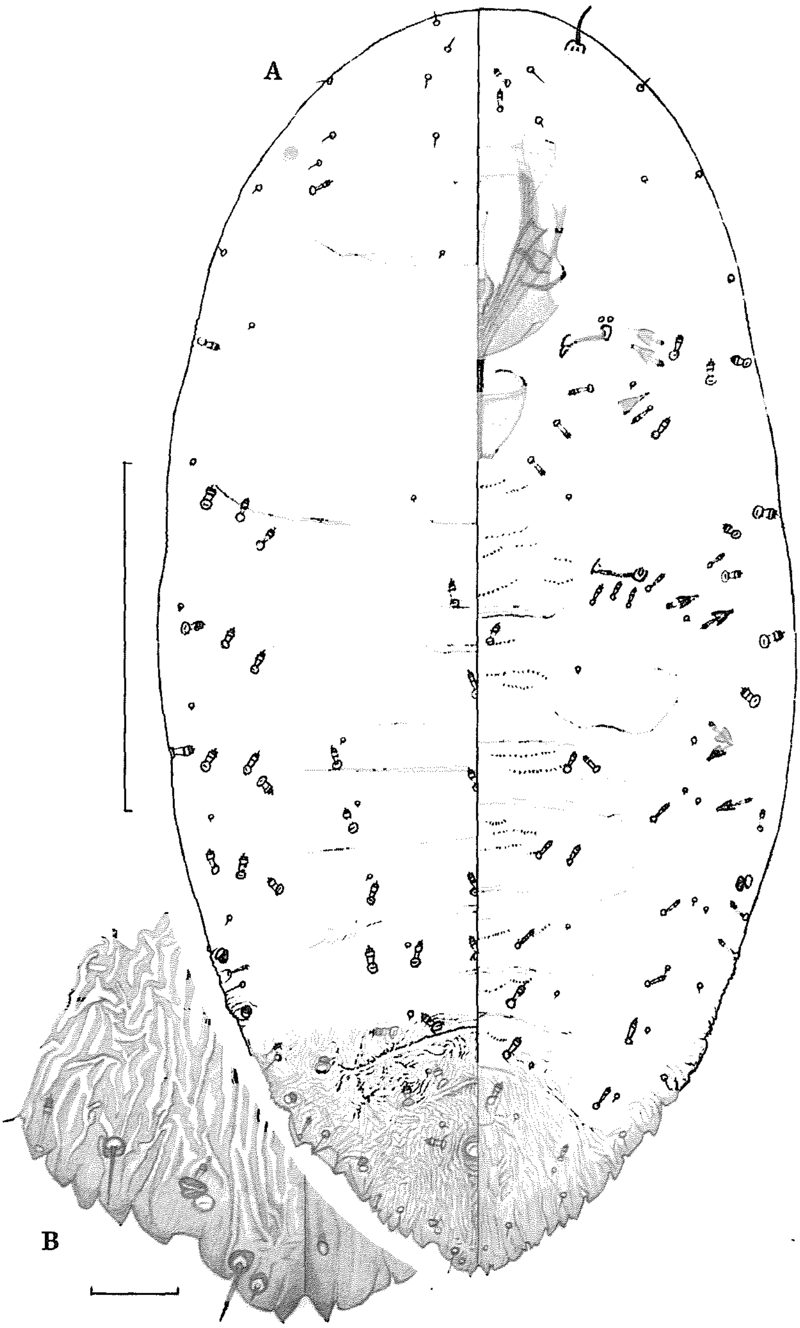

Fig. 16. *Pinnaspis serrulata*: second-instar male. B: pygidial margin of abd VII and VIII, dorsal surface. Scales: A, 100µm; B, 10µm.

Fig. 17. *Pinnaspis simplior*: adult female. B: anterior spiracle; C: pygidium. Scales: A, 100μm; B and C, 10μm.

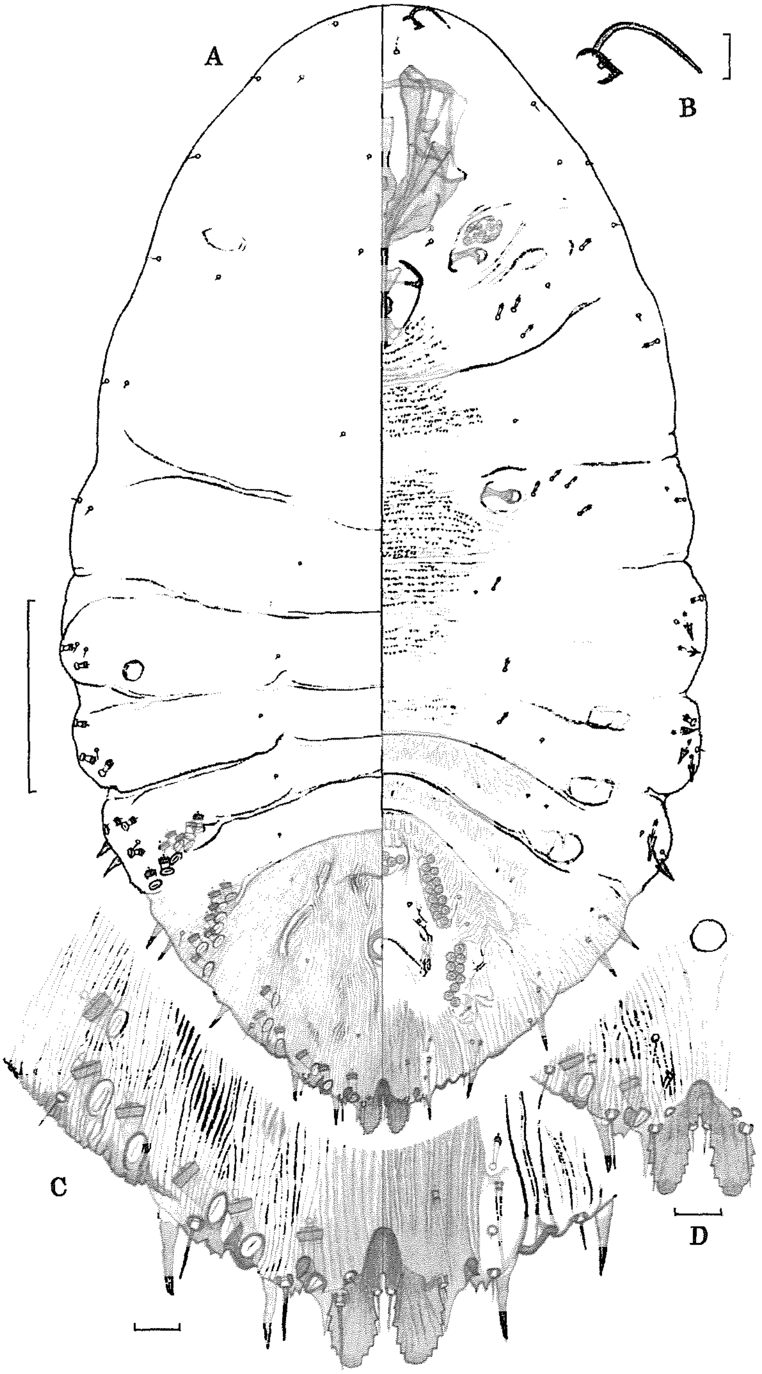

Fig. 18. *Mayonia callicarpae*. A–C: adult female; B: antenna; C: pygidial margin. D: exuvial cast of the second-instar female, apex of the pygidium. Scales: A, 100µm; B–D, 10µm.

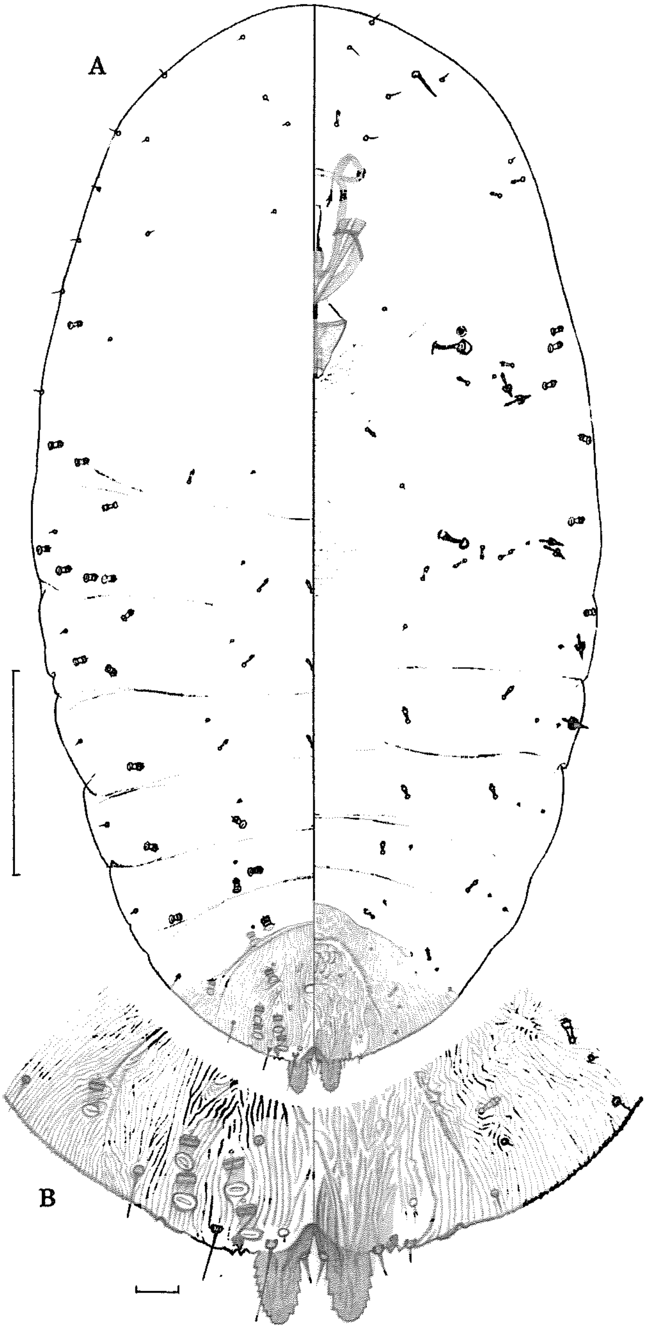

Fig. 19. *Mayonia callicarpae*: second-instar male. B: pygidial margin. Scales: A, 100µm; B, 10µm.

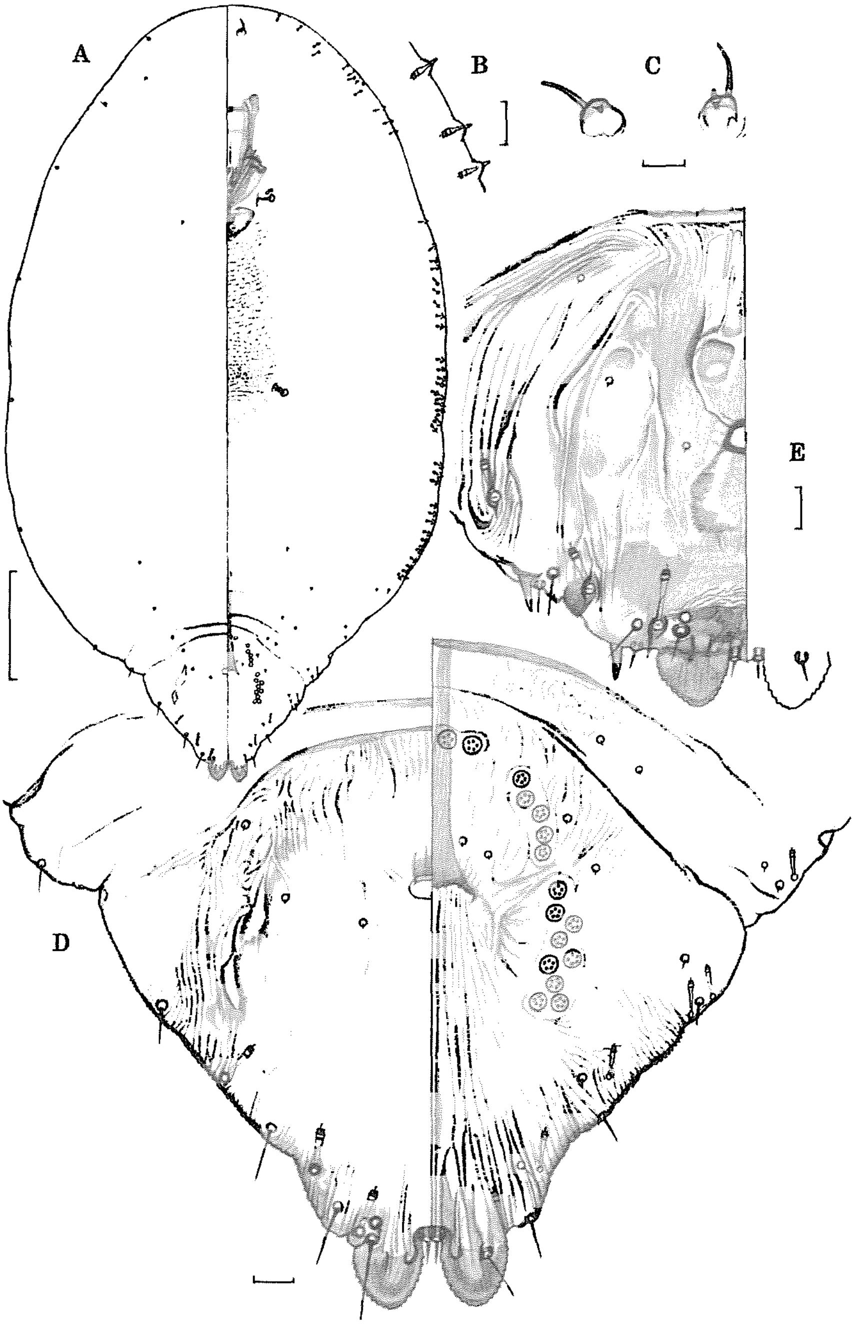

Fig. 20. *Bayokaspis luzonensis*. A–D: adult female [94PL-90]; B: tubercular gland spines on the margin of the prosoma; C: antennae; D: pygidium. E: exuvial cast of the second-instar female [94PL-145], dorsal surface of the pygidium. Scales: A, 100μm; B–E, 10μm.

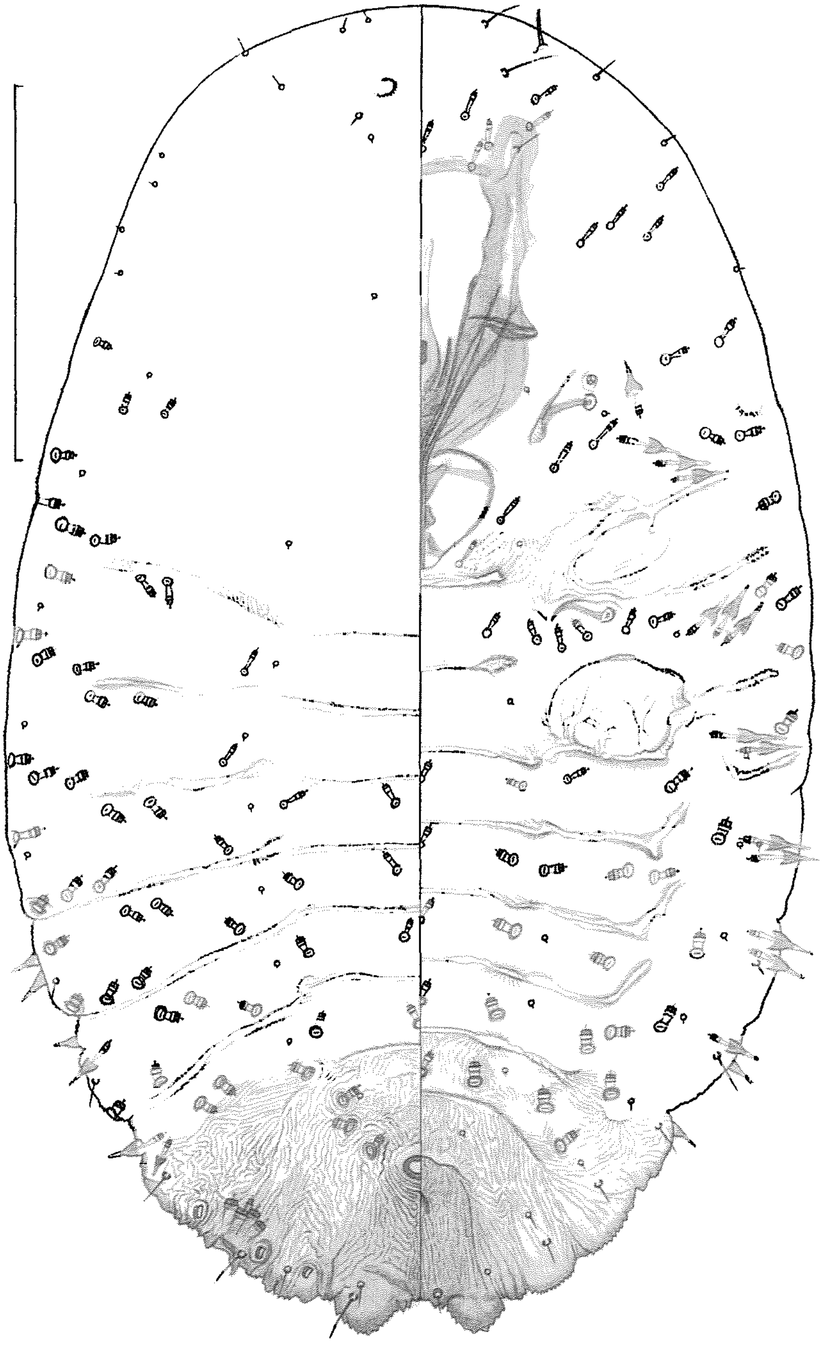

Fig. 21. *Bayokaspis luzonensis*: second-instar male [92PL-104]. Scale: 100µm.

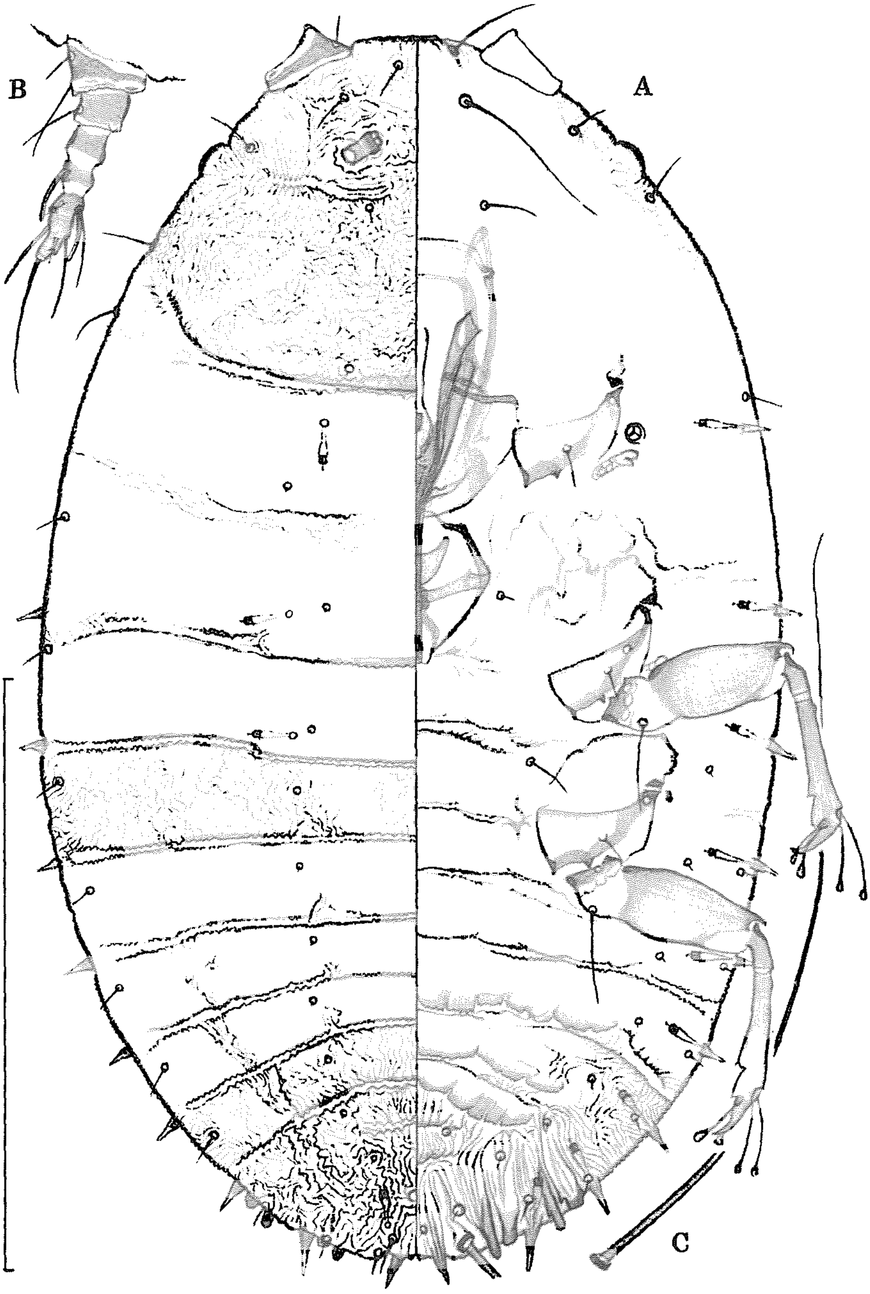

Fig. 22. *Bayokaspis luzonensis*: first-instar nymph [92PL-104]. B: antenna; C: caudal seta. Scale (for A–C): 100μm.

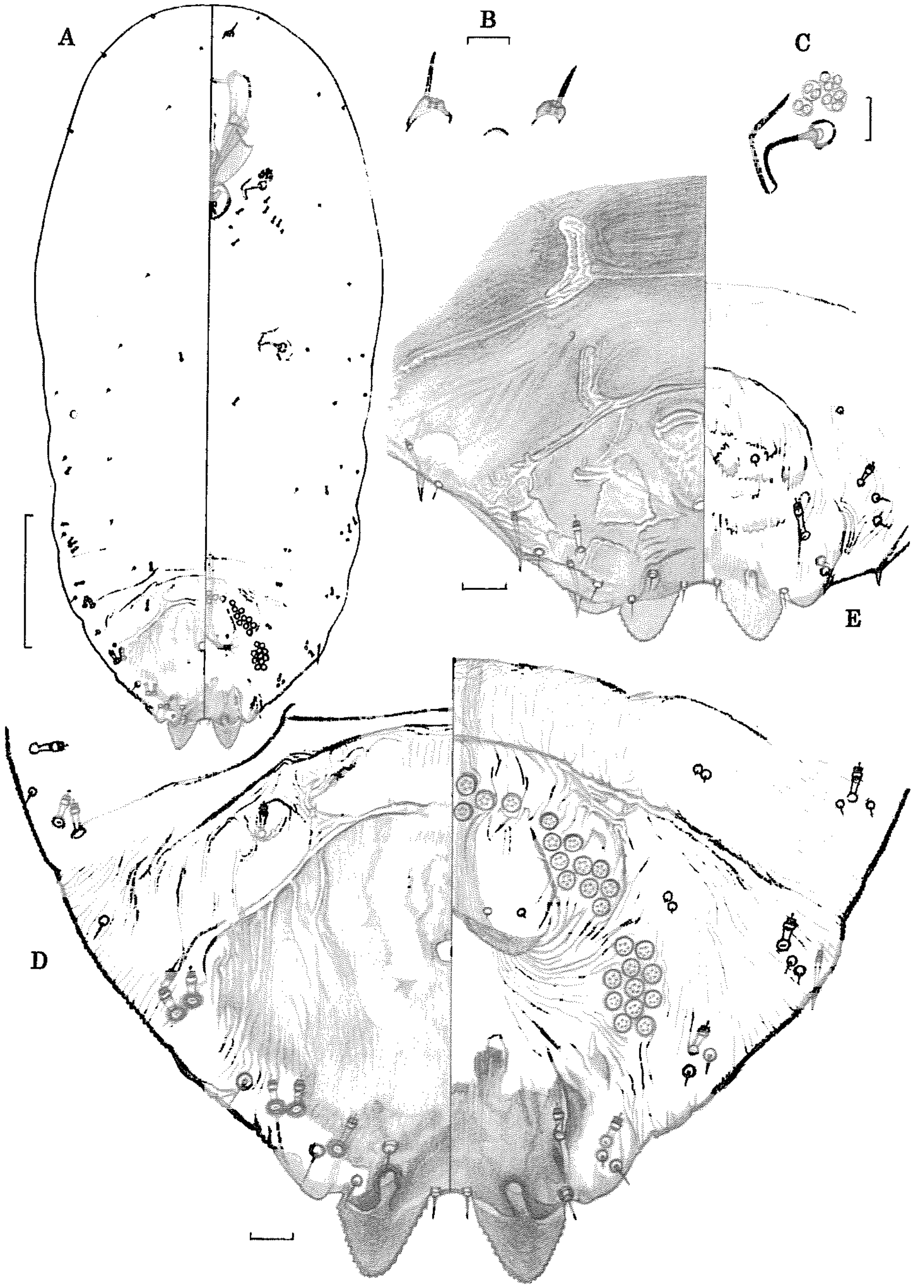

Fig. 23. *Kulatinganaspis quezonensis*. A–D: adult female; B: antennae; C: anterior spiracle; D: pygidium. E: exuvial cast of the second-instar female, pygidium. Scales: A, 100μm; B–E, 10μm.

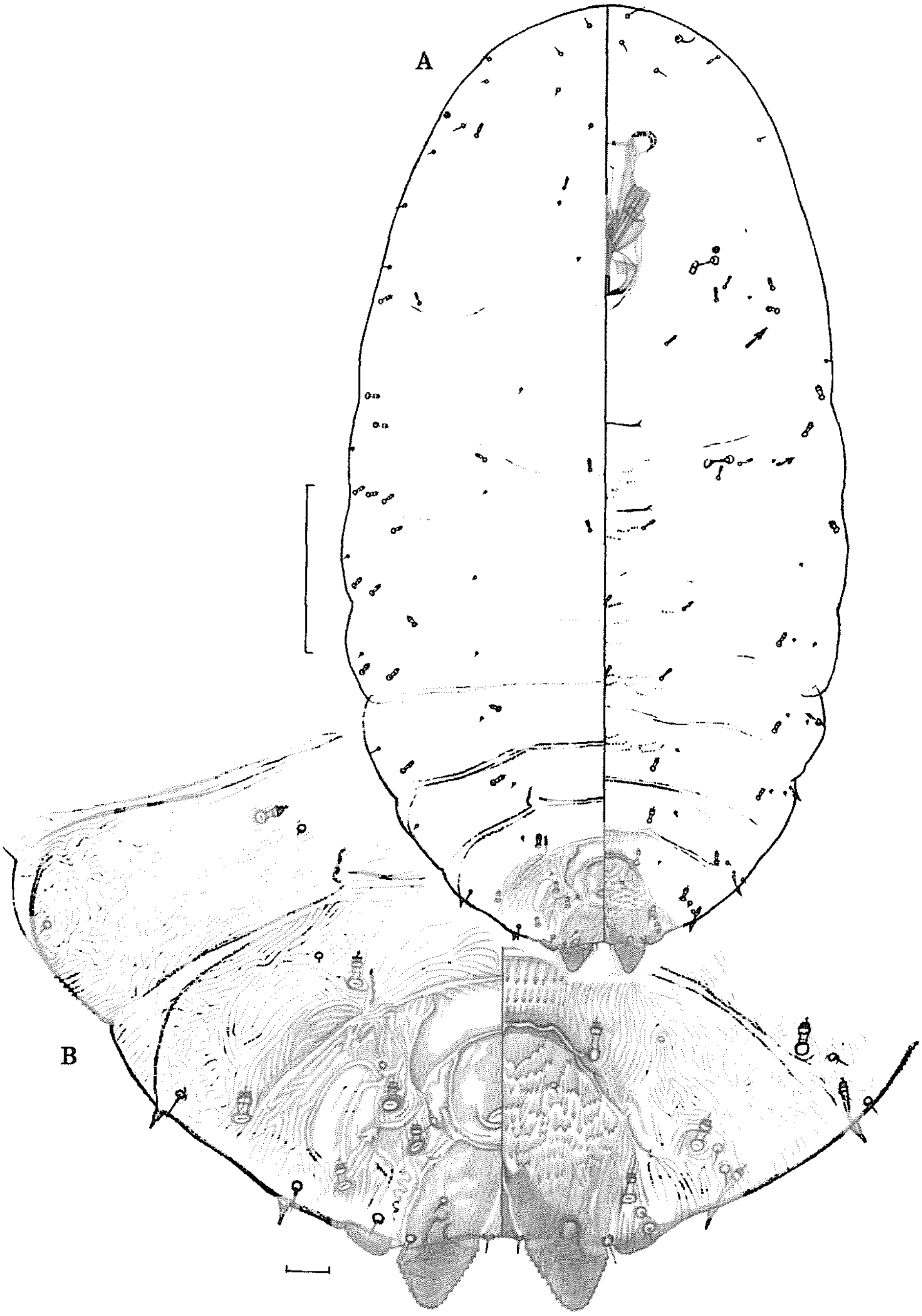

Fig. 24. *Kulatinganaspis quezonensis*: second-instar male. B: pygidium. Scales: A, 100μm; B, 10μm.

Fig. 25. *Kulatinganaspis quezonensis*: first-instar nymph. B: antenna; C: caudal seta. Scales: A (also for C), 100μm; B, 10μm.

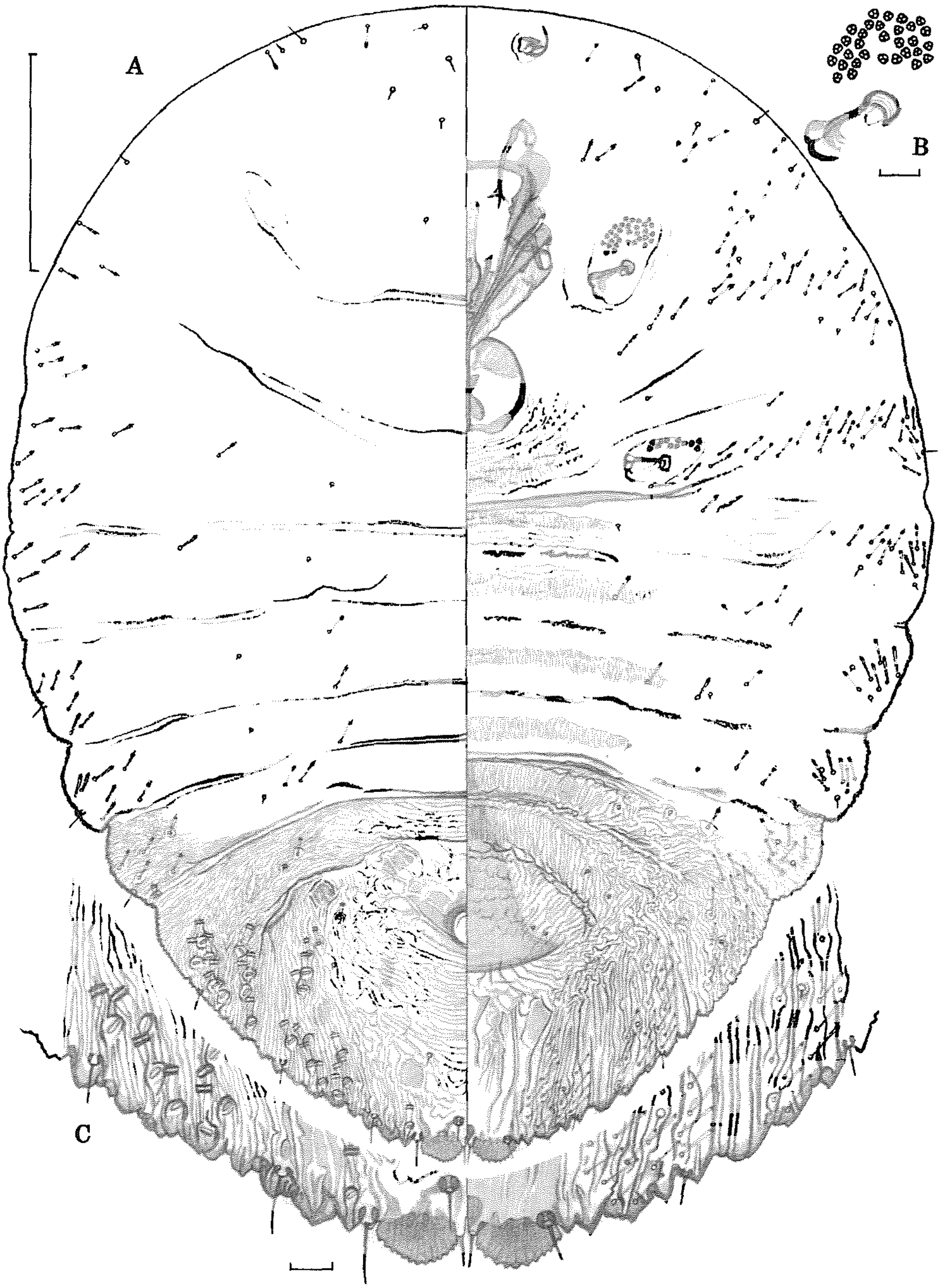

Fig. 26. *Singapuraspis lasianthi*: adult female, figured from an immature specimen. B: anterior spiracle; C: pygidial margin. Scales: A, 100µm; B and C, 10µm.

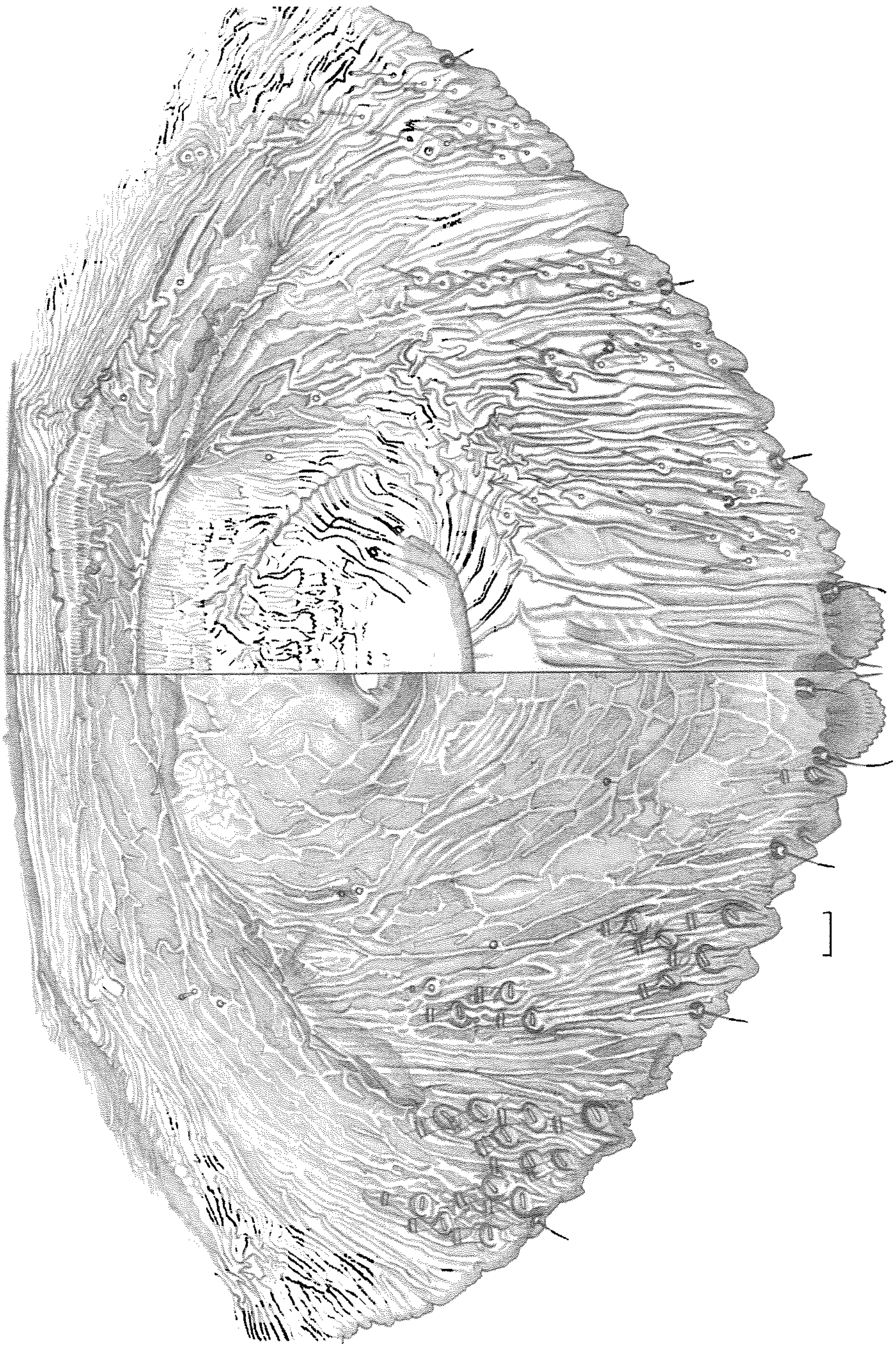

Fig. 27. *Singapuraspis lasianthi*: adult female, pygidium, figured from a full-grown specimen. Scale: 10μm.

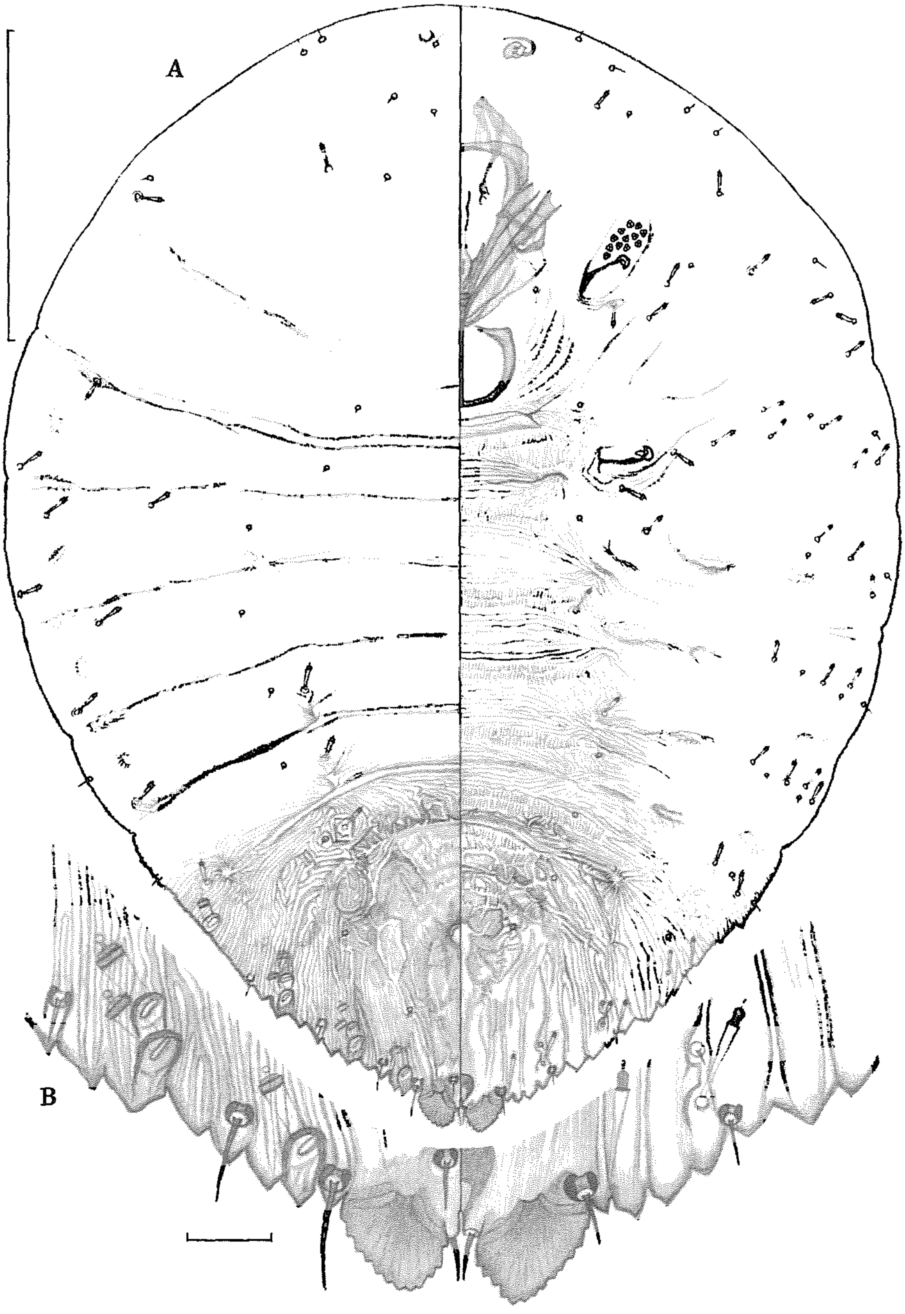

Fig. 28. *Singapuraspis lasianthi*: second-instar female. B: pygidial margin. Scales: A, 100μm; B, 10μm.

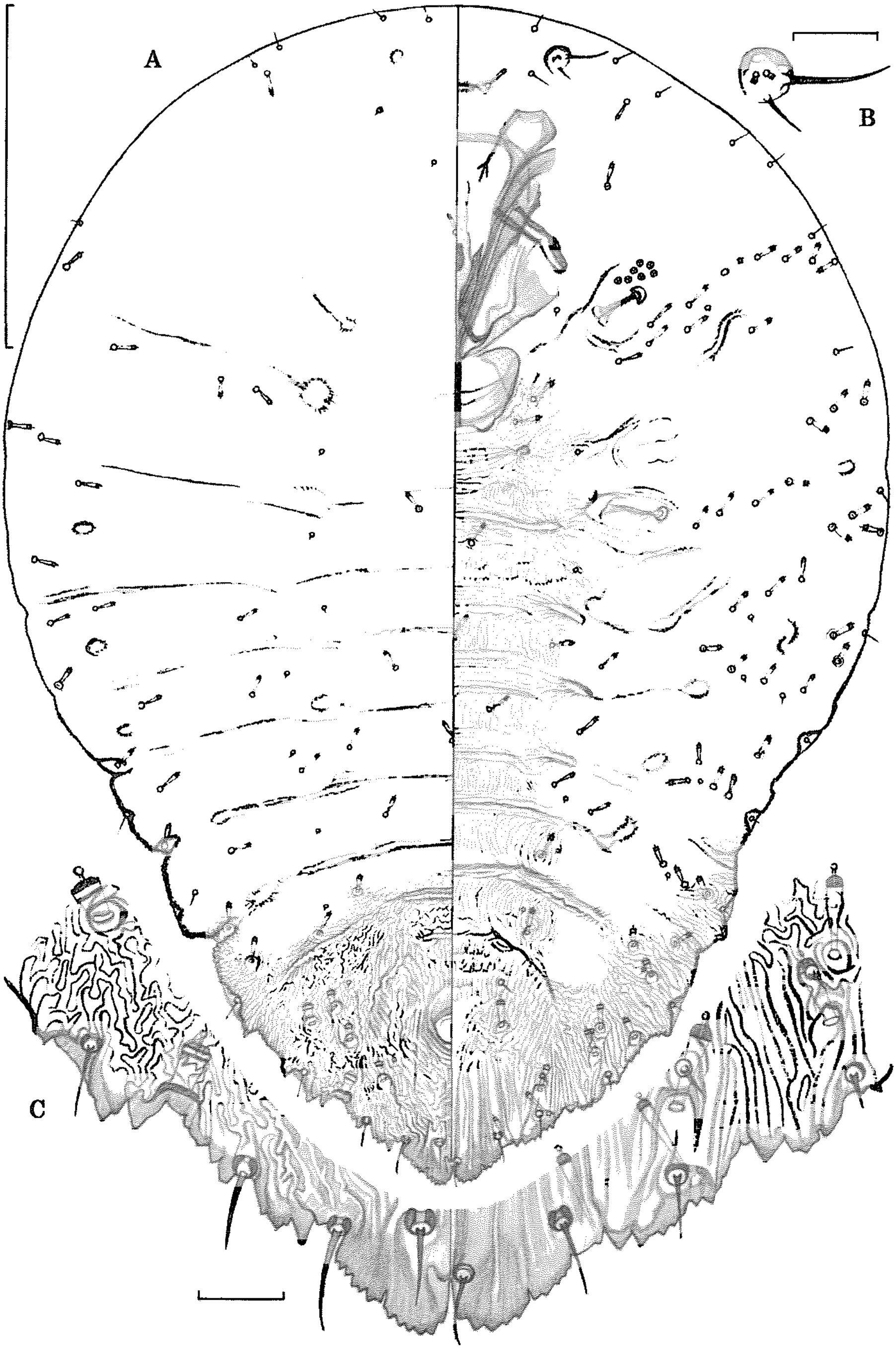

Fig. 29. *Singapuraspis lasianthi*: second-instar male. B: antenna; C: pygidial margin. Scales: A, 100μm; B and C, 10μm.

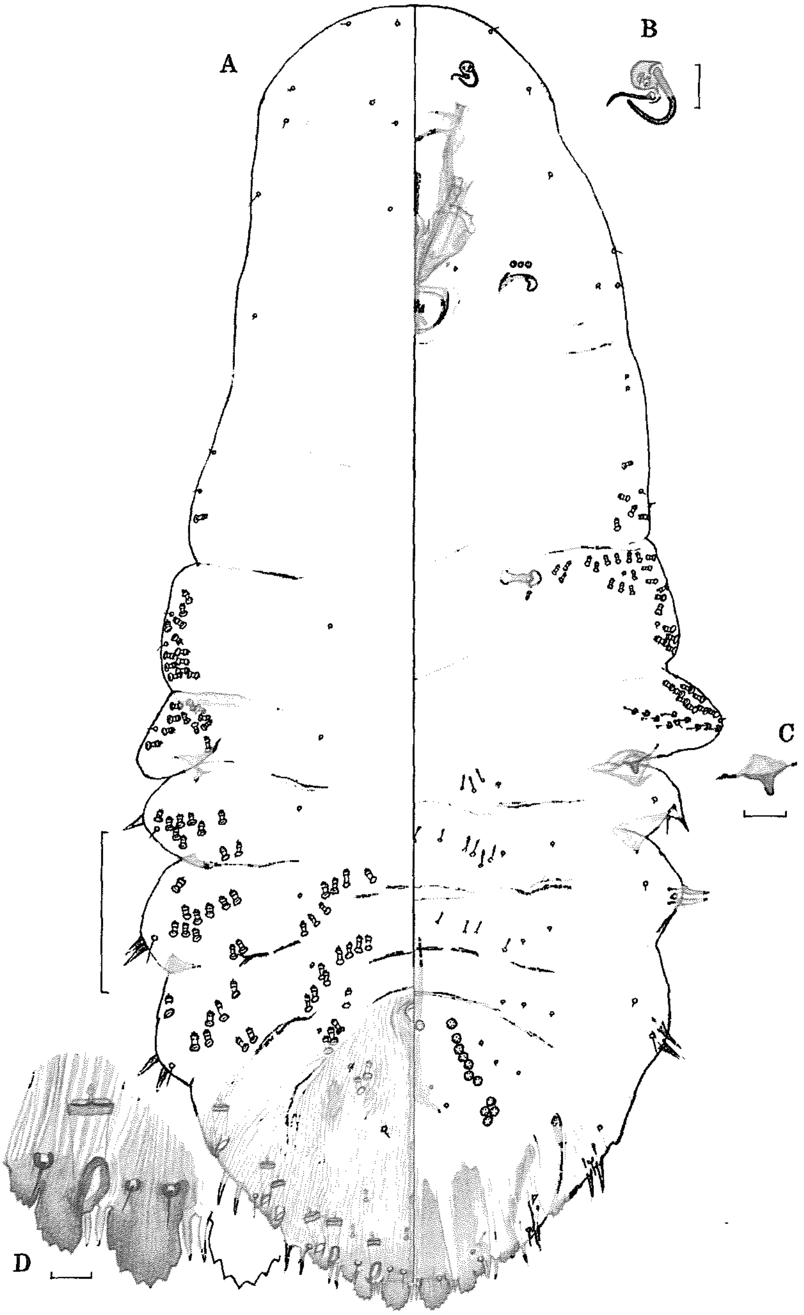

Fig. 30. *Lepidosaphes crotonifolii*: adult female. B: antenna; C: lateral spur between abd I and II; D: apex of the pygidium, dorsal surface. Scales: A, 100µm; B–D. 10µm. (The lateral lobe of abd I on the left side of Figure A is bent down, so that it is not produced beyond that of abd II.)

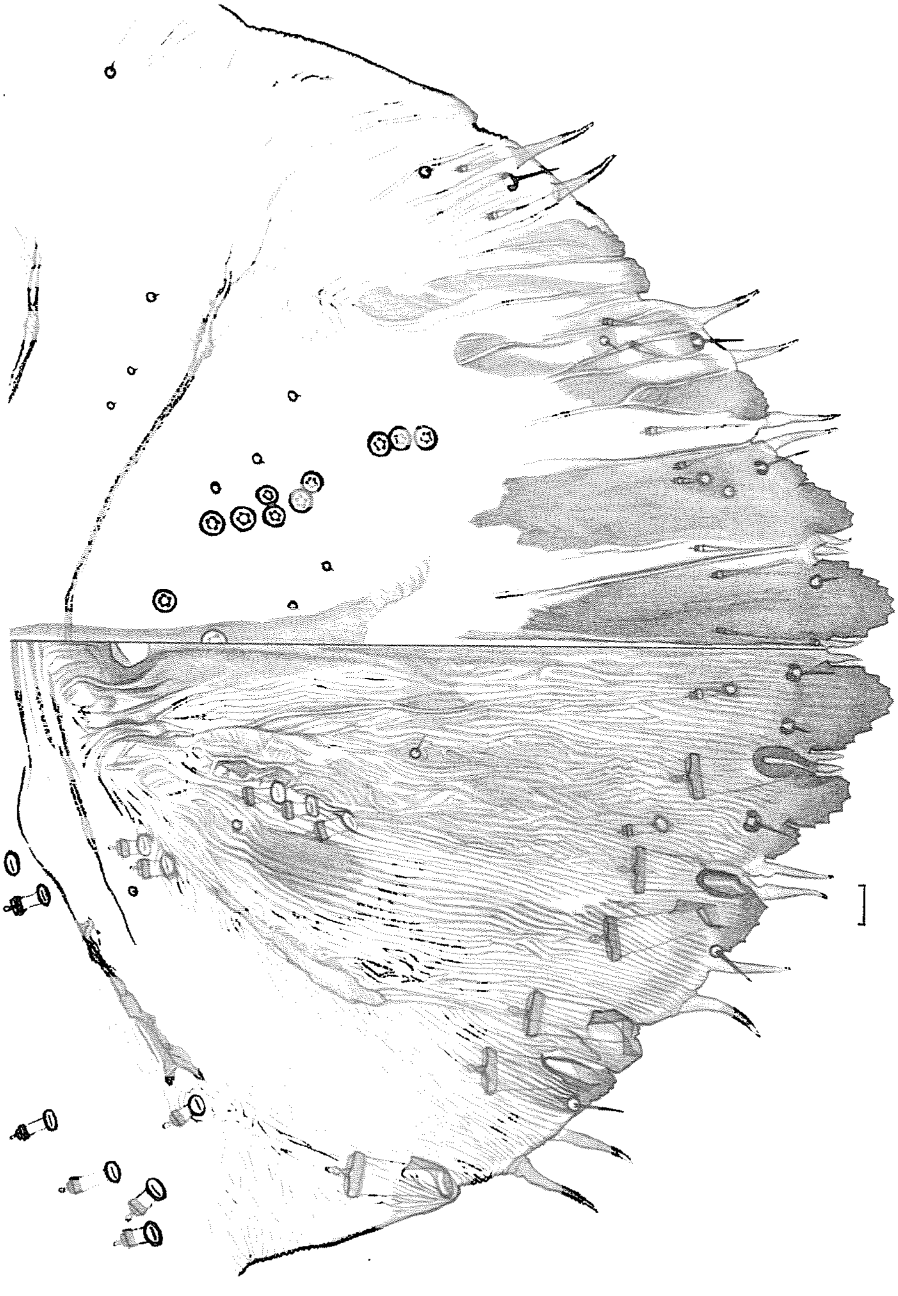

Fig. 31. *Lepidosaphes crotonifolii*: adult female, pygidium. Scale: 10µm.

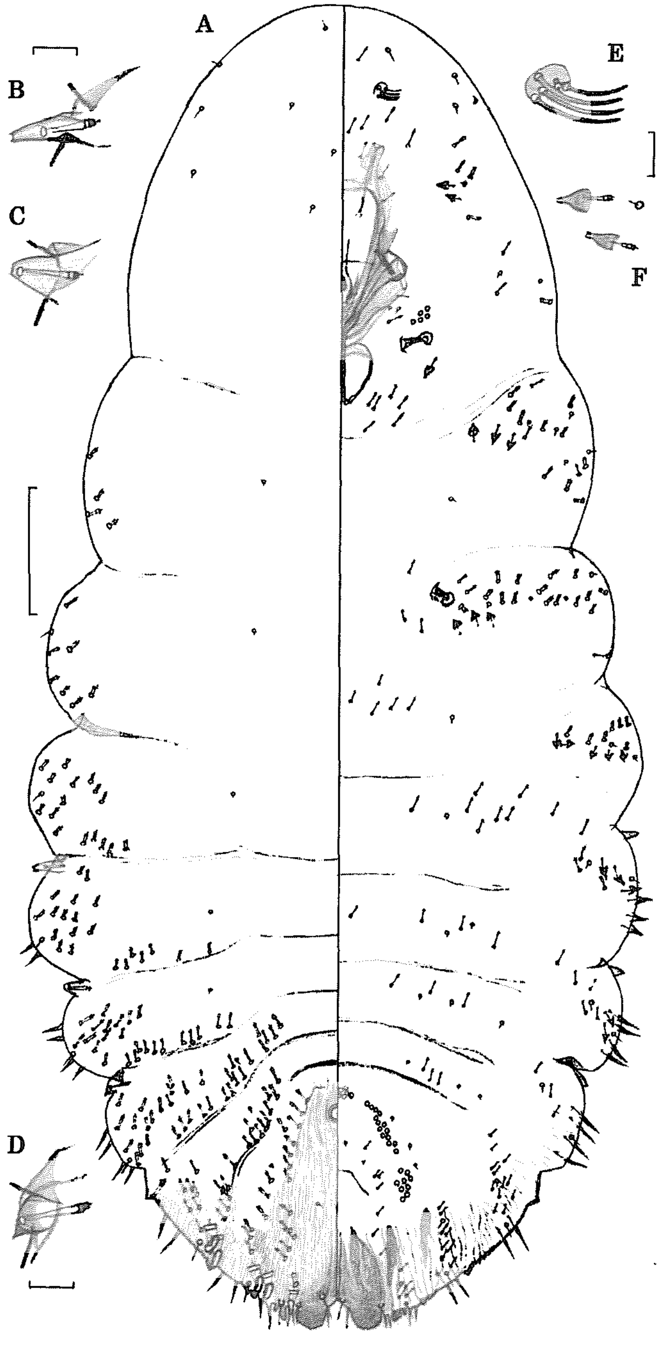

Fig. 32. *Lepidosaphes clerodendri*: adult female. B–D: lateral tubercles between Abd I and II, II and III, and III and IV; E: antenna; F: gland spines on the prothorax. Scales: A, 100µm; B–F, 10µm.

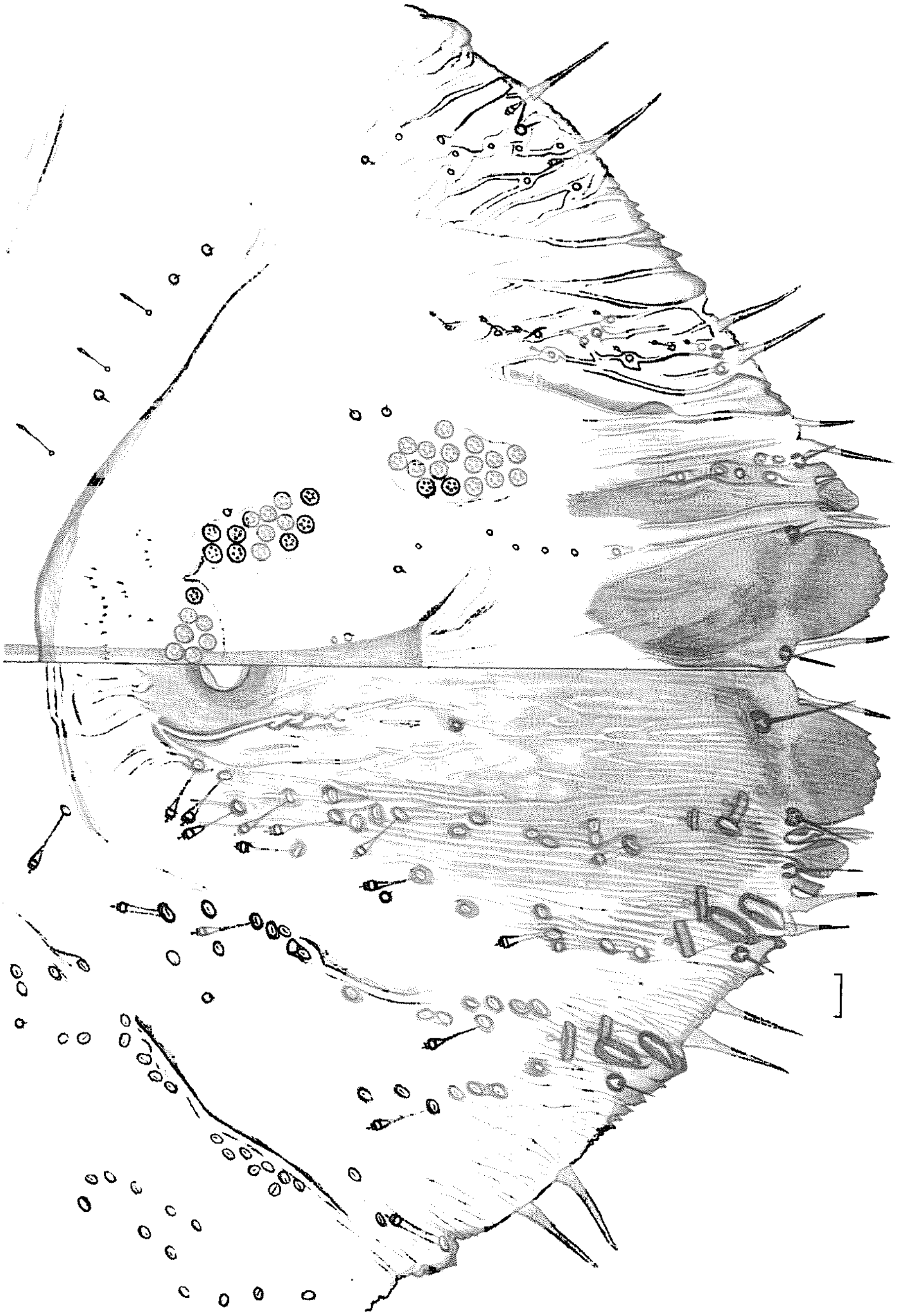

Fig. 33. *Lepidosaphes clerodendri*: adult female, pygidium. Scale: 10µm.

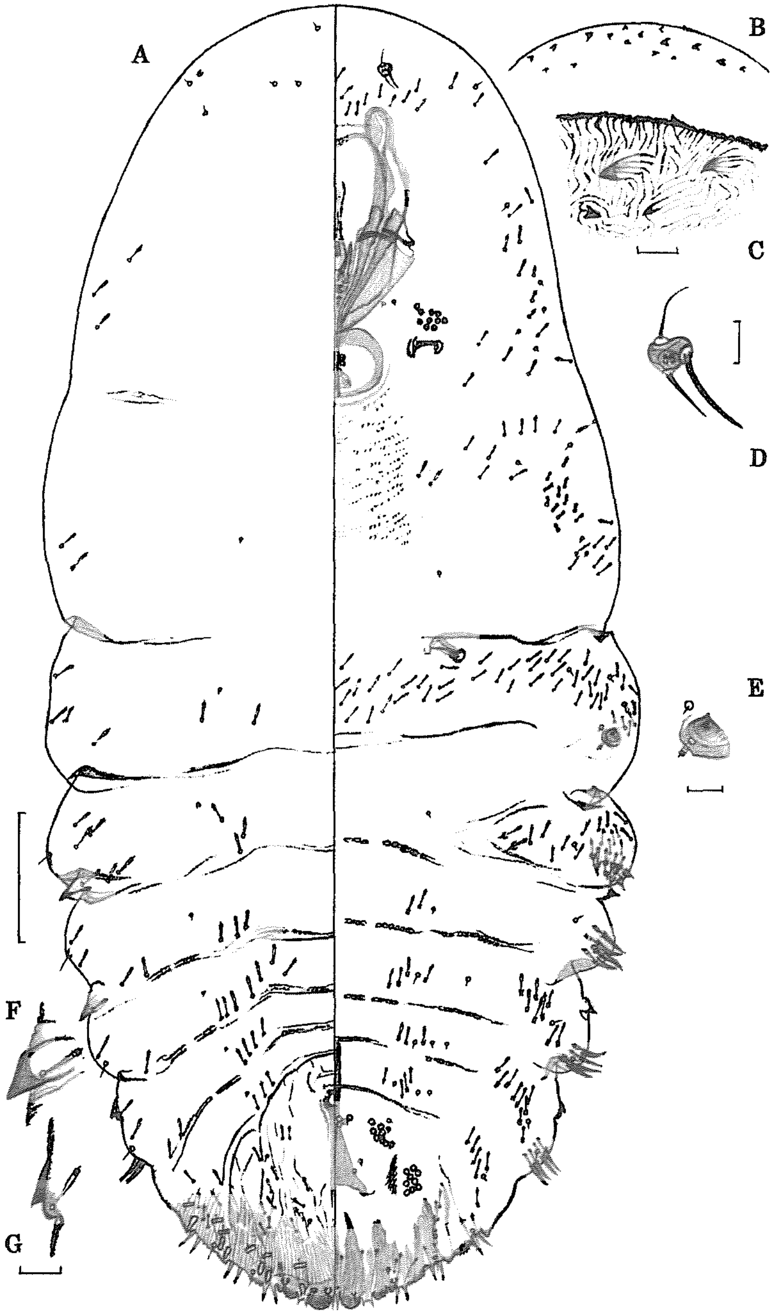

Fig. 34. *Lepidosaphes yakusimana*: adult female. B: head in another specimen, with conical processes; C: same as B, detail; D: antenna; E: sclerotized patch of derm on the lateral lobe of the metathorax; F and G: lateral tubercles between abd II and III and on the base of abd IV. Scales: A (also for B), 100μm; C–G, 10μm.

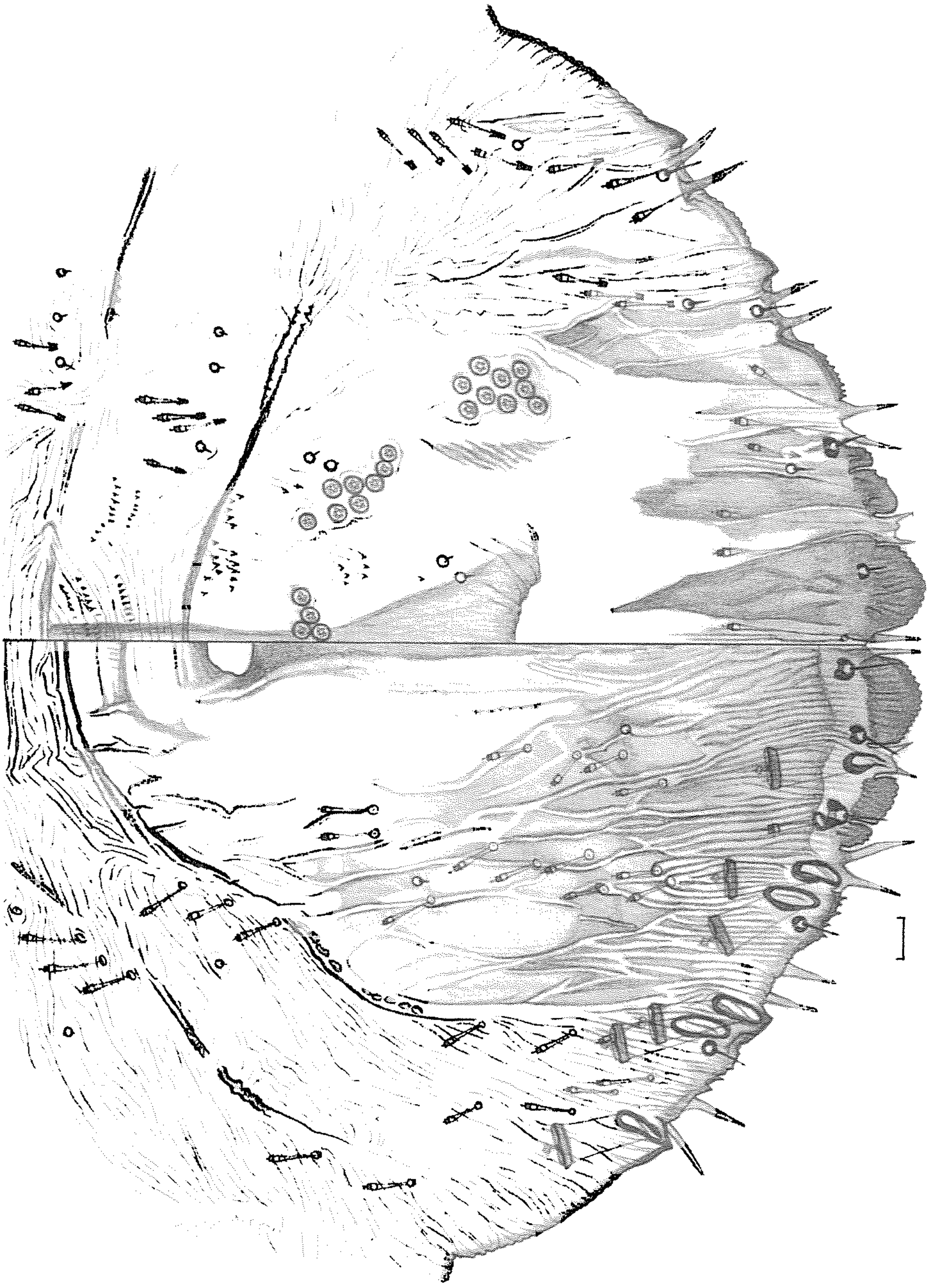

Fig. 35. *Lepidosaphes yakusimana*: adult female, pygidium. Scale: 10µm.

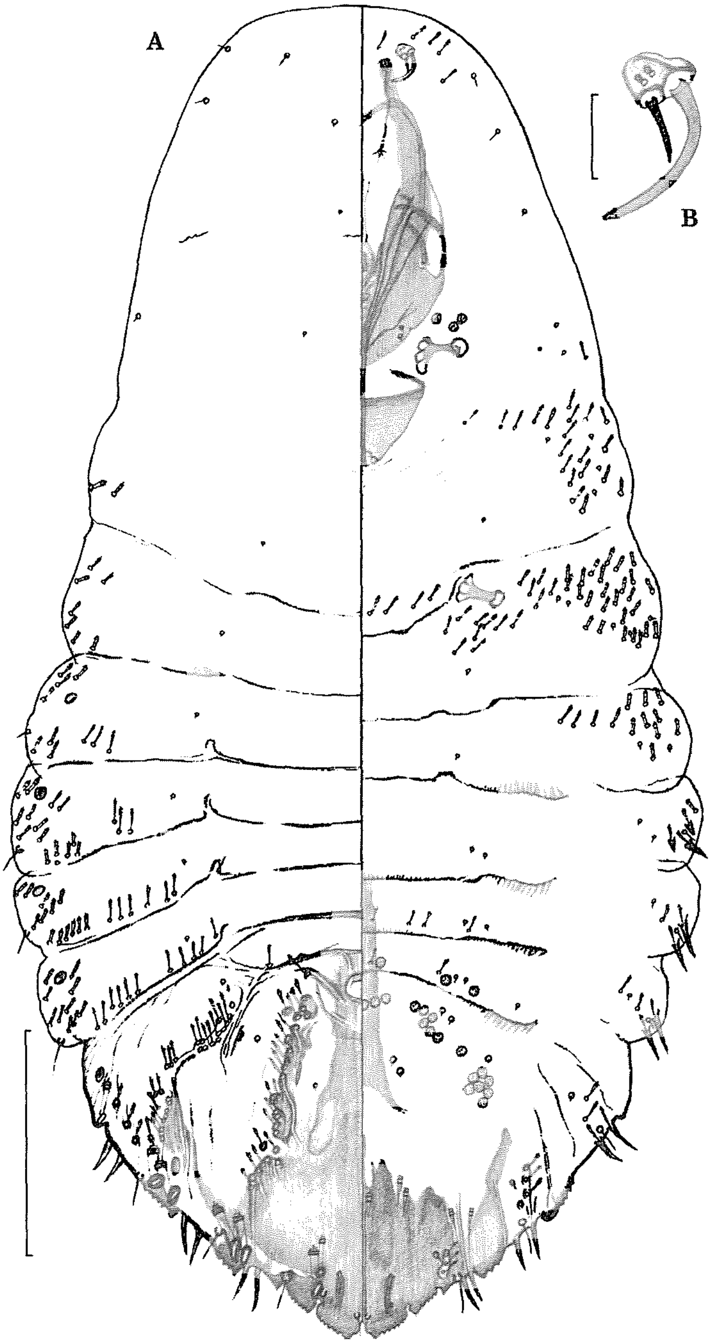

Fig. 36. *Andaspis glutae*: adult female. B: antenna. Scales: A, 100µm; B, 10µm.

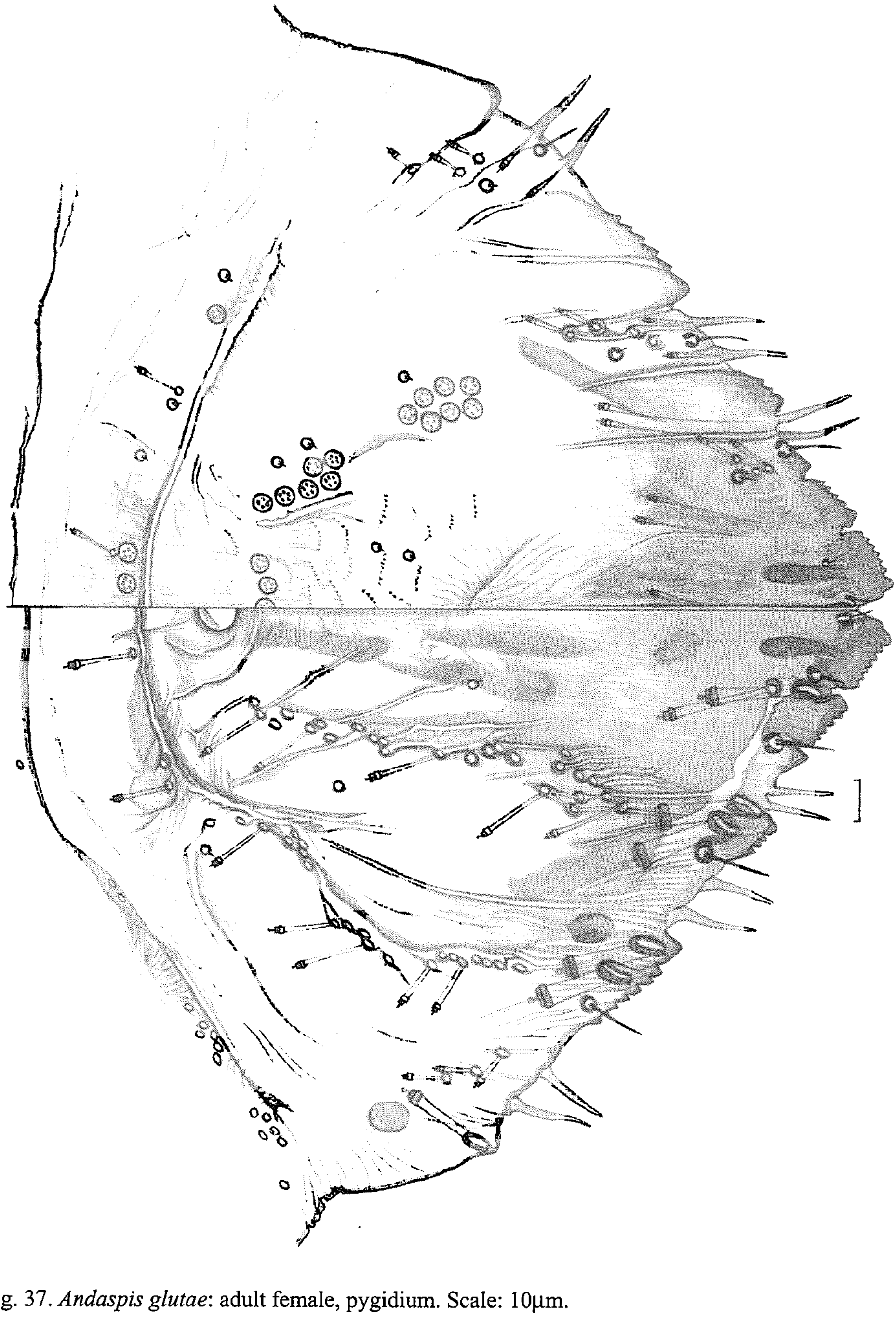

Fig. 37. *Andaspis glutae*: adult female, pygidium. Scale: 10µm.

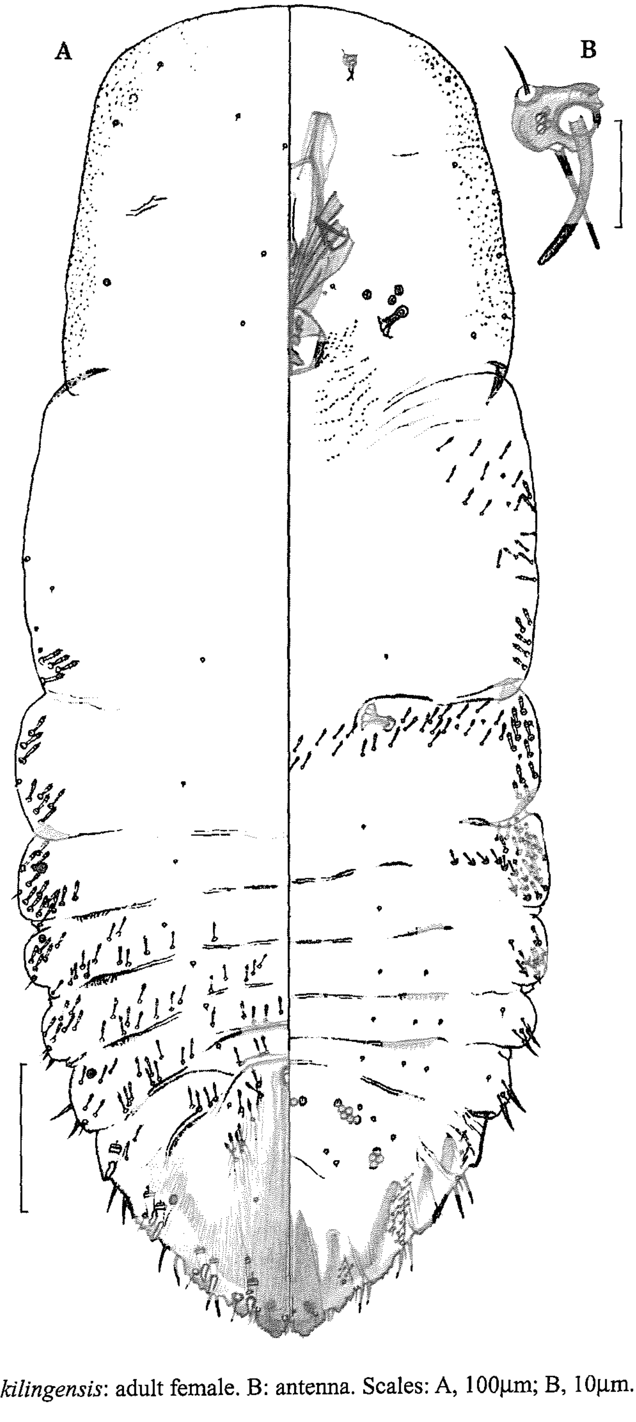

Fig. 38. *Andaspis makilingensis*: adult female. B: antenna. Scales: A, 100µm; B, 10µm.

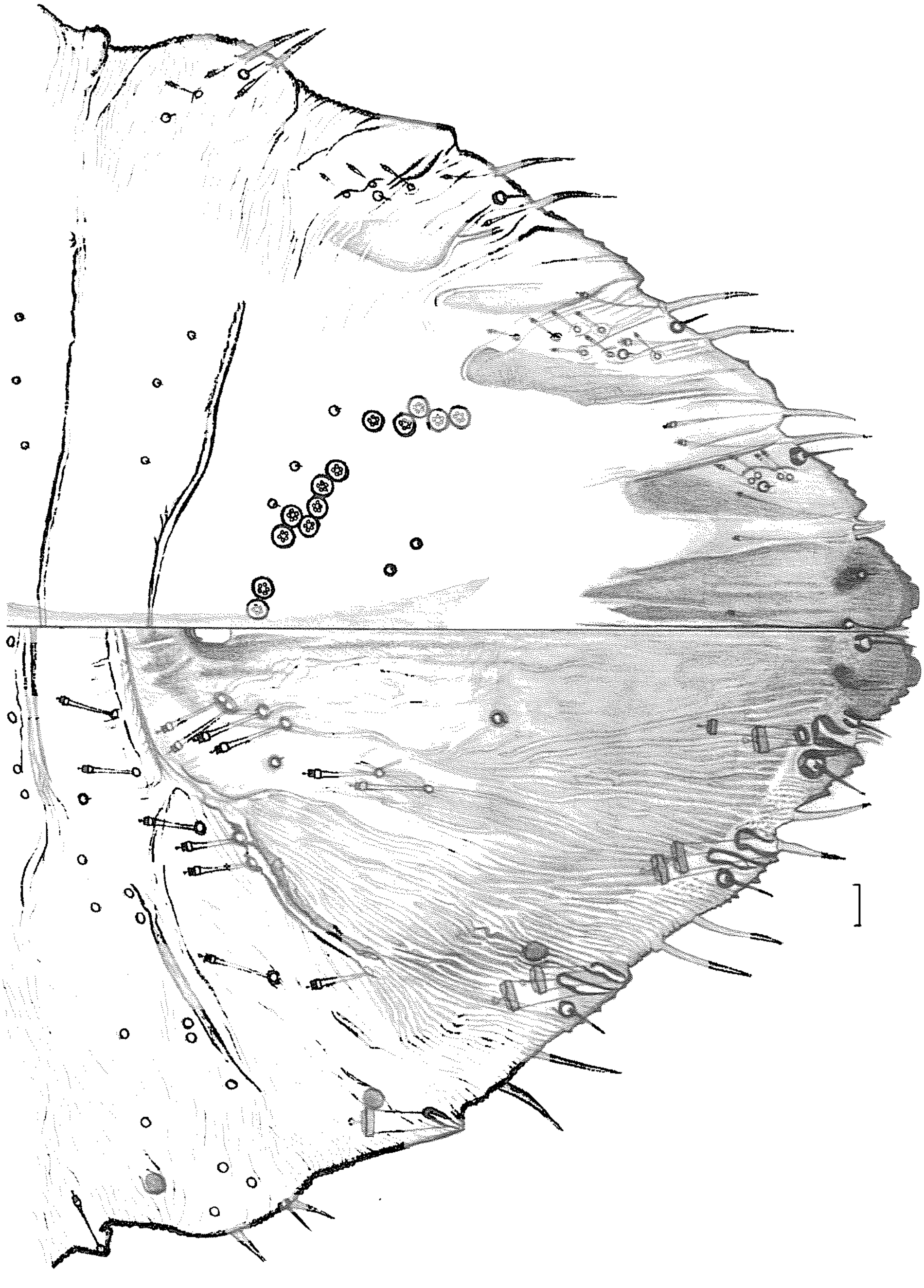

Fig. 39. *Andaspis makilingensis*: adult female, pygidium. Scale: 10µm.

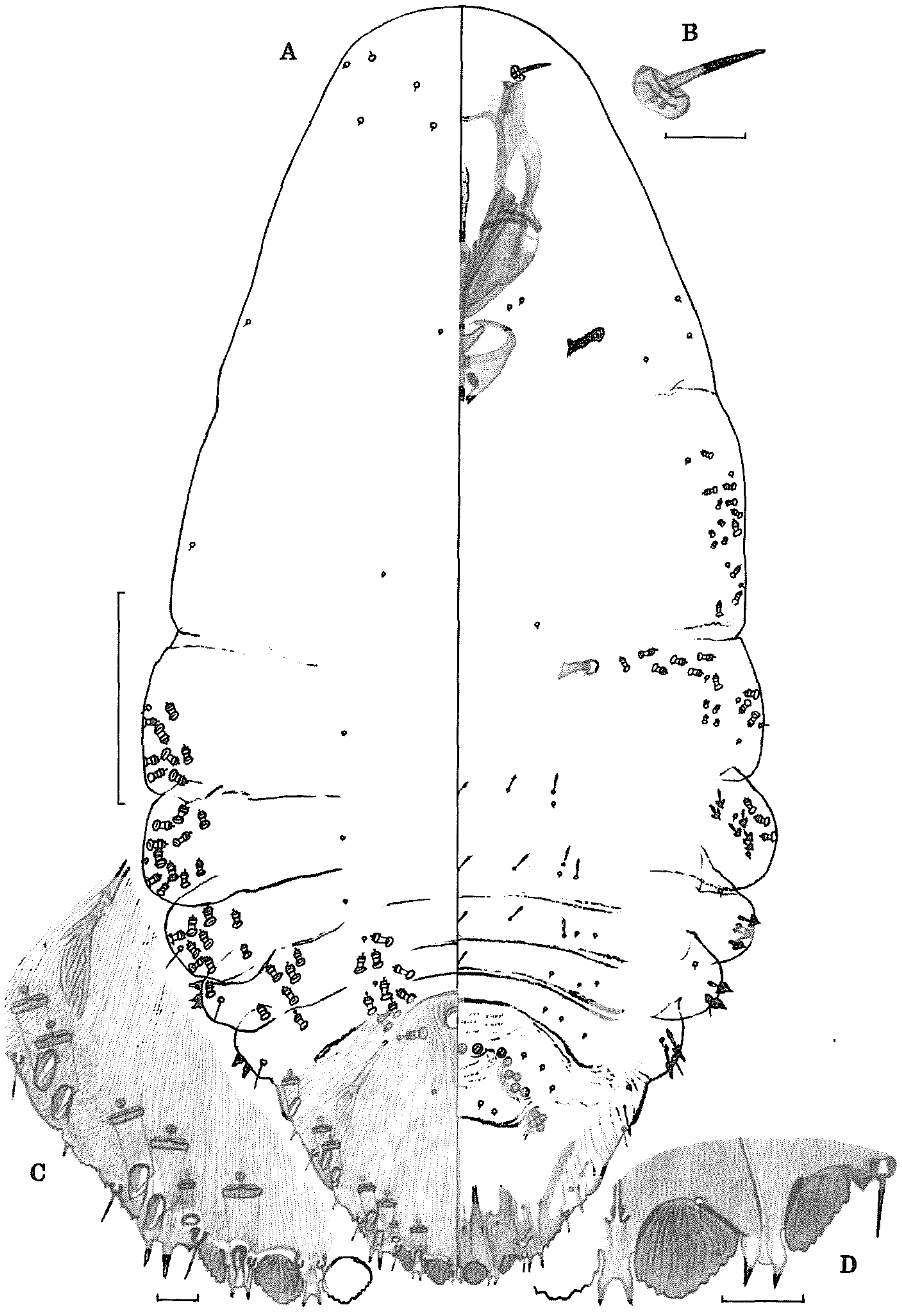

Fig. 40. *Andaspis conocarpi*: adult female. B: antenna; C: pygidial margin, dorsal surface; D: median and second trullae, ventral surface. Scales: A, 100μm; B–D, 10μm.

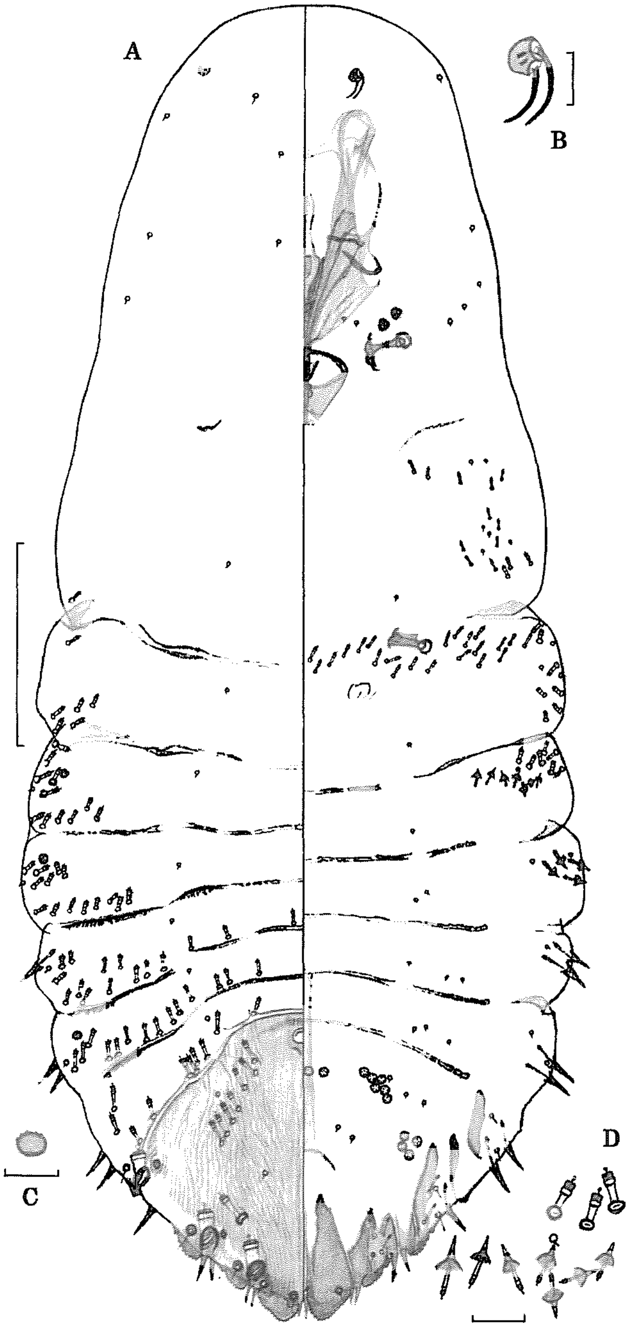

Fig. 41. *Hexandaspis bataanensis*: adult female [94PL-90]. B: antenna; C: dorsal boss on abd IV; D: ducts and tubercular gland spines on abd I. Scales: A, 100μm; B–D, 10μm.

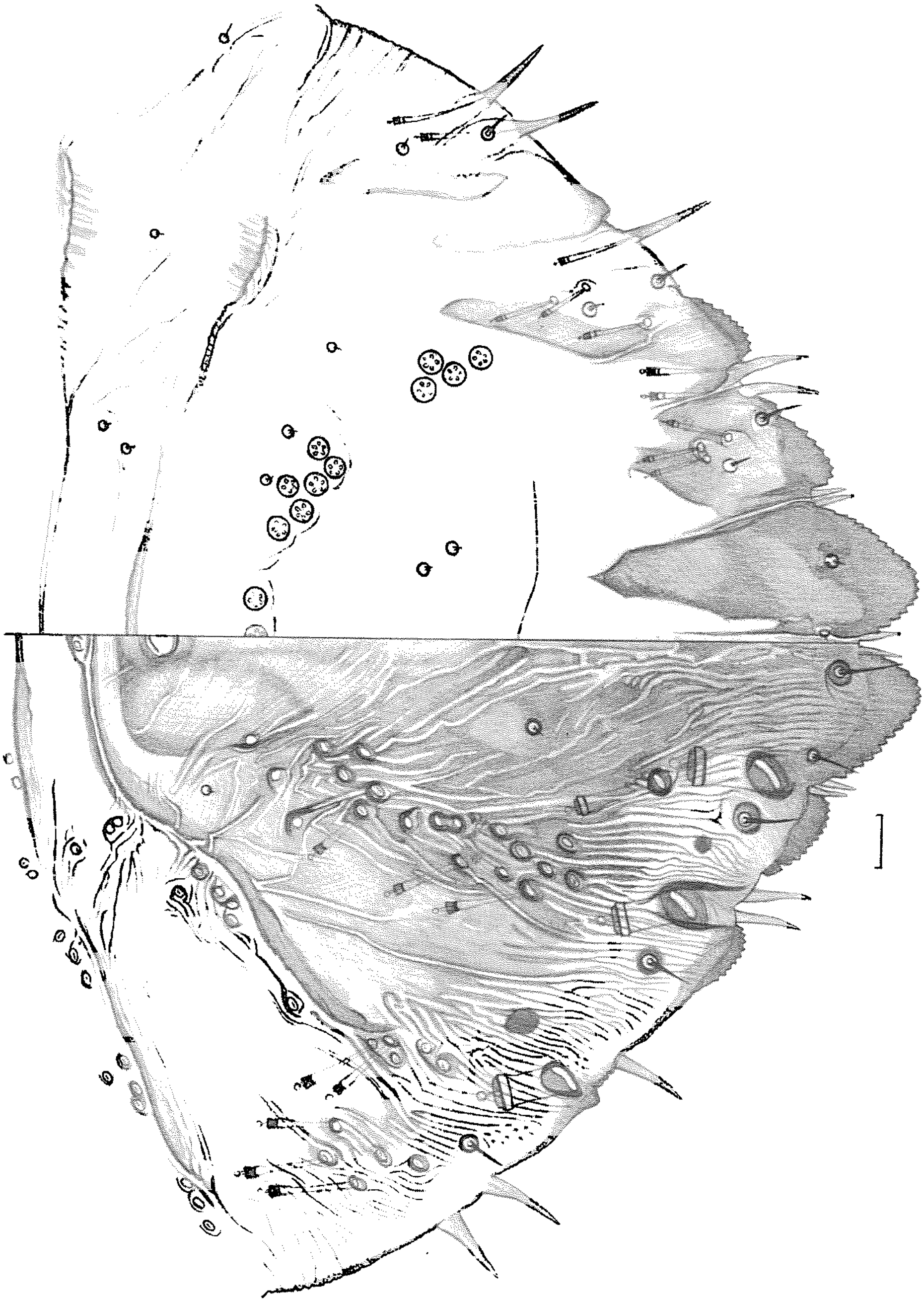

Fig. 42. *Hexandaspis bataanensis*: adult female, pygidium [94PL-145]. Scale: 10μm.

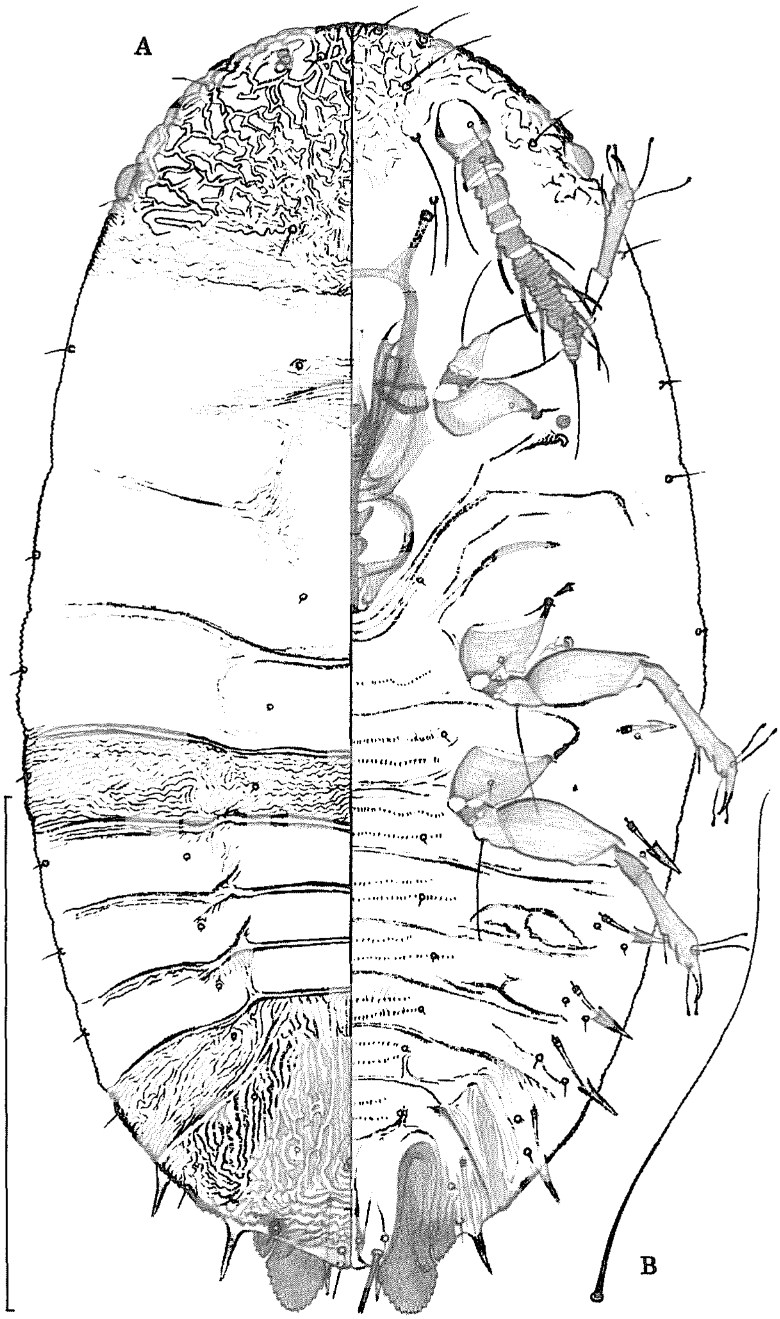

Fig. 43. *Hexandaspis bataanensis*: first-instar nymph [94PL-145]. B: caudal seta. Scale: 100μm.

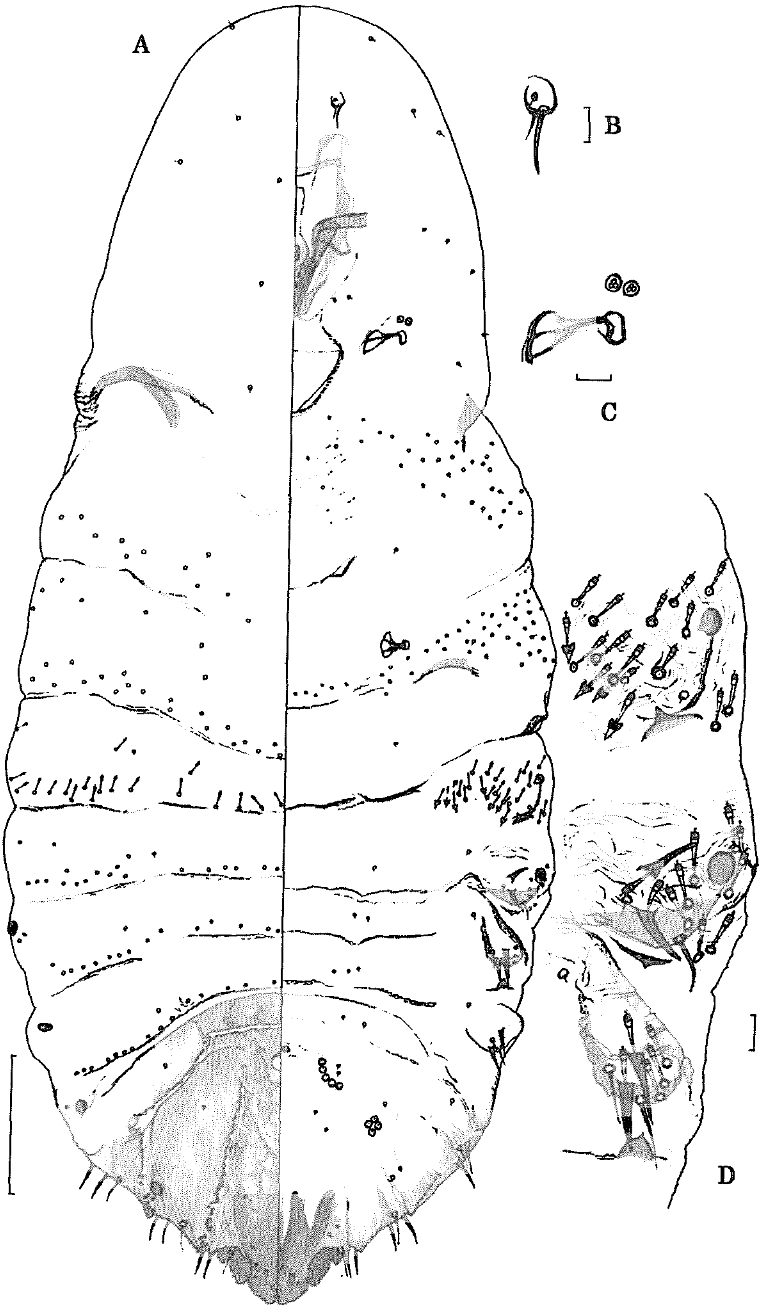

Fig. 44. *Santubongia swintoniae*: adult female. B: antenna; C: anterior spiracle; D: lateral lobes of abd I–III, ventral surface, showing ducts, gland spines, lateral tubercles, and dorsal bosses. Scales: A, 100µm; B–D, 10µm. (In D, the dorsal bosses are brought onto the ventral side due to the specimen being flattened on the slide.)

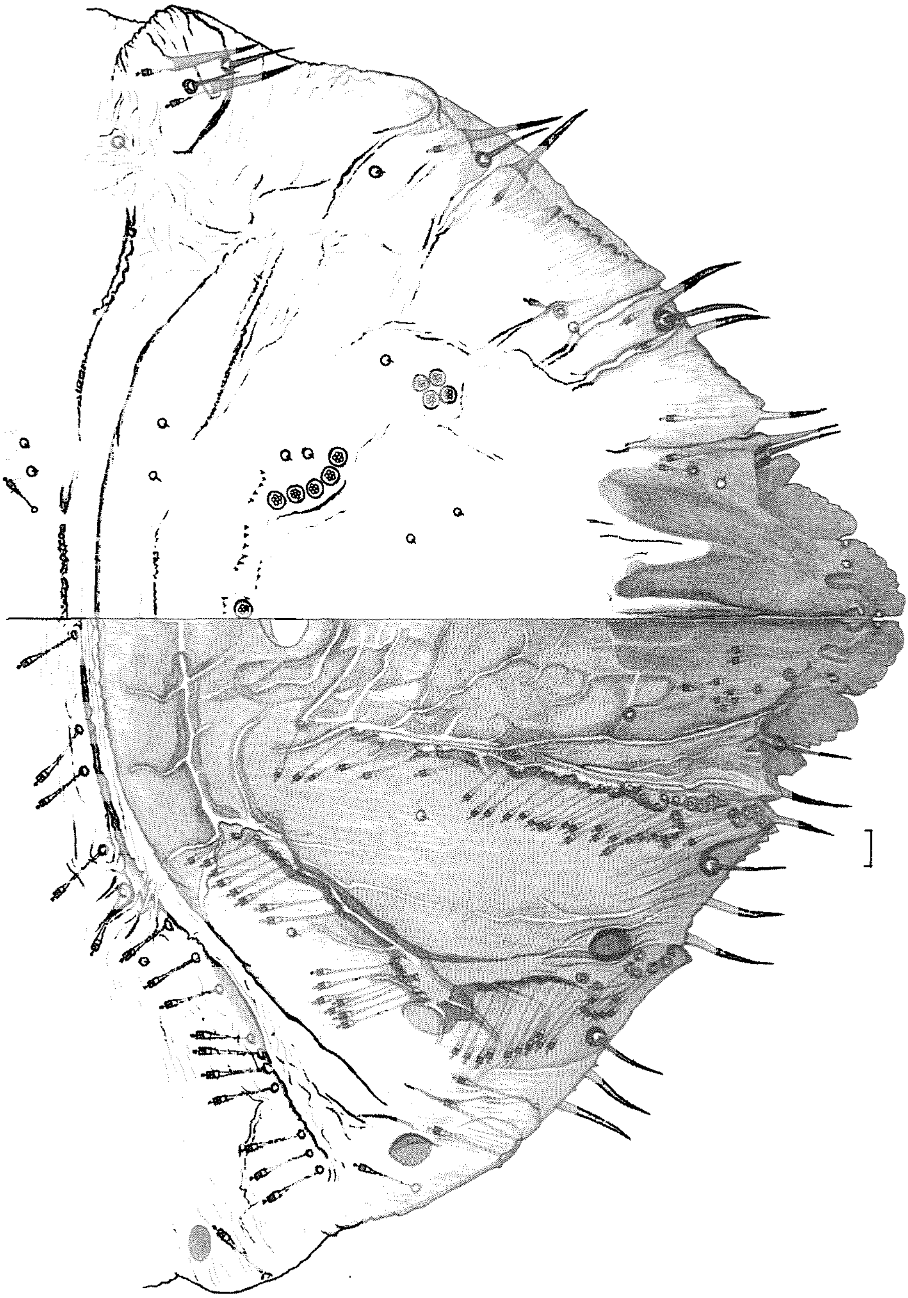

Fig. 45. *Santubongia swintoniae*: adult female, pygidium. Scale: 10µm.

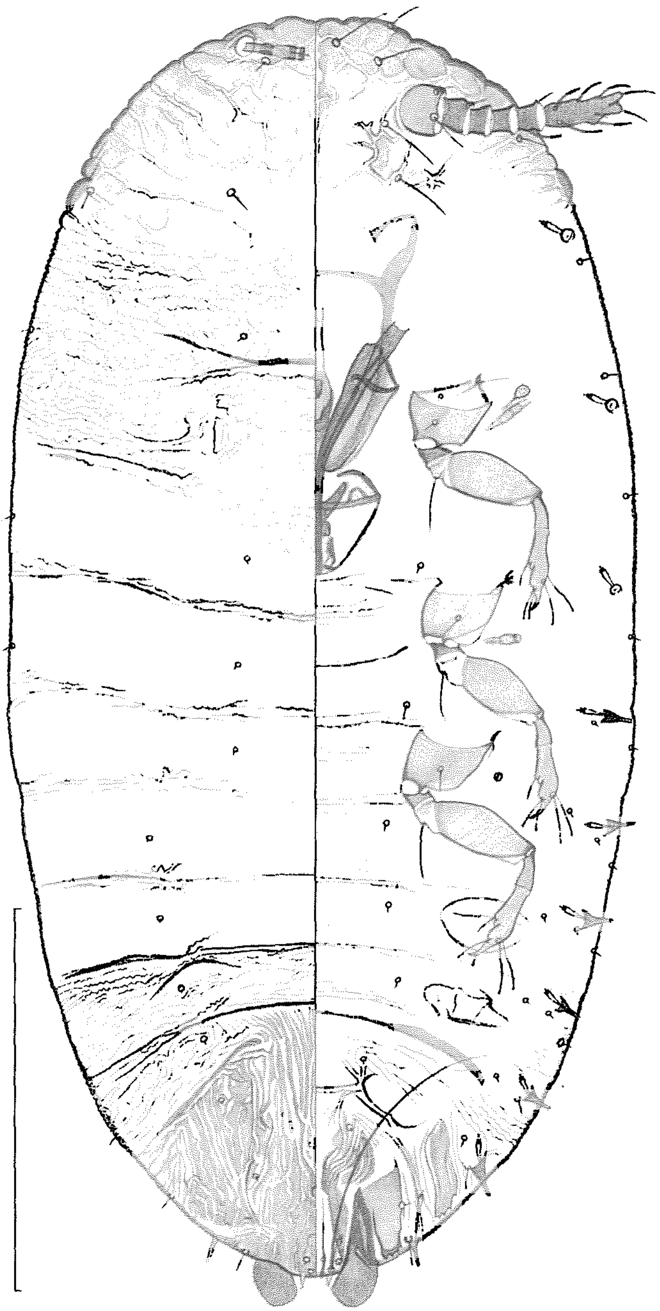

Fig. 46. *Santubongia swintoniae*: first-instar nymph. Scale: 100μm.

Fig. 47. *Bayuraspis javanensis* [=*Metandaspis javanensis* Williams]: adult female, pygidium. Scale: 10µm.

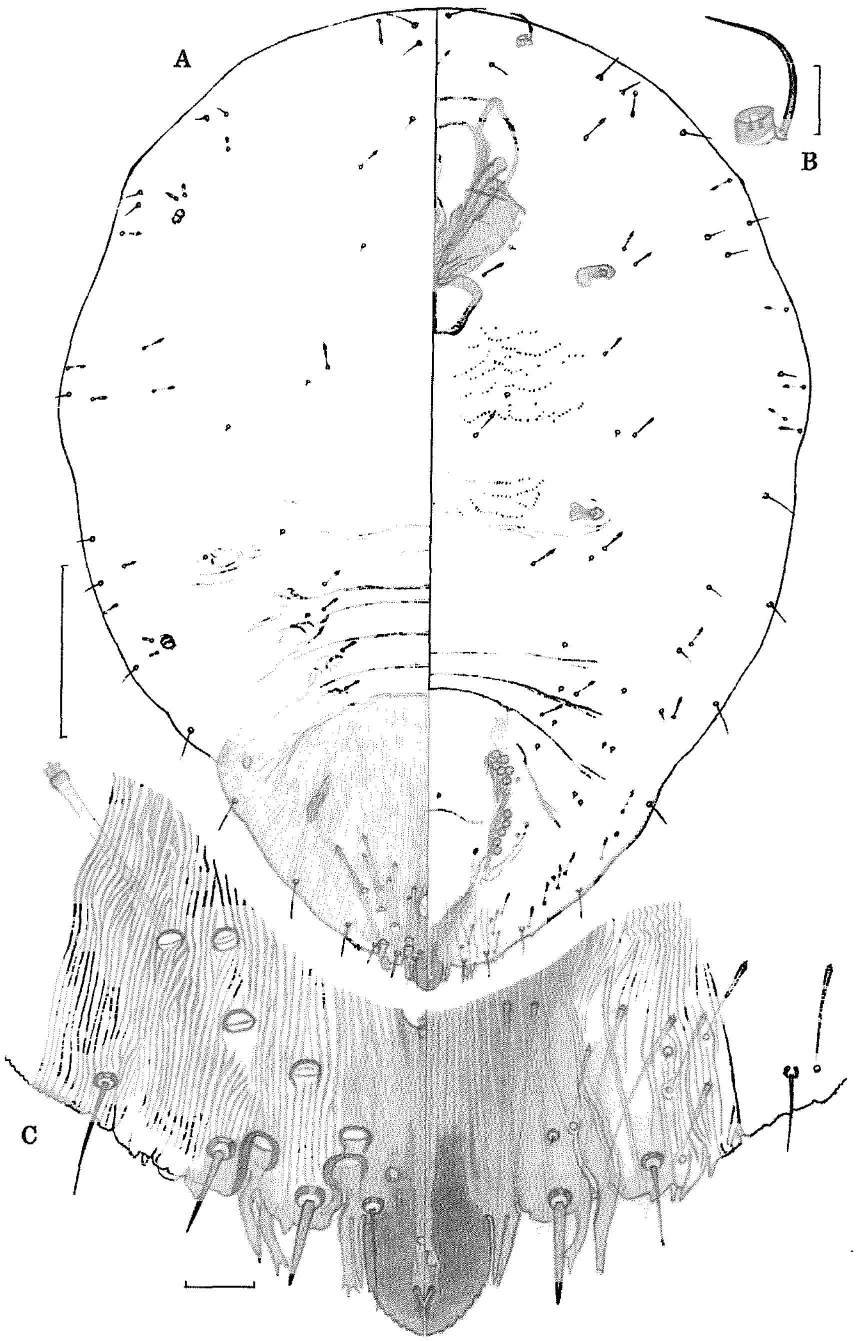

Fig. 48. *Banahaoa bayokana*: adult female. B: antenna; C: pygidial margin. Scales: A, 100µm; B and C, 10µm.

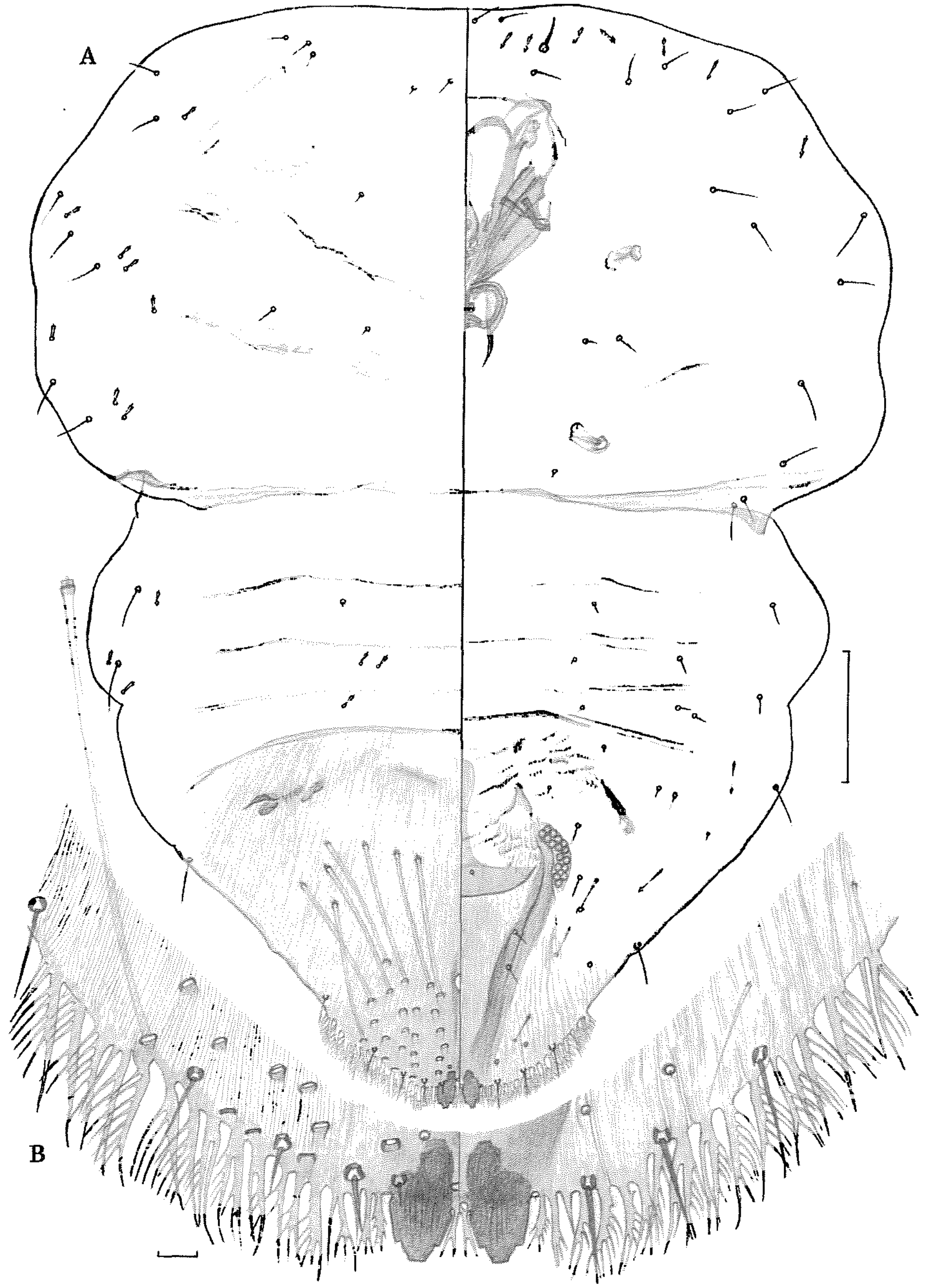

Fig. 49. *Cephalaspidiotus palaquii*: adult female [91ML-148]. B: pygidial margin. Scales: A, 100µm; B, 10µm.

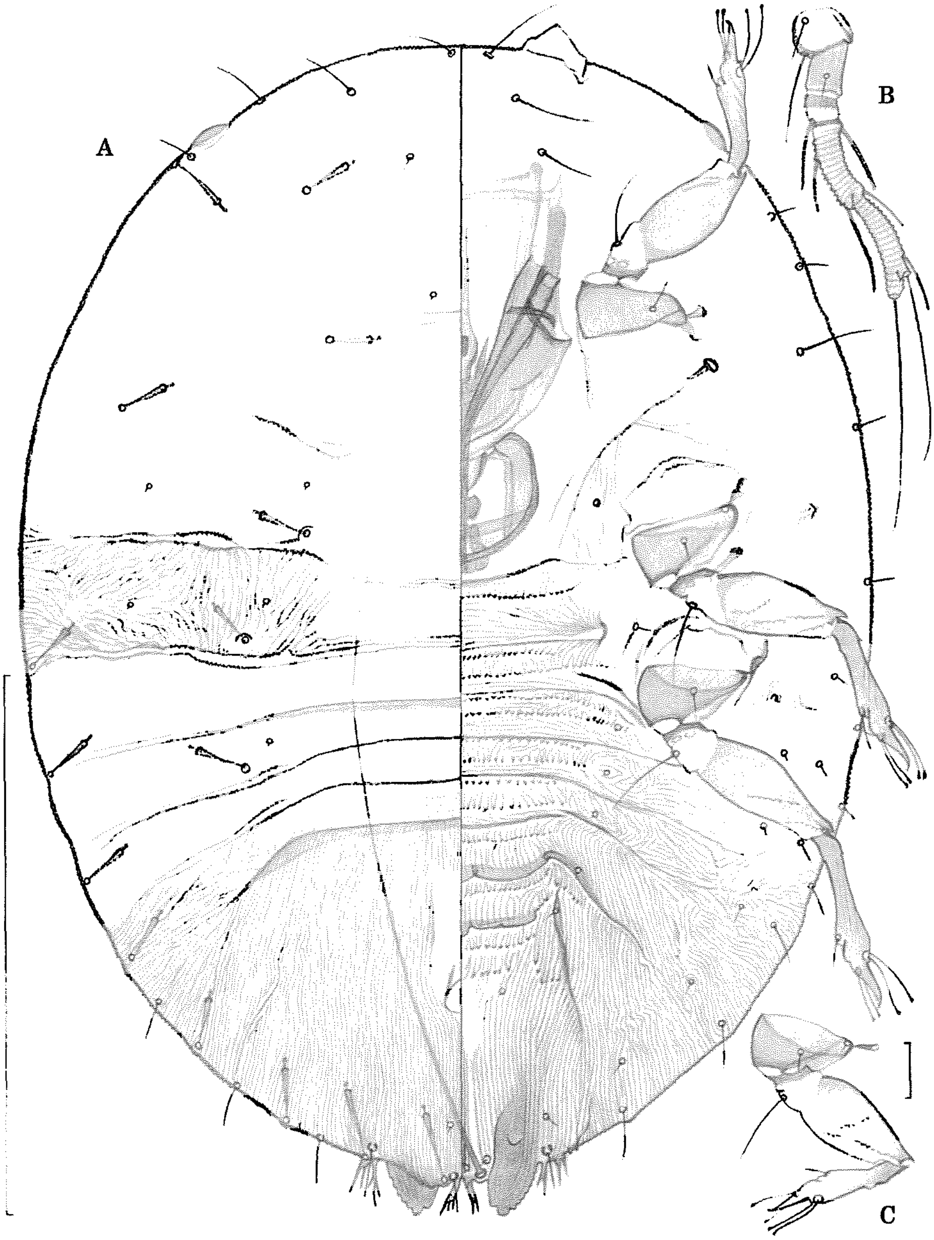

Fig. 50. *Cephalaspidiotus palaquii* [91ML-148]. A and B: first-instar female; B: antenna (figured from another specimen). C: first-instar male, hind leg (magnification as for A and B). Scales: A (also for B), 100μm; C, 10μm.

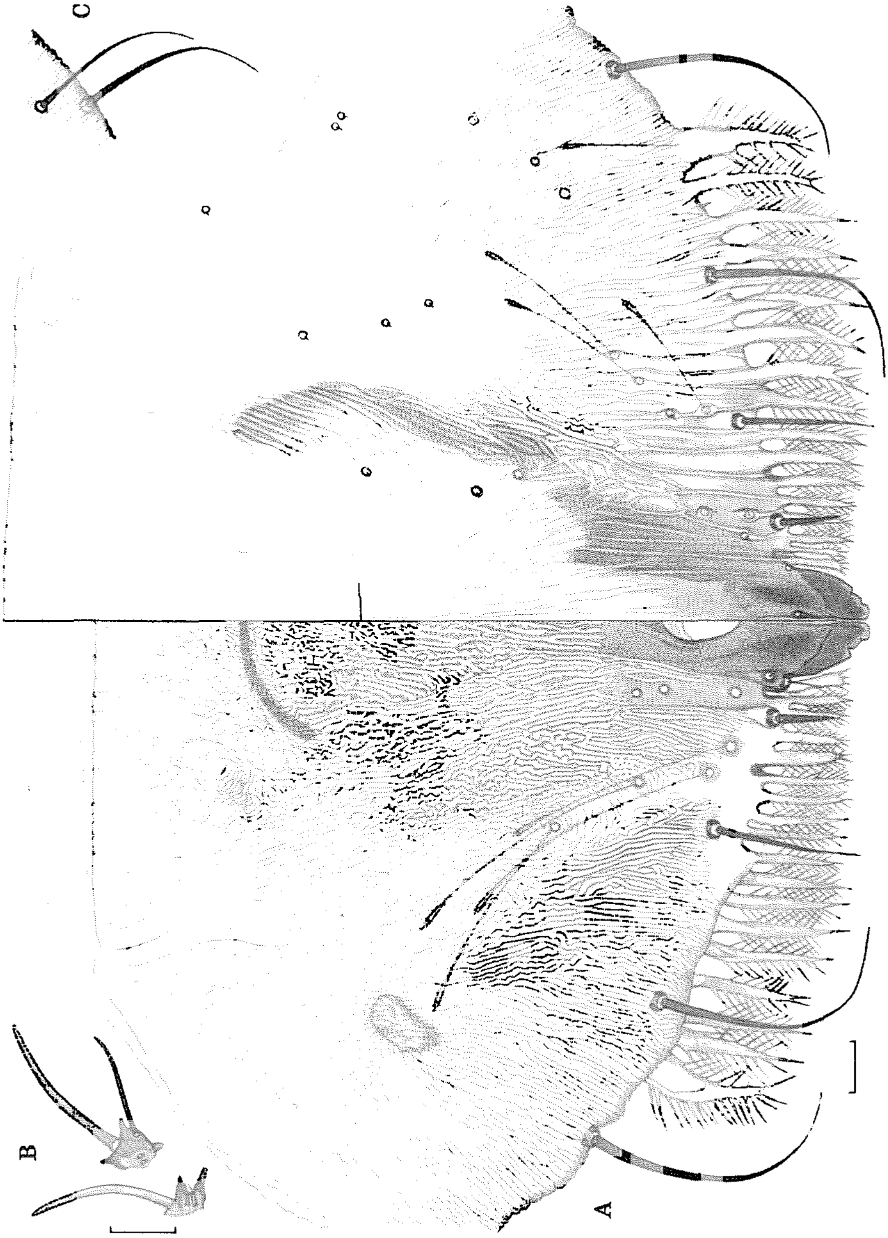

Fig. 51. *Morganella polyctena*: adult female [94PL-90]. A: pygidium; B: antennae; C: ventral and dorsal marginal setae on abd III. Scales: A (also for C), 10μm; B, 10μm.

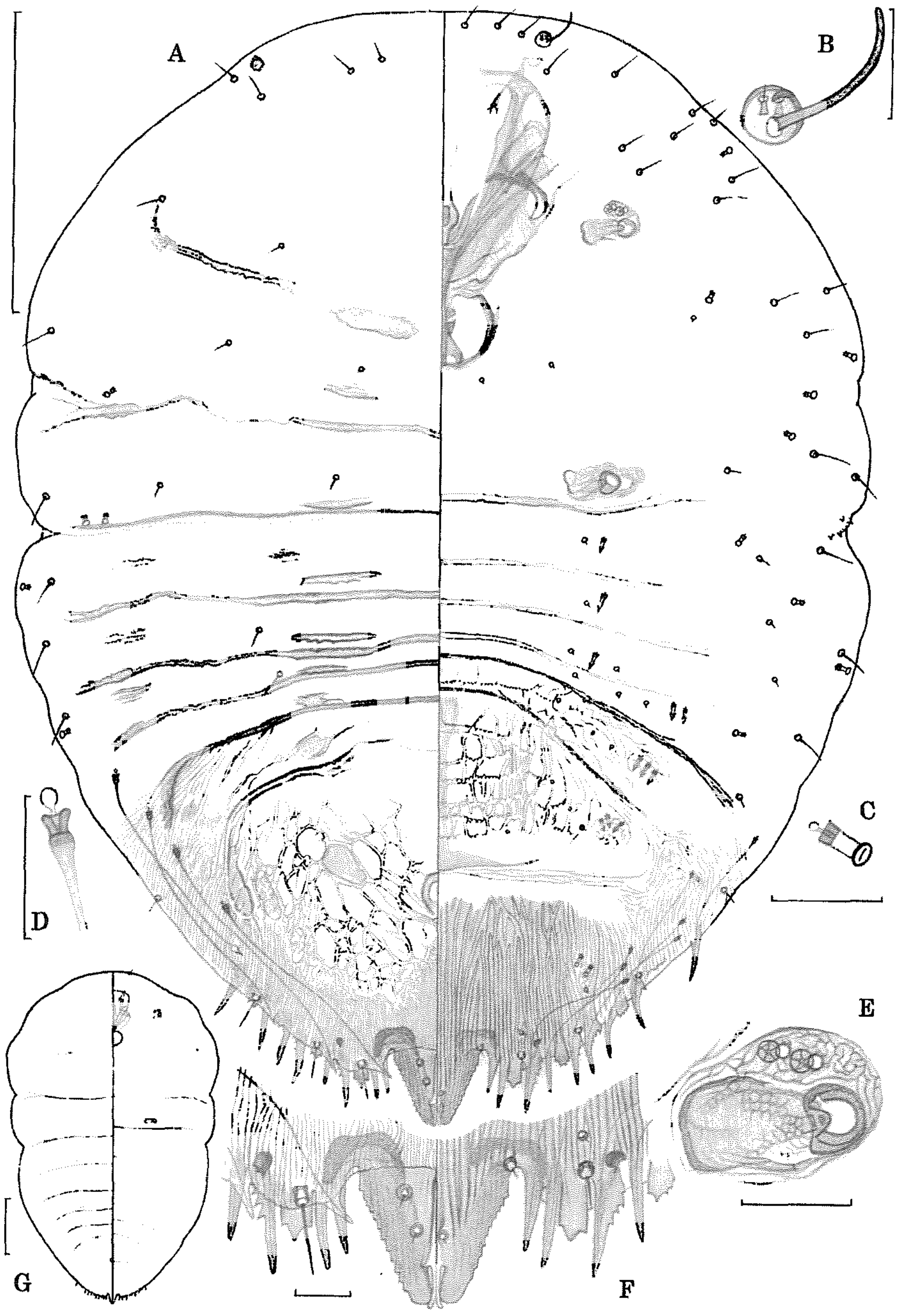

Fig. 52. *Kochummenaspis filiorum*: adult female [91ML-455]. A–F: figured from a teneral specimen; B: antenna; C: prepygidial duct; D: inner end of a dorsal duct arising from the pygidial margin; E: anterior spiracle [also see Fig. 57]; F: apex of the pygidium. G: body shape of a full-grown specimen. Scales: A and G, 100μm; B–F, 10μm.

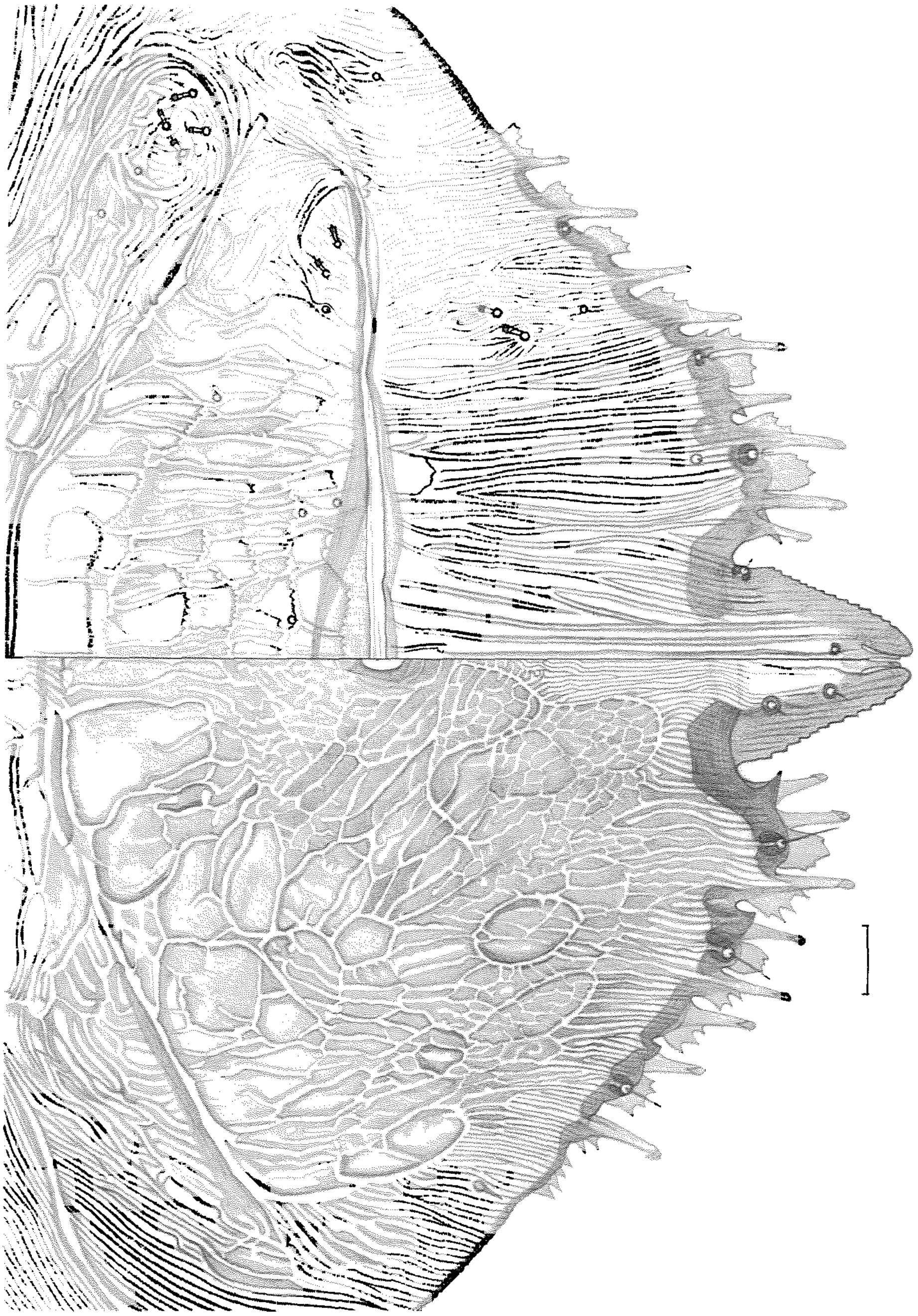

Fig. 53. *Kochummenaspis filiorum* : adult female, pygidium [91ML-455]. Figured from a full-grown specimen. Scale: 10μm. (The ducts observed in teneral specimens are not clearly visible in full-grown specimens owing to the sclerotized derm, so that they are not drawn in the figure.)

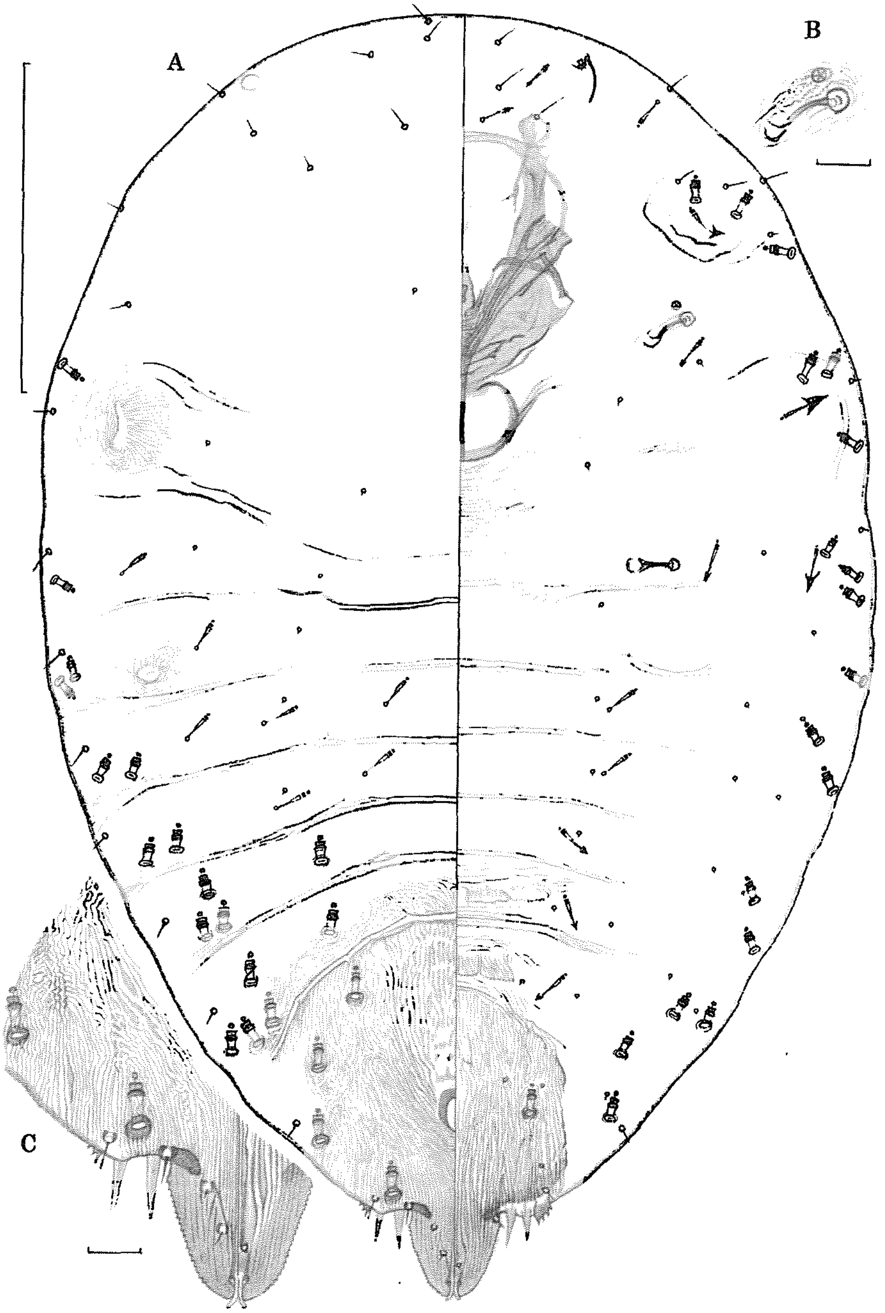

Fig. 54. *Kochummenaspis filiorum*: second-instar male [91ML-455]. B: anterior spiracle; C: apex of pygidium, dorsal surface. Scales: A, 100μm; B and C, 10μm.

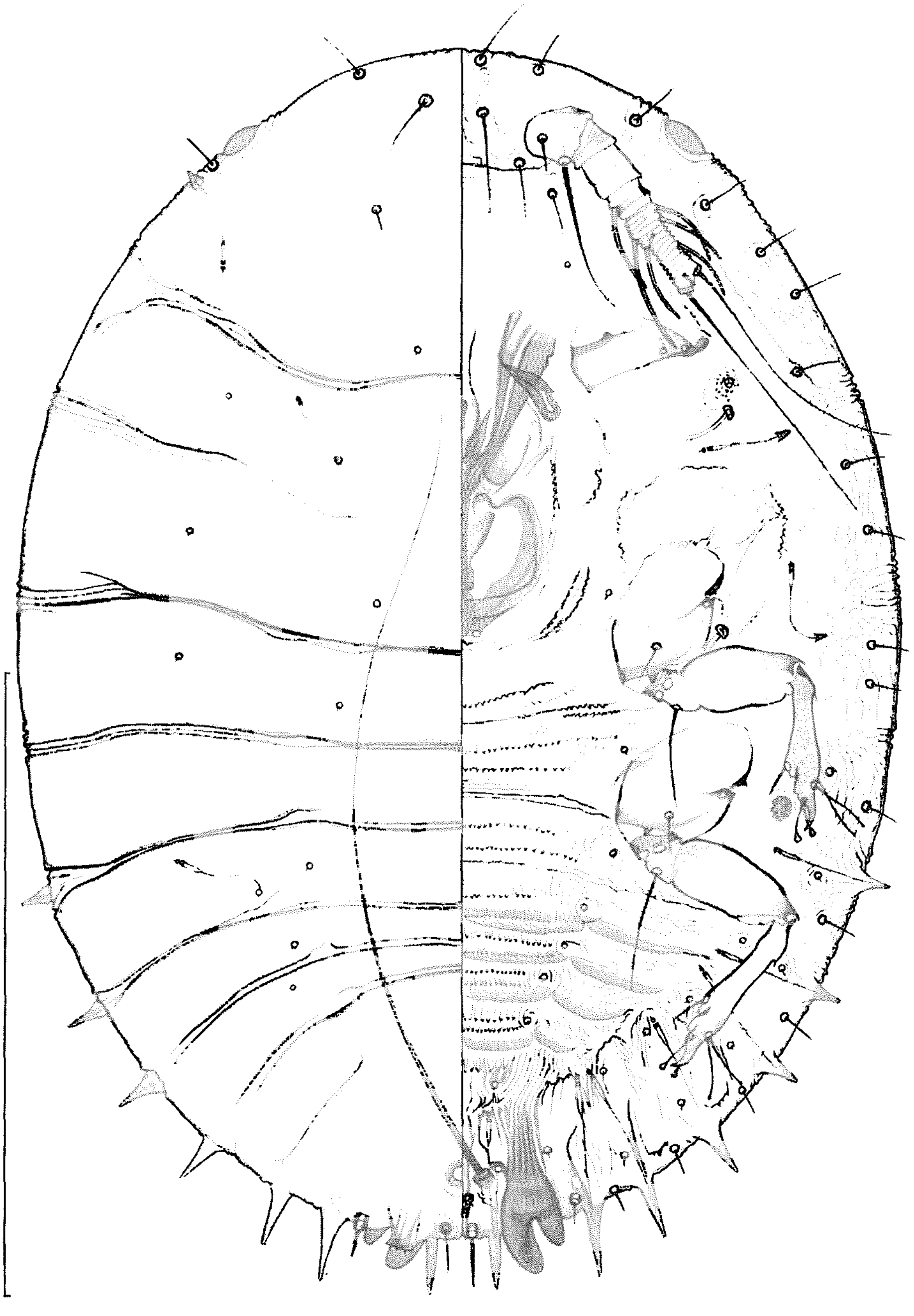

Fig. 55. *Kochummenaspis filiorum*: first-instar female [90ML-503]. Scale: 100µm.

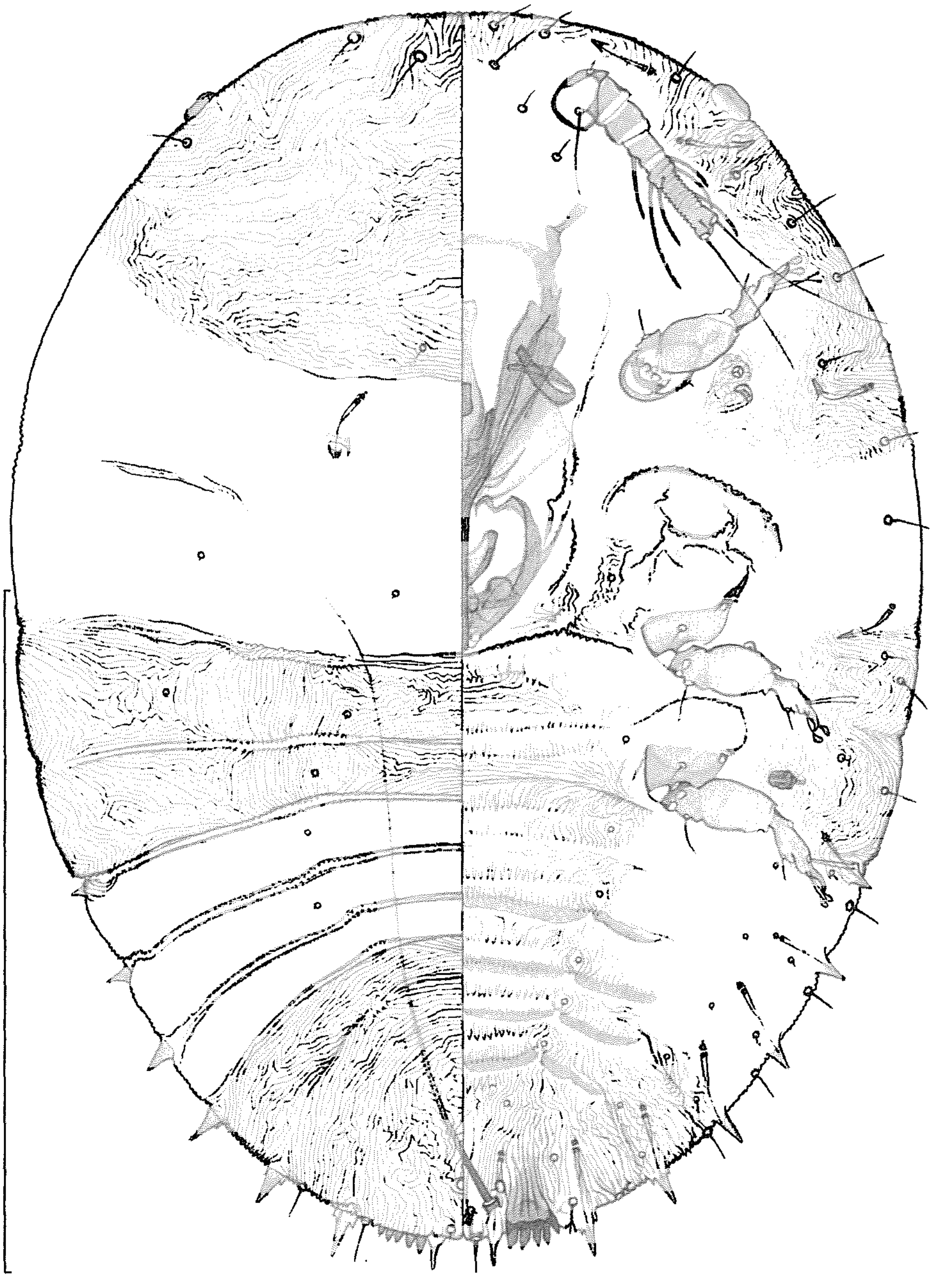

Fig. 56. *Kochummenaspis filiorum*: first-instar male [90ML-503]. Scale: 100μm.

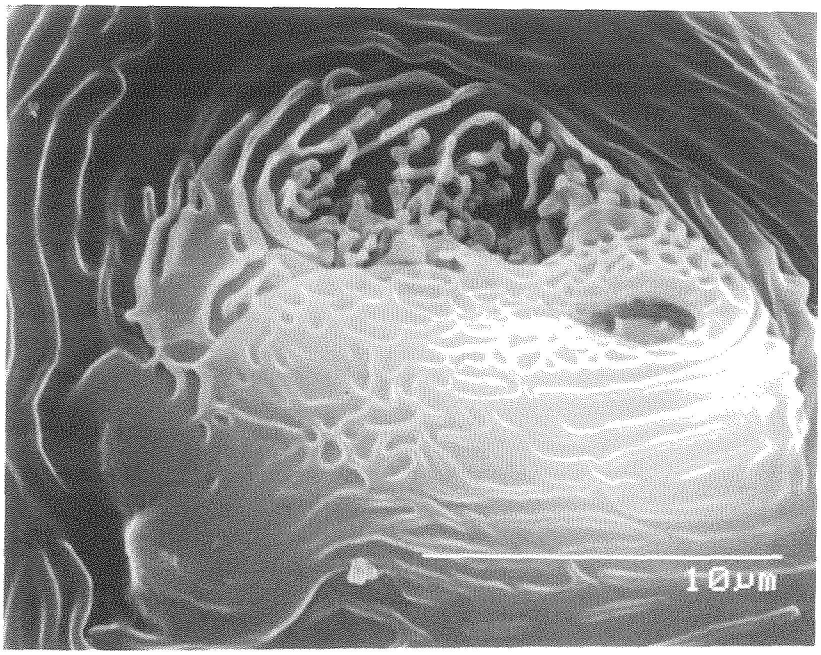

Fig. 57. *Kochummenaspis filiorum*: adult female, anterior spiracle [also see Fig. 52, E] [91ML-455].

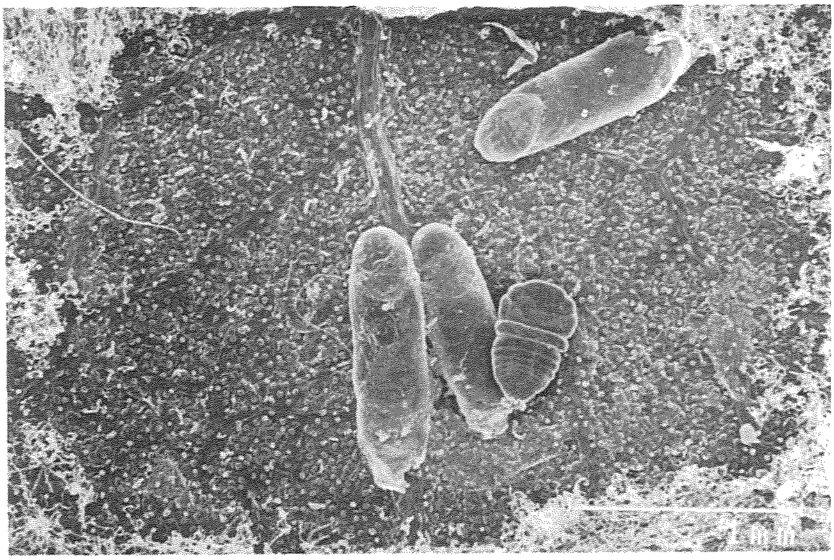

Fig. 58. *Kochummenaspis filiorum*: familial burrow, with mother and the tests of her sons [91ML-455].

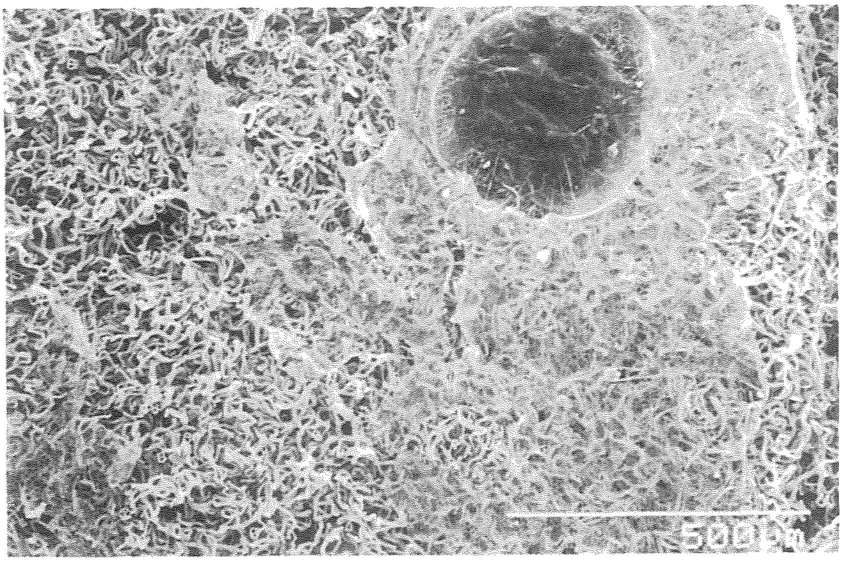

Fig. 59. *Kochummenaspis filiorum*: ceiling of a burrow, with the second exuvial cast of the female (above on the right) and a thin film around it [91ML-455].

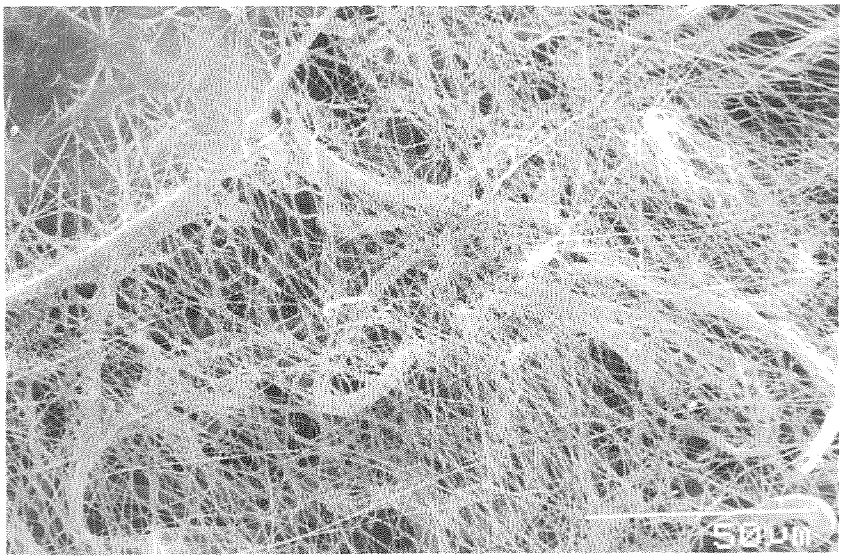

Fig. 60. *Kochummenaspis filiorum*: part of Fig. 59, showing wax filaments near the second exuvial cast, with entangled trichomes forming the background.

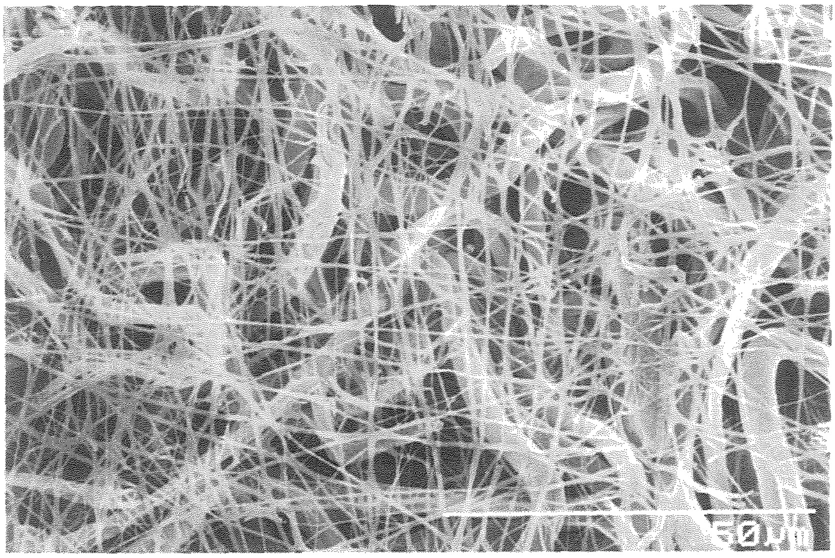

Fig. 61. *Kochummenaspis filiorum*: part of Fig. 59, showing wax filaments near the periphery of the film, with entangled trichomes forming the background.

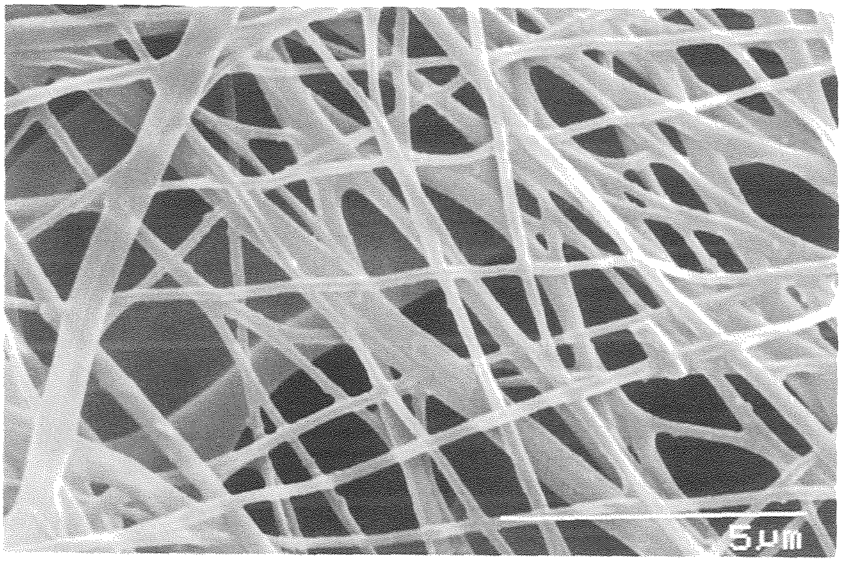

Fig. 62. *Kochummenaspis filiorum*: part of Fig. 59, wax filaments near the periphery of the film, more magnified than in Fig. 61 to show filaments different in thickness.

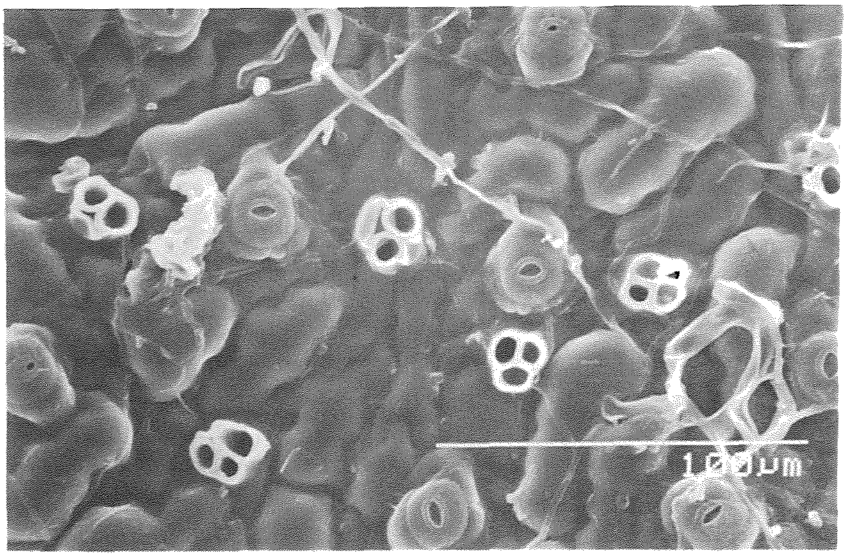

Fig. 63. *Kochummenaspis filiorum*: floor of the burrow, with bases of trichomes [91ML-455]. (These trichomes were cut away to form the ceiling of the burrow, leaving their tri- or quadrilocular bases.)

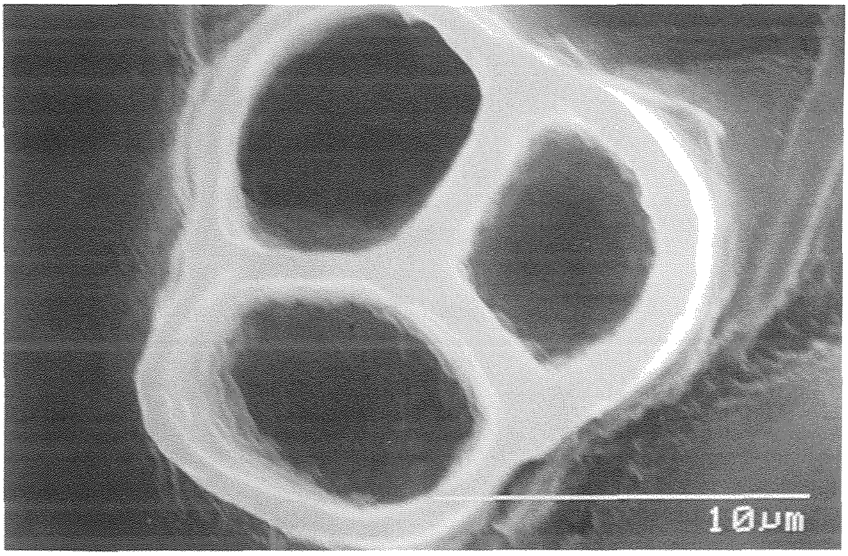

Fig. 64. *Kochummenaspis filiorum*: part of Fig. 63, showing the base of a trichome.