INSECTA MATSUMURANA

NEW SERIES 68: 17–115 OCTOBER 2012

ATYPICAL SPECIES OF AULACASPIS (STERNORRHYNCHA: COCCOIDEA: DIASPIDIDAE)

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Abstract

TAKAGI, S., 2012. Atypical species of *Aulacaspis* (Sternorrhyncha: Coccoidea: Diaspididae). *Ins. matsum. n. s*. 68: 17–115, 44 figs.

'Atypical' species of *Aulacaspis*, scale insects referable to the genus but not conforming with the type species in body shape, are dealt with; 21 species including 17 new species are described, three undetermined and seven known species are briefly noted, and 10 published names are mentioned. Not all of them are closely related to each other, so that the atypical species do not form their own taxonomic group within the genus. The *calcarata* species group is composed of nine species similar to each other in certain pygidial characters; five of them are typical and the other four atypical in body shape, the latter exhibiting two types of body shapes. These species suggest the emergence of the different body shapes within the group. The antennae of the first instar are six-segmented in six species, whereas five-segmented in many others; the possibility that the number of the antennal segments sometimes changes between closely related species is not excluded.

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Scientific Report for the projects: Hokkaidô University Expeditions to the Himalaya; Research Trips for Agricultural and Forest Insects in the Subcontinent of India; Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia.

Contents

1. Introduction

The scale insects dealt with in this paper are referred to *Aulacaspis* in spite of the fact that their full-grown adult females are anomalous in body shape in view of the traditional concept of the genus. They are lumped together under the title 'Atypical species of *Aulacaspis*', which simply means that they do not conform with the type species of the genus, *Aulacaspis rosae*, in body shape. Not all of them agree in their body shapes, which are not only atypical but also various. They are not uniform in other features, which do not vary in correlation with the body shapes. The atypical species, therefore, do not form their own taxonomic group or groups in the genus.

The inclusion of such various atypical forms in *Aulacaspis* may be supposed to make the genus too heterogeneous and to add unnecessary confusion to the genus. In fact, not all the species dealt with are included in the genus without question, and I do not think that none of them are erroneously referred to the genus. However, I think that in the present state of our knowledge these species are better referred to the genus than to any others. Furthermore, there is no obvious boundary between the typical and atypical species.

The genus *Aulacaspis* as represented by the type species and many other species is outstanding in having a swollen prosoma. This character is not restricted to the genus but known also in several other genera of the tribe Diaspidini, which are not closely related to *Aulacaspis*. The swollen prosoma should have emerged independently in all these genera with some adaptive significance. The atypical species of *Aulacaspis* may give a concrete basis for understanding the emergence of the typical body shape in the genus.

1.1. Establishment of the traditional concept of *Aulacaspis*

The genus *Aulacaspis* was originally proposed by Cockerell (1893) as a separation from *Diaspis* and for three species, with emphasis on the possession of a strongly tricarinate male test (so that the genus was named *Aulacaspis*). Newstead (1901) criticized the division based on that state of the male test as 'a most unnatural one', though he accepted *Aulacaspis* as represented by *Diaspis rosae* (which was the only species referred to *Aulacaspis* by both these authors and, therefore, is the type species) and another species he added to the genus. In response to Newstead's criticism, Cockerell (1902) recomposed these genera on the basis of the arrangement of the dorsal macroducts in the adult female; he transferred eight species from *Diaspis* to *Aulacaspis* and found that these genera were different in geographical distribution: '*Diaspis* became an American genus, *Aulacaspis* an Old World one'. However, *Aulacaspis* understood by him at that time (and also by Newstead, 1901) included *Pseudaulacaspis*, which was erected later and is recognized as a distinct genus in the current classification. Moreover, even if accepted, *Aulacaspis* was regarded as an infrageneric group of *Diaspis* by some authors (for example, 'the *Aulacaspis* section of *Diaspis*' in Green, 1922, p. 460). On the other hand, MacGillivray (1921) treated *Aulacaspis* as a genus and proposed *Pseudaulacaspis* as a separation from *Aulacaspis* in one of his tables for identification, in which these genera were placed in a pair and separated from each other by the presence or absence of a concavity at the apex of the pygidium.

Kuwana (1926) recognized *Aulacaspis* as a genus quite distinct from *Diaspis* and also from his new genus *Sasakiaspis* (which he described formally in replacement of

MacGillivray's *Pseudaulacaspis*), and compared the body shapes of the 'typical forms' of *Aulacaspis*, *Phenacaspis*, *Sasakiaspis*, and *Chionaspis*. Ferris (1937) regarded *Aulacaspis* as having no immediate connection with *Diaspis* and as distinct from *Pseudaulacaspis* (which was accepted as valid also in nomenclature). Both these authors attached weight to the enlarged prosoma ('cephalothorax' in Kuwana) in recognizing *Aulacaspis*. As foreseen by Cockerell (1902), many species of *Aulacaspis* were discovered in tropical and subtropical Asia and warm-temperate eastern Asia (while further species of *Diaspis* were described mostly from southern North America to tropical America and also from Africa). In the middle of the twentieth century, the concept of *Aulacaspis* was well established (Scott, 1952), and the genus was unanimously accepted by authors as a distinct one having a number of species in Asia. The species comprised in the genus were especially characteristic in the body shape of the adult female at full growth, having the prosoma swollen into a prominent mass and the postsoma abruptly narrowed behind the prosoma. In a rough outline, their bodies were shaped like a mushroom. Being outstanding and easily observable, this body shape was generally adopted as a useful diagnostic character of the genus.

1.2. *Phenacaspis* Problem and *Aulacaspis*

The concept and composition of *Aulacaspis* had to be revised again in a new situation brought about by a problem originally posed for settling the biological relationships between some forms of *Chionaspis* and *Phenacaspis*. The '*Chionaspis* or *Phenacaspis*' problem, or the *Phenacaspis* problem for short, was raised at the middle of the twentieth century (Takahashi, 1952, 1953), completely ignored once (Ferris, 1955, 1956), and carried to a final settlement after decades (Takagi, 1985). The core of the problem was the question whether *Phenacaspis*, a considerably large group long accepted by authors as a genus, was an entity or an artifact. (All taxa are artifacts in a sense, but we expect or hope that they reflect or approach entities.)

The nominifer ('the type species') of *Phenacaspis*, occurring in North America, was presumed to be the leaf-associated form of a species that had on the same host plant another form, the branch-associated form, under *Chionaspis*, and *Phenacaspis* was suppressed as a synonym of *Chionaspis* (Takagi and Kawai, 1967; Takagi, 1967; later, the presumption was confirmed experimentally by Knipscher et al., 1976). These leaf- and branch-associated forms appeared to be so discrete especially in the state of the median trullae that they had long been supposed to belong not only to different species (in spite of the deciduous host plant) but also to different genera. It was found that these forms embraced individuals that were somewhat variable in each of them; intermediate individuals were also found, and they connected the other individuals to form a broad and continuous series of variation. The other native forms of *Phenacaspis* in North America, with or without branch-associated counterparts under *Chionaspis*, were also referred to *Chionaspis* (Takagi and Kawai, 1967; later, Liu et al., 1989, re-examined the North American forms of *Chionaspis* and *Phenacaspis* and rearranged all of them in *Chionaspis*).

The phenomenon of ecophenotypic variation in '*Chionaspis* or *Phenacaspis*', caused by feeding on different parts of the plant body, was first noticed in Japan, where the problem extended to another genus and assumed another phase. The forms known at that time in Japan under *Chionaspis* and *Phenacaspis* were recomposed into two distinct

groups, which were found by combining characters from different instars, especially from the adult female and the second-instar male. One of the groups was identified with *Chionaspis*, and the other was united with *Pseudaulacaspis* (Takagi and Kawai, 1967). The *Phenacaspis* problem brought forth not only the obliteration of *Phenacaspis* and the recomposition of *Chionaspis* but also a renewed and broadened concept of *Pseudaulacaspis*.

The examined second-instar males of *Chionaspis* and *Pseudaulacaspis* suggested a remote relationship between these genera, which belong to the Chionaspidina and the Fioriniina, respectively, in a recent classification. It became apparent that the ecophenotypic effect in the stage of the adult female sometimes produced not only different forms within the same species but also parallel forms between the remotely related genera. *Phenacaspis* as composed by authors proved to be an assemblage of pieces (species) and fragments (ecophenotypic infraspecific forms) picked out from different taxonomic groups (genera and higher taxa) and put together in the same 'genus' on account of their superficial resemblance in the stage of the adult female. Needless to say, 'the subtribe Phenacaspidina' (Borchsenius, 1965, 1966) lost all meaning.

Finally and inevitably, the *Phenacaspis* problem required re-examinations of all the forms that remained under *Chionaspis* or *Phenacaspis* with their generic positions left unrevised and undetermined (Takagi, 1985). This involved *Aulacaspis*, another genus of the Chionaspidina, because not a few of the forms in question, mostly occurring in tropical Asia, appeared to be referable to the genus when the body shapes of their adult females at full growth were ignored. They agreed with the typical species of the genus especially in having 'Gland spines and small ducts found in varying numbers laterally on the second and third abdominal segments' (Scott, 1952, 'Definition of *Aulacaspis*'), while lacking these features laterally on the preceding segments except for the occasional presence of a few diminished ones. The occurrence of lateral macroducts and gland spines restricted to the second and third abdominal segments, called the 'localization' hereafter, was adopted as a useful diagnostic character for recognizing *Aulacaspis* in preference to the body shape (Takagi, 1985).

The localization of the lateral macroducts and gland spines is not a result of a general reduction of these features, because the absence of them on the first abdominal segment (and the preceding segments) is often combined with their abundant occurrence on the second segment (and the third), the contrast between the first and second segments being quite striking. The localization is apparently deeply rooted in the organization of the body, whereas the shape of the body is formed as a result of growth during the stage of the adult female. When thus qualified, the localization and the body shape should not be equivalent in taxonomic practice and the former should have importance over the latter. The combination of the localization with another character, the absence of well-developed marginal setae between the median trullae, was evaluated as a clue in deciding which species should be included in the genus (Williams and Watson, 1988). A revised diagnostic description of *Aulacaspis* was given, a species group (the *calcarata* species group; see 6.1.) was composed of typical and atypical species, all these species having been referred to the genus according to the revised concept, and the group was deemed to be a natural one in spite of its heterogeneous composition (Takagi, 1999).

However, adhering to the localization of the lateral macroducts and gland spines in assigning species to *Aulacaspis* may sometimes be misleading. The same character may appear as a result of a reduction of the lateral macroducts and gland spines throughout

the prepygidial segments. In this case, the lateral macroducts and gland spines remaining on the second and third abdominal segments should be very few. This statement does not necessarily imply that *Aulacaspis* should not include species with very few lateral macroducts and gland spines.

In the present study, I have noticed that the localization is not always held in its primary state in the species referred to *Aulacaspis*. In the present paper, 17 species are described as new. One of the new species has no lateral macroducts and gland spines on the second abdominal segment as well as on the preceding segments, while possessing these features in good numbers on the third segment (see 2.1.). Another species has a few lateral macroducts and gland spines only on the third segment (2.14.), and four other species are not stable in the occurrence of these features on the second segment, which is often devoid of macroducts or gland spines or both (2.12., 2.13., 2.15., and 2.21.). These six new species are referred to *Aulacaspis* in consideration of other characters. The absence of lateral macroducts and gland spines on the second abdominal segment in these species is apparently a secondary loss within the genus. It is attributable to a general reduction of these features on the second and third segments except for one species, which has many lateral macroducts and gland spines on the third segment (2.1.).

2. Atypical Species of *Aulacaspis*

The full-grown adult female of the type species, *Aulacaspis rosae*, has the prosoma (composed of the head and the pro- and mesothorax all fused together) swollen into an eminent mass exceeding the postsoma in width, and represents the '*rosae*-type' in body shape. In reality, however, the species referable to this type are various in the enlargement of the prosoma, forming a graded series, and at one end of the series some species have the prosoma little broader than the postsoma. The distinction between the typical and atypical species is, therefore, rather arbitrary. There also exist a few species belonging to the *rosae*-type but having the body unusually slender, and they are treated as atypical species in this paper.

The full-grown adult female of *Aulacaspis vitis* (=*Chionaspis vitis*) has the thoracic region, especially the mesothorax, extraordinarily expanded laterally and thus making the whole body roughly rhombic in outline. It represents the '*vitis*-type' in body shape. (The growth of the body of this type is shown in Takagi, 1999, Fig. 2.) There are other species referable to *Aulacaspis* and less peculiar in body shape. In these species the adult females are fusiform (elongate, broadest about the middle, and tapering to each end), oblong (elongate and parallel-sided for most length), or obovate (moderately expanded laterally in the thoracic region) at full growth. In the species of the *vitis*-type the adult females do not always grow fully enough to reveal the characteristic shape of the type. It is, therefore, not always easy to distinguish between the species of the *vitis*-type and those shaped less peculiar. Rarely, the full-grown adult females are much elongated and slender; the body of this type may represent an elongated variation of the fusiform or oblong body. Two other species have the whole cephalothorax swollen into a round or transversely oblong mass.

Some of the atypical species are occasionally or usually provided between the antennae with a broad transverse tubercle, called in this paper the 'interantennal tubercle', which is often divided into a pair of swellings, the 'interantennal swellings', situated just mesad of the antennae. Less frequently, they have a pair of small dermal

invaginations, the ‘interantennal derm pockets’, which are sometimes not complete, one of the pair being lost; they are situated just behind the interantennal tubercle or swellings when these are present.

The abbreviations ‘abd I’–’abd VIII’ stand for the first to eighth abdominal segments. The term ‘trullae’ is used in place of the ‘pygidial lobes’ of authors; the term ‘dorsal macroducts’ means the submedian and submarginal macroducts combined together (several species have no submedian macroducts); the ‘lateral macroducts’ and ‘lateral gland spines’ occur on the lateral lobes of the second and third abdominal segments. The length of the pygidium is measured along the midline between the anterior border of the fifth abdominal segment and the level of the apices of the median trullae. (The length of the pygidium should properly exclude the median trullae, which are appendages of the pygidium. In most species dealt with in this paper, however, the median trullae are sunken into the pygidium, forming a notch on the apex of the latter, so that they are included in the length of the pygidium.) The numbers of disc pores, macroducts, and gland spines are given for each side of the body except for the total number of the dorsal macroducts and that of the perivulvar disc pores. (The total number of the perivulvar disc pores cannot be given for each side owing to the presence of the median group in addition to the antero- and posterolateral groups. The combination of the total number of the dorsal macroducts occurring on both sides of the body and that of the perivulvar disc pores in all the five groups affords a simple but useful numerical index for specimens and samples especially on a scatter diagram.) Specimens mounted from the leaves of the host plants are ‘foliicolous’, and those from the twigs and branches are ‘ramicolous’. In two species (2.9. and 2.10.) the feeding sites are divided further.

The present study is based on the adult females, but notes are added to the number of the antennal segments in the first instar (see 6.2.). In most of the species dealt with, the adult female specimens are membranous and not stained well, so that they were observed by phase-contrast microscopy.

Four figures drawn by Dr D. J. Williams are published in this paper with his approval.

Most of the host plants were identified by botanists in India (Botanical Survey of India), Nepal (Department of Medicinal Plants), Malaysia (Mr K. M. Kochummen, Forest Research Institute of Malaysia; Forest Research Centre, Sabah), Singapore (Dr Hsuan Keng, University of Singapore), and the Philippines (Dr Edwino S. Fernando, University of the Philippines at Los Baños).

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

2.1. *Aulacaspis gracilis*, n. sp. (Fig. 7)

Material. Collected on Mt. Kinabalu, alt. 2500m, Sabah (northeastern Borneo), Malaysia, on *Actinodaphne pruinosa* (Lauraceae), 2.X.1988 [lot no.: 88ML-32]. Female tests occurring on the lower surface of leaves, rather large, flat, thin but not transparent. The description below is based on four adult females, three of them being fully grown, with the derm sclerotized throughout. Holotype: FRIM.

Adult females. Body of the *rosae*-type, with prosoma swollen into a mass distinctly broader than postsoma, but the whole body unusually narrow for a species of this type, 2.2–2.6 times as long as wide, 1400–1620μm long; pygidium 330–350μm long. Prosoma as long as or a little shorter than wide, gradually broadening caudad, broadest subbasally, prosomatic tubercles low and inconspicuous; metathorax well lobed laterally; abdomen narrower than metathorax, slender, abd I and II moderately lobed laterally, lateral lobes of abd III flattish marginally; pygidium as long as wide, little rounded on free margin. Peribuccal scleroses well developed. Anterior spiracles each accompanied with a rather compact cluster of 13–26, mean 16.3 (n=8), disc pores; posterior spiracles each with a loose cluster of about 2–10 disc pores laterally (these disc pores were not always exactly counted owing to a sclerotized dermal fold associated with them). Perivulvar disc pores 14–16 in median, 24–30 in each anterolateral, and 17–23 in each posterolateral group; total 101–117, mean 106.5 (n=4). Meso- and metathorax and abd I and II each scattered with some small and short ducts on ventral surface submarginally (abd II with 5–9 on each side), these ducts being nearly as large as microducts but broader. Abd II with no macroducts and no gland spines on lateral lobe; III with 9–11, mean 9.5 (n=8), macroducts and 9–11, mean 9.5 (n=8), gland spines arranged on margin of lateral lobe; IV with 4–6, mean 5.0 (n=8), gland spines marginally. Abd III–V with submedian and submarginal dorsal macroducts; submedian macroducts few, 2 or 3 on each of III and IV and 1 or 2 on V; submarginal rows single, row on III oblique, with 3 or 4 macroducts, rows on IV and V nearly perpendicular, with 4–6 and 6 macroducts, respectively; total of dorsal macroducts on both sides 40–44, mean 42.0 (n=4). Median trullae much longer than lateral trullae, largely sunken into pygidium, divergent, slender, obscurely serrate on mesal margins, with a small basal zygosis not produced anteriorly beyond bases of trullae. Second and third trullae well represented, each lobule dilated, with a pair of linear scleroses basally. Pore prominences rather low.

Recognition characters (foliicolous adult female). Body of the *rosae*-type, but unusually slender. Peribuccal scleroses well represented. Posterior spiracles each with a loose cluster of disc pores laterally. Lateral macroducts and gland spines absent on abd II, rather abundant on III. Submedian and submarginal dorsal macroducts on abd III–V; submedian macroducts few; submarginal macroducts in single rows. Median trullae much longer than lateral trullae, sunken into apex of pygidium, divergent, slender, with a small basal zygosis not produced anteriorly.

Remarks. This species represents an unusually narrow form of the *rosae*-type. In this genus, a narrow or slender body is occasionally seen in species or individuals occurring along the veins or margin of leaves, but this is not the case with *A. gracilis*.

The absence of macroducts and gland spines on the lateral lobes of the second abdominal segment is another remarkable character of this species. This character is not a result of a general reduction of lateral macroducts and gland spines in this species, because these features are represented rather abundantly on the third segment. As a possibility, it may be associated with the movement of the narrow body in test construction, but how the body moves is no more than speculation in the present state of our knowledge.

2.2. *Aulacaspis loranthi* (Figs 3, 8)

Diaspis loranthi Green, 1900: 254 [‘On under surface of leaves of *Loranthus tomentosus*;

sometimes also on the young stems; Pundaluoya; Banderawella.', Sri Lanka].

Aulacaspis loranthi: Cockerell, 1902: 59.

Aulacaspis loranthi: Green, 1937: 315 ['On under surface of leaves *Loranthus tomentosus*. Pundaluoya: Bandarawela. Recorded also from India, on the same plant.']. (For the record from India, see *Remarks*.)

Material. Collected in Nepal on lauraceous plants. The samples are largely divided into two groups according to collection localities.

Group I. Bagmati Zone. Gokarna Forest, alt. 1350–1380m, Kathmandu Valley, on *Cinnamomum bifaria*, *Lindera latifolia*, *Lindera nacusua*, and *Neolitsea cuipala*, 16.VIII.1975 [lot no.: 75NPL-8, -9, -10, -14], 16.X.1975 [75NPL-325, -327], and 15.X.1983 [83NPL-47]. Sundarijal, alt. 1530–1600m, Kathmandu Valley, on *Lindera nacusua*, 23.X.1983 [83NPL-100, -102]. On the way from Dunche to Syabru, alt. 1770m, on *Machilus duthiei*, 19.IX.1975 [75NPL-237]. The numbers of main wax-secreting organs have been counted in about 20 specimens for each of the samples from [75NPL-9], [75NPL-237], and [83NPL-47].

Group II. Gandaki Zone. Malepatan, alt. 750–800m, Pokhara District, on *Lindera* sp. and *Neolitsea cuipala*, 7.XII.1983 [83NPL-299, -304]. The numbers of main wax-secreting organs have been counted in 20 specimens from each of the two samples.

Female and male tests occurring on the lower surface (female tests sometimes on the upper surface) of leaves. Female tests mostly occurring along leaf veins and narrow, with exuvial casts terminal; broader when occurring on the blade off the veins. Male tests tricarinate.

Adult females (Group I). Body elongate, attaining a little more than twice as long as broad, about 1500μm long at maximum; pygidium 210–260μm long. Oblong, with the lateral sides nearly parallel, a little constricted on metathorax and abd I; mesothorax clearly demarcated from prothorax and metathorax dorsally, well lobed laterally, a little broader than prothorax, metathorax, and abd I; metathorax and abd I weakly, and abd II strongly, lobed laterally; pygidium broader than long, little rounded on free margin. Derm remaining membranous, or tending to be sclerotized on prothorax, metathorax and abd I; sclerotized patches (irregularly shaped) and spots (more or less rounded) often appearing clearly on dorsal surface, prosoma with a number of scar-like patches, meso- and metathorax and abd I with a submedian pair of spots and a submarginal pair of patches. Anterior spiracles each accompanied with 7–25 disc pores (not always exactly counted). Posterior spiracles each with 1–6 (usually 2–4) disc pores laterally or anterolaterally; 2–6 disc pores, mean 3.6 (n=34) in sample from [75NPL-9], 1–6, mean 2.7 (n=40) in [83NPL-47], 1–4, mean 2.6 (n=36) in [75NPL-237]. Perivulvar disc pores 11–24 in median, 16–30 in each anterolateral, and 13–29 in each posterolateral group; total 85–123, mean 109.6 (n=20) in sample from [75NPL-9], 85–127, mean 98.3 (n=20) in [83NPL-47], 75–126, mean 103.6 (n=20) in [75NPL-237]. Abd II with 2–7 macroducts and 1–6 gland spines at apex of lateral lobe; III with 2–7 macroducts and 4–10 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 6–10, mean 8.3 (n=39) in sample from [75NPL-9], 5–11, mean 8.0 (n=40) in [83NPL-47], 5–12, mean 9.4 (n=40) in [75NPL-237]. Total of lateral gland spines on each side 7–14, mean 10.2 (n=39) in sample from [75NPL-9], 5–11, mean 9.2 (n=41) in [83NPL-47], 7–14, mean 11.2 (n=40) in [75NPL-237]. Abd IV with 3–6 gland spines marginally; 3–6, mean 4.1 (n=40) in sample from [75NPL-9], 3–5, mean 3.8 (n=42) in [83NPL-47], 3–5, mean 4.2 (n=40) in [75NPL-237]. Submedian macroducts on abd III–V, tending to be divided into segmental and infrasegmental series on III and IV; 1–8, 1–6, and 1–5 on III, IV, and V, respectively;

1 macroduct present (in 20–43% of the examined cases) or absent on VI. Submarginal macroducts in single rows, 1–11, 2–7, and 2–8 on abd III, IV, and V, respectively. Total of dorsal macroducts on both sides: 30–62, mean 50.6 (n=20) in sample from [75NPL-9], 25–69, mean 46.2 (n=20) in [83NPL-47], 24–80, mean 58.0 (n=20) in [75NPL-237]. Median trullae much larger than lateral trullae, sunken into apex of pygidium, divergent, slender, with mesal margins obscurely serrate; basal zygosis small but distinct. Lateral trullae well represented, each lobule with a pair of short linear scleroses basally. Pygidial margin on abd V and VI nearly straight, with pore prominences little produced.

Adult females (Group II). Characterized substantially the same as the samples from the Bagmati Zone, with the main wax-secreting organs tending to be fewer but largely overlapping in range with those in the latter. Disc pores associated with each posterior spiracle 1–4, mean 2.3 (n=38) in sample from [83NPL-299], 2–4, mean 3.4 (n=37) in [83NPL-304]. Total of perivulvar disc pores 67–114, mean 91.7 (n=20) in sample from [83NPL-299], 73–122, mean 94.3 (n=20) in [83NPL-304]. Total of lateral macroducts on each side 4–9, mean 6.5 (n=40) in sample from [83NPL-299], 3–10, mean 7.0 (n=38) in [83NPL-304]. Total of lateral gland spines on each side 7–11, mean 8.1 (n=40) in sample from [83NPL-299], 6–13, mean 8.3 (n=38) in [83NPL-304]. Abd IV with 2–5 gland spines marginally; 2–5, mean 3.4 (n=40) in sample from [83NPL-299], 3–5, mean 3.7 (n=40) in [83NPL-304]. Total of dorsal macroducts on both sides 22–60, mean 39.1 (n=20) in sample from [83NPL-299], 12–57, mean 39.0 (n=20) in [83NPL-304]. Submedian macroducts sometimes (18–20%) absent on abd III. In contradiction, 1 submedian macroduct occurring on abd VI more frequently (50–58%) than in the samples from the Bagmati Zone.

Recognition characters (foliicolous adult female). Body narrowly oblong, nearly parallel-sided; mesothorax clearly demarcated from prothorax dorsally, well lobed laterally, and a little broader than prothorax, metathorax and abd I; abd II strongly lobed laterally. Posterior spiracles each with a few disc pores. Submedian macroducts on abd III–V, 1 present or absent on VI; submarginal macroducts in single rows on III–V. Median trullae much larger than lateral trullae, sunken into apex of pygidium, divergent, slender, obscurely serrate on mesal margins, with a small basal zygosis. Pygidial margin on abd V and VI nearly straight, with pore prominences little produced.

Remarks. This scale insect is unique in having a narrowly oblong body and an incompletely formed prosoma, in which the mesothorax is clearly demarcated from the mass composed of the head and prothorax on the dorsal surface. In the other characters of the adult female, however, it is not extraordinary for a member of *Aulacaspis* (see also 6.2.).

Diaspis loranthi was described from *Loranthus tomentosus*, family Loranthaceae. On this plant, the females burrow beneath ‘the tomentose covering of the leaf, which is continuous over the surface of the scale’ (Green, 1900). The specimens examined in the present study are all from Lauraceae, on which they occur on the glabrous leaf surface, not burrowing, and mostly along veins. In consideration of the host association, it is doubtful that they belong to *D. loranthi*. However, in comparing them with a figure drawn by Dr D. J. Williams from a specimen of the type series (Fig. 3), I have failed to find any difference distinct enough to separate them from *D. loranthi*. They should be identified with *D. loranthi*, but tentatively unless this species proves to be a polyphagous species. The placement of this species in *Aulacaspis*, too, is rather tentative because not only of the body shape and the incomplete prosoma in the adult female but also of

another reason (see 6.2.).

Green (1919) recorded *Diaspis loranthi* as from '*Loranthus cordifolius*: Paresnath, Bihar, 4000 ft.', India. According to Dr D. J. Williams, this record was based on a misidentification and should refer to another species, *Aulacaspis peresnathae* (manuscript name) (Fig. 4). (In the caption of *A. peresnathae*, the locality is written 'West Bengal, Peresnath', not 'Paresnath, Bihar' as in Green, 1919, but I have no doubt that these names point to the same locality.) *A. peresnathae* is remarkably different from *A. loranthi* in having a robust body, which seems to belong to the *rosae*-type; it has the mesothorax not clearly demarcated from the prothorax, and differs also in the median trullae, which are shorter and broader. Green (1900) observed that *Diaspis loranthi* occurred on the leaves and 'sometimes also on the young stems' of *Loranthus tomentosus*, but he stated nothing about the morphological traits of the stem-associated individuals. The feeding site of *A. peresnathae* on the host plant is unknown, but the possibility that this form represents the branch-associated form of *A. loranthi* may not definitely be excluded in the present state of our knowledge on ecophenotypic variation in armoured scale insects.

This study has left two questions: whether the Himalayan form associated with Lauraceae is really conspecific with the *Loranthus*-associated form occurring in Sri Lanka; and whether *A. peresnathae* from northeastern India is really distinct from the forms occurring in Sri Lanka and the Himalayas.

If *A. peresnathae* is distinct from the forms occurring in Sri Lanka and the Himalayas and yet closely related to the latter two, it follows that the typical body shape and an atypical one can occur in closely related species. If *A. peresnathae* represents the branch-associated form of *A. loranthi*, it is apparent that ecophenotypic effect sometimes produces the *rosae*-type and another type within the same species.

2.3. *Aulacaspis litzeae* (Fig. 9)

Chionaspis eugeniae var. *litzeae* Green, 1896: 2 ['Found on under surface of leaves of *Litzea zeylani*ca. … Locality Punduloya.' Sri Lanka].

Chionaspis litzeae Green, 1899: 144 ['Habitat on leaves of *Litzea zeylani*ca. Pundaluoya; Nuwara Eliya.' Sri Lanka].

*Chionaspis litsea*e Green, 1937: 319 ['The alteration in the spelling of the specific name, as originally published, is necessitated by the fact that the host-plant is '*Litsea*' (not '*Litzea*').].

Phenacaspis litzeae: Ferris, 1956: 70 ['A single specimen of this species has been available …, this from Pundaluoya, Ceylon, collected and determined by E. E. Green but not indicated as from the type material although it probably is so.'].

*Aulacaspis litsea*e: Takagi, 1985: 47.

Material. Collected in South India on plants of *Actinodaphne* (Lauraceae). Nadubattam, alt. 1930m, Nilgiri Hills, Tamil Nadu, India, on *Actinodaphne* sp., 28.XI.1978 [lot no.: 78IND-223]. Periyar Tiger Reserve, alt. ca. 900m, Thekkady, Kerala, on *Actinodaphne* sp. (*A. hookeri*?), 19.XII.1978 [78IND-397]. Female and male tests occurring on the lower surface of leaves. Female test very thin, variable in outline, narrow when occurring along the veins and margin of leaves; male tests with a faint median carina. About 20 mounted specimens are available from each of the two samples.

Adult females from the Periyar Tiger Reserve. Body elongate, growing 975µm long and a little more than twice as long as wide; pygidium 160–190µm long. Roughly oblong, with body sides nearly parallel and free segments weakly lobed laterally, or,

when fully grown, with mesothorax a little broader than metathorax and abdomen; pygidium little rounded on free margin. Anterior spiracles each accompanied with a compact cluster of 12–37 disc pores (not always exactly counted); posterior spiracles each accompanied with a cluster of 3–10 (usually 3–6), mean 4.5 (n=37), disc pores laterally. Perivulvar disc pores 6–10 in median, 12–24 in each anterolateral, and 8–19 in each posterolateral group; total 59–91, mean 72.8 (n=19). Abd II with 1–4 (usually 2 or 3) macroducts and 1–4 (usually 1 or 2) gland spines on lateral lobe; III with 3 or 4 (usually 3) macroducts and 4–7 (usually 5 or 6) gland spines on lateral lobe. Total of lateral macroducts on each side 4–8, mean 5.8 (n=33). Total of lateral gland spines on each side 6–10, mean 7.3 (n=33). Abd IV with 2–5 (usually 3) gland spines marginally. Submedian macroducts few: abd III often without submedian macroducts, sometimes (19%, n=38) with 1; IV usually with 1 macroduct, rarely with 2, sometimes with none; V usually with 2, sometimes with 1, rarely with 3; VI with none. Submarginal macroducts also few; 1 or 2 (rarely none) on abd III; 1 or often 2 on IV; 2, rarely 1 or 3, on V. Total of dorsal macroducts on both sides 10–19, mean 15.7 (n=18). Median trullae very large as compared with lateral trullae, deeply sunken into apex of pygidium, elongate, with mesal margins gradually divergent from their bases, curved, and minutely serrate; bases thick, completely fused together, without distinct, strongly sclerotized zygosis. Lateral trullae well represented; mesal lobules with basal linear scleroses ill developed. Abd IV and V flattish marginally, without prominent processes.

Adult females from the Nilgiri Hills. Characterized substantially the same as the specimens from the Periyar Tiger Reserve. Anterior spiracles each with about 16–40 disc pores (not always counted exactly). Posterior spiracles each with 4–11, mean 6.9 (n=36), disc pores. Total of perivulvar disc pores 69–97, mean 81.4 (n=18). Total of lateral macroducts on each side 2–6, mean 4.4 (n=36). Total of lateral gland spines on each side 4–10, mean 6.8 (n=36). Total of dorsal macroducts 8–19, mean 13.9 (n=18).

Recognition characters (foliicolous adult female). Body oblong; when fully grown, mesothorax a little broader than metathorax and abdomen. Posterior spiracles each with a small cluster of disc pores laterally. Submedian macroducts few; 1 occasionally present on abd III, 1 or rarely 2 on IV, and 1–3 on V. Submarginal macroducts on abd III–V, not numerous. Median trullae much larger than lateral trullae, elongate, divergent, the bases thick, completely fused together.

Remarks. The examined specimens are identified mainly on the basis of the description in Green (1899). These specimens from South India disagree with the form described and figured by Green from Sri Lanka in having fewer perivulvar disc pores in the median and anterolateral groups and fewer submarginal macroducts on the third and fourth abdominal segments, but the differences are not great. They agree with the figures given by Green in the body oblong and a little swollen in the mesothorax and in the median trullae with the bases thick and completely fused together. The examined specimens may be sufficiently numerous to show that the adult female remains almost fusiform. (See also 6.2.)

Green (1919) recorded '*Chionaspis litsea*e' from 'Darjiling District', northeastern India, as occurring on 'Ghumti'. Tang (1986) described a new species from China under the name '*Aulacaspis litsea*e'.

2.4. *Aulacaspis malabarica*, n. sp. (Figs 1, 10–12)

Material. Collected at hilly areas in South India, on lauraceous plants. Periyar Tiger Reserve, alt. ca. 900m, Thekkady, Kerala, on *Cinnamomum zeylanicum* (*C. verum*), 21.XII.1978 [lot no.: 78IND-425]. Coonoor, alt. ca. 1600m, Nilgiri Hills, Tamil Nadu, on *Neolitsea* sp., 29.XI.1978 [78IND-240]. Top Slip, alt. ca. 750m, Anaimalai Hills, Tamil Nadu, on *Cinnamomum* sp. and *Cinnamomum malabratum*, 2.XII.1978 [78IND-272, -273]. Female and male tests occurring on the lower surface of leaves, female tests sometimes also on the upper surface and along the midrib. Examined specimens of the adult female: 18 from material [78IND-425]; about 10 from each of the other lots of material. Holotype, from [78IND-425]: SEHU.

Adult females from the Periyar Tiger Reserve. Body, when fully grown, of the *vitis*-type, with mesothorax much expanded laterally; pygidium broadly triangular in outline, about 240–250μm long. Anterior spiracles each accompanied with 13–30 disc pores (not always exactly counted); posterior spiracles each accompanied with a compact group of 8–20, mean 12.9 (n=32), disc pores laterally. Perivulvar disc pores 13–20 in median, 24–37 in each anterolateral, and 15–31 in each posterolateral group; total 100–148, mean 126.2 (n=18). Abd II with 4–8 (usually 4 or 5) macroducts and 3–9 gland spines on lateral lobe; abd III with 3–6 (usually 5 or 6) macroducts and 5–10 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 7–12, mean 9.8 (n=31). Total of lateral gland spines on each side 10–16, mean 12.8 (n=32). Abd IV with 2–4 (usually 3) gland spines marginally. Submedian macroducts on abd III–V, rarely 1 on VI, those on III and IV tending to be divided into segmental and infrasegmental series; 1–5 on III, 2–4 on IV, 1–3 on V. Submarginal macroducts in single rows on abd III–V, 2–8 on III, 2–6 on IV, and 2–5 on V. Total of dorsal macroducts on both sides 31–56, mean 39.9 (n=17). Median trullae much larger than lateral trullae, sunken into apex of pygidium, slender, with mesal margins nearly parallel or slightly divergent on about basal half, then divergent, curved, and minutely serrate, with basal zygosis horseshoe-shaped and a little produced anteriorly beyond their bases. Second and third trullae well represented, mesal lobule of second trulla with a pair of slender but distinct scleroses basally, other lobules with basal scleroses less developed. Abd IV and V flattish marginally.

Adult females from Top Slip, *Anaimalai Hills*. Characterized substantially the same as the females from the Periyar Tiger Reserve. Body attaining 1360μm long. Posterior spiracles with disc pores tending to be fewer, each with 6–13, mean 9.0 (n=28). Total of perivulvar disc pores 81–158, mean 128.0 (n=17). Total of lateral macroducts on each side 5–11, mean 8.1 (n=32). Total of lateral gland spines on each side 8–18, mean 11.8 (n=32). Total of dorsal macroducts 19–45, mean 32.2 (n=17). Abd VI usually with 1 submedian macroduct, occasionally with 2 or none. Median trullae divergent from their bases.

Adult females from Coonoor, Nilgiri Hills. Posterior spiracles with disc pores tending to be fewer, each with 6–9, mean 8.0 (n=17). Total of perivulvar disc pores 99–121, mean 111.8 (n=11). Total of lateral macroducts on each side 5–8, mean 6.7 (n=20). Total of lateral gland spines on each side 10–17, mean 13.3 (n=19). Total of dorsal macroducts 38–59, mean 48.0 (n=10). Abd VI with no submedian macroducts. Median trullae divergent from their bases.

Recognition characters (foliicolous adult female). Body, when fully grown, of the *vitis*-type, with mesothorax expanded laterally. Posterior spiracles each with a small cluster of disc pores laterally. Submedian macroducts on abd III–V, a few to several on

each segment; 0–2 on VI. Submarginal macroducts in single rows on abd III–V. Median trullae larger than lateral trullae, divergent, with mesal margins minutely serrate; basal zygosis horseshoe-shaped, a little produced anteriorly.

Remarks. The specimens from the two localities in Tamil Nadu (Coonoor, Nilgiri Hills; Top Slip, Anaimalai Hills) differ from those collected in Kerala (Periyar Tiger Reserve) in the median trullae, which have the mesal margins divergent from the bases in the former and on about apical half in the latter. In the correlation between the total number of the dorsal macroducts and that of the perivulvar disc pores (Fig. 1), the samples from the two localities in Tamil Nadu form distinct groups, whereas the sample from the Periyar Tiger Reserve, Kerala, comes between them, the three samples being united to form a larger group.

Three interpretations are possible for the three forms. First, they belong to three species; second, the sample from the Periyar Tiger Reserve represents a distinct species, whereas the specimens from the two localities in Tamil Nadu belong to another species and represent two local forms; third, all these forms belong to one and the same species, which is variable locally in the shape of the median trullae and in the number of the dorsal macroducts. The available samples are not amply sufficient to show that they represent more than one species, and I adopt the third interpretation tentatively. Any way, it seems that there is in the hilly areas of South India a compact group of forms of *Aulacaspis* associated with Lauraceae, the *malabarica* complex, which should also include two other species, *Aulacaspis anaimala* (2.5.) and *Aulacaspis nilagirica* (2.6.).

2.5. *Aulacaspis anaimala*, n. sp. (Figs 1, 13, 14)

Material. Collected at Top Slip, alt. ca. 750m, Anaimalai Hills, Tamil Nadu, India, on undetermined trees of the family Lauraceae, 2.XII.1978 and 3.XII.1978 [lot no.: 78IND-263, -285]. Female and male tests occurring on the lower surface of leaves, female test with exuvial casts terminal. Nine and 20 adult females from material [78IND-263] and [78IND-285], respectively, have been examined, and they are united together in the description. Holotype, from [78IND-285]: SEHU.

Adult females. Body, when fully grown, of the *vitis*-type, with meso- and metathorax eminently expanded laterally; attaining about 1500μm in length; pygidium roundish on free margin, 240–280μm long. Interantennal tubercle sometimes present. Anterior spiracles each accompanied with a cluster of 5–15, mean 8.1 (n=51), disc pores; posterior spiracles each accompanied with 1–4 (usually 1 or 2) disc pores anteriorly. Perivulvar disc pores 14–17 in median, 15–35 in each anterolateral, and 13–25 in each posterolateral group, total 86–131, mean 109.8 (n=29). Abd II with 5–8 macroducts and 5–10 gland spines on lateral lobe; III with 3–6 macroducts and 4–9 gland spines on margin of lateral lobe. Total of lateral macroducts on each side 8–13, mean 10.7 (n=51). Total of lateral gland spines on each side 10–18, mean 13.8 (n=48). Abd IV with 2–4 (usually 2 or 3) gland spines marginally. Abd I and II each with a transverse row of several microducts submedially on dorsal surface. Submedian macroducts on abd III–V and usually also on VI, those on III, and sometimes also those on IV, tending to be divided into segmental and infrasegmental series; 3–9, 3–7, and 2–7 on III, IV, V, respectively; usually 1, at times 2 or 3, or none, on VI. Submarginal macroducts 5–11, 3–8, and 1–4 on abd III, IV, and V, respectively, usually in single rows, sometimes in a partly double row on III and also on IV. Total of dorsal macroducts 46–87, mean 65.0 (n=28). Median trullae

somewhat larger than lobules of lateral trullae, sunken into apex of pygidium, divergent, robust, expanded caudad, rounded and obscurely serrate marginally, basal zygosis represented by a pair of small sclerotized pieces united with each other at their anterior ends. Second and third trullae with both lobules well developed and tending to be dilated, their mesal lobules each with a pair of linear scleroses basally, lateral lobule of second trulla with short scleroses. Abd IV and V with margin flattish or slightly roundish, with processes not prominent.

Recognition characters (foliicolous adult female). Body, when fully grown, of the *vitis*-type. Anterior spiracles each with a small cluster of disc pores; posterior spiracles each with a few disc pores anteriorly. Submedian macroducts on abd III–V; 1 or 2 usually present on VI. Submarginal macroducts on abd III–V, rather numerous. Median trullae somewhat larger than lobules of lateral trullae, sunken into apex of pygidium, divergent, expanded caudad, rounded and obscurely serrate marginally, basal zygosis represented by a pair of small pieces.

Remarks. This species may be closely related to *Aulacaspis malabarica* and *Aulacaspis nilagirica* (see *Remarks* under 2.6.).

2.6. *Aulacaspis nilagirica*, n. sp. (Figs 1, 15)

Material. Collected at Doddabetta, alt. ca. 2600m, Nilgiri Hills, Tamil Nadu, India, on *Litsea* sp. (Lauraceae), 24.XI.1978 [lot no.: 78IND-189]. Two specimens of the adult female were obtained from the lower surface of a leaf, and one from a twig. Holotype, one of the foliicolous specimens: SEHU.

Foliicolous adult females. The two available specimens are probably at an early stage of growth; body about 1050µm long and about 500µm wide (across abd II); pygidium broadly triangular in outline, about 250µm long. Body nearly oblong, broadest in abd II, which is produced laterally. Antennae each composed of a flattish tubercle and a slender seta. Anterior spiracles each accompanied with 12–18, mean 15.5 (n=4), disc pores; posterior spiracles each accompanied with 5 or 8 disc pores laterally. Perivulvar disc pores 16 or 20 in median, 32–38 in each anterolateral, and 26–31 in each posterolateral group; total 140 or 147. Abd II with 8 or 9 macroducts and 5–9 gland spines on lateral lobe; III with 7 or 8 macroducts and 5–10 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 15–17, mean 16.0 (n=4). Total of lateral gland spines on each side 13–17, mean 14.8 (n=4). Abd IV with 3–5, mean 4.0 (n=4), gland spines marginally. Abd I and II each scattered with several submedian microducts dorsally; III with 1 microduct anteriorly to row of submedian macroducts. Submedian macroducts on abd III–VI, those on III–V tending to be divided into segmental and infrasegmental series, 4–8 on III, 4–9 on IV, 6 or 7 on V, and 1–3 on VI. Submarginal macroducts on abd III–V, those on III in a partly double row; 7–9 on III, 6–8 on IV, and 4–6 on V. Total of dorsal macroducts on both sides 84 or 86. Median trullae distinctly larger than lobules of lateral trullae, sunken into apex of pygidium, robust, divergent, separated from each other by a good space basally, with mesal margins parallel for about basal half, then strongly divergent, minutely serrate; basal zygosis not developed in one of the specimens (Fig. 15, I), but well represented in the other, shaped like an inverted U (Fig. 15, D, upper). Second and third trullae well represented; mesal lobule of second trulla with a pair of linear scleroses basally, that of the third with shorter scleroses. Abd IV and V flattish marginally, with no prominent processes.

Ramicolous adult female. The single specimen examined in this study appears to be more aged than the foliicolous specimens, but is still roughly oblong in outline, with the prepygidial region of the body nearly of the same breadth through the meso- and metathorax and prepygidial abdomen; body 1220μm long and 640μm wide (across abd II); pygidium 300μm long. Anterior spiracle with 24 or 30 disc pores; posterior spiracle with 8 or 11 disc pores laterally. Perivulvar disc pores: 38 in median, 44 or 45 in anterolateral, and 37 or 38 in posterolateral group; total 202. Abd II with 11 or 12 macroducts and 9 or 13 gland spines on lateral lobe; III with 8 macroducts and 10 or 13 gland spines along margin of lateral lobe; IV with 4 or 6 gland spines marginally. Abd I and II each with several submedian microducts dorsally; III with 3 or 5 microducts anteriorly to row of submedian macroducts. Submedian macroducts on abd III–VI, divided into segmental and infrasegmental series on III–V; 7 or 11 on III, 10 or 11 on IV, 9 or 10 on V, and 3 on VI. Submarginal macroducts on abd III–V, in partly double rows especially on III and IV; 12 or 14 on III, 10 on IV, 5 or 7 on V. Total dorsal macroducts on both sides 122. Pygidial margin as in the foliicolous specimens; median trullae with basal zygosis well developed (Fig. 15, D, lower).

Recognition characters (foliicolous and ramicolous adult females). The examined specimens are nearly oblong in body outline (but it is possible that the adult female grows to the *vitis*-type ultimately). Posterior spiracles with a small cluster of disc pores laterally. Submedian macroducts on abd III–VI; submarginal macroducts on III–V. Median trullae distinctly larger than lobules of lateral trullae, sunken into apex of pygidium, robust, basally separated from each other by a good space, then divergent and minutely serrate (basal zygosis well developed in one of the foliicolous specimens, probably representing the normal state in the species).

Remarks. The ramicolous specimen is different from the foliicolous specimens in the spiracular and perivulvar disc pores and the dorsal macroducts much more numerous, but it agrees with the latter in the characters of the pygidial margin, especially of the median trullae, which are robust and separated from each other by a good space basally.

Aulacaspis malabarica (2.4.), *A. anaimala* (2.5.), and *A. nilagirica* are closely similar and distinguished by rather trifling differences. *A. malabarica* may be recognized by having disc pores laterally (not anteriorly) to the posterior spiracles, and by the median trullae slender, with the basal zygosis horseshoe-shaped and produced anteriorly beyond the bases of the trullae. *A. anaimala* has a few disc pores anteriorly (not laterally) to each posterior spiracle and is characterized by the median trullae rounded, with the basal zygosis represented by a pair of small sclerotized pieces. *A. nilagirica* differs from *A. anaimala* and agrees with *A. malabarica* in the disc pores associated with the posterior spiracles situated laterally, and differs from the latter two species in the median trullae separated basally from each other by a good space. The material of *A. nilagirica* was collected near the summit of Doddabetta, one of the highest peaks of the Nilgiris, and this fact suggests the possibility that *A. nilagirica* differs from the other two species in its adaptation to the high-altitude environment. All these species appear distinct also in the correlation between the total number of the dorsal macroducts and that of the perivulvar disc pores (Fig. 1). They should form a species group, the *malabarica* complex, which may include unknown forms occurring on lauraceous plants in the hilly areas of South India (see also *Remarks* under 2.4.).

2.7. *Aulacaspis machili* (Figs 1, 16, 17)

Diaspis machili Takahashi, 1931: 1 [‘Host.–*Machilus kusanoi*. Hab.–Maruyama near Taihoku.’ Taiwan].

Phenacaspis obovata Takagi and Kawai, 1966: 112 [Idu-Ôsima, Japan, on *Machilus japonica*].

Chionaspis machili: Takagi, 1970: 72 [Taiwan, on *Machilus* spp.].

Phenacaspis machili: Chen, 1983: 76 [Sichuan, China, on *Phoebe nanmu*].

Aulacaspis machili: Takagi, 1985: 47.

Material. Collected in Taiwan and Japan on lauraceous plants of the genus *Machilus* (now *Persea*).

Taiwan (Yangming Shan; Kuantzuling; Fenchihu; Kenting) on *Machilus japonica*, *M. kusanoi*, and *M.* sp., 1965 (part of the specimens were studied in Takagi, 1970; the other specimens were prepared for the present study). Foliicolous specimens are available from the localities other than Fenchihu; ramicolous specimens from Fenchihu and Kenting.

Japan, on *Persea thunbergii* (=*Machilus thunbergii*). Utatu-yama, Kanazawa, Isikawa-ken, 6.X.1982; E-no-Sima, Huzisawa [Fujisawa], Kanagawa-ken, 27.III.1995; Tasiro, Kagosima-ken, 17.I.1975. Foliicolous specimens alone are available from these localities. One of the slides used for the description of *Phenacaspis obovata*, with eight specimens of the adult female, is also at hand.

Foliicolous and ramicolous adult females. The specimens are variable in the shape of the body, in the shape of the median trullae, and in the numbers of wax-secreting organs.

The body shape changes with growth owing to the broadening of the cephalothorax. At full growth the cephalothorax is transversely oblong in outline, with the frontal margin flat and the mesothorax strongly expanded laterally; the body is, thus, nearly as broad as long, with the abdomen gradually narrowing caudad (Fig. 17). However, not all individuals grow in that way, and many apparently fully grown adult females remain more or less oblong (Fig. 16), obovate, or obpyriform. Pygidium broadly triangular in outline, about 180–270μm (usually about 200–250μm) long.

The median trullae are usually sunken into the pygidium in the foliicolous specimens, whereas they are broader and more or less produced at the apex of the pygidium in the ramicolous specimens. They are, however, variable within the foliicolous specimens and also within the ramicolous specimens, thus forming a continuous series of variation through all these specimens. A broad variation has been observed in the single sample collected on the leaves of *Persea thunbergii* at Kanazawa (the opposite extremes in the variation are shown in Fig. 17, D and G), almost covering the whole range of the continuous variation formed by the other foliicolous and ramicolous specimens.

The macroducts, disc pores, and gland spines were counted in 20 individuals from each of the following four localities: foliicolous specimens from Kanazawa (central Honsyû), Tasiro (southern Kyûsyû, about 800km distant from Kanazawa), and Kenting (southern Taiwan, about 1400km distant from Tasiro), and ramicolous specimens from Fenchihu (central Taiwan).

In the correlation between the total number of the dorsal macroducts and that of the perivulvar disc pores (Fig. 1), the specimens from Kanazawa and those from Tasiro are considerably different from each other, and may represent the northern and southern populations of the species in Japan. Unexpectedly, the specimens from Kenting largely

overlap with those from Kanazawa and Tasiro. The foliicolous specimens from these widely separated localities are thus united together to form an indivisible group on the scatter diagram. On the other hand, the ramicolous specimens from Fenchihu are almost isolated on the diagram from the foliicolous specimens owing to the perivulvar disc pores tending to be more numerous. Dorsal macroducts, total: 28–72, mean 44.6 in the specimens from Kanazawa; 58–103, mean 82.2, Tasiro; 34–95, mean 69.0, Kenting; 47–84, mean 66.3, Fenchihu. Perivulvar disc pores, total: 80–115, mean 96.5, Kanazawa; 104–155, mean 125.6, Tasiro; 77–139, mean 109.6, Kenting; 120–188, mean 163.6, Fenchihu.

The ramicolous specimens have the disc pores associated with the spiracles also tending to be more numerous. The disc pores associated with each anterior spiracle range from about 30 to about 50 in the specimens from Fenchihu, but usually do not exceed 30 in the foliicolous specimens (these disc pores are crowded so closely that they were not always exactly counted). Disc pores associated with each posterior spiracle: 1–8 (usually 2–4), mean 2.9 in the specimens from Kanazawa; 1–9, mean 3.4, Tasiro; 2–10, mean 7.0, Kenting; 5–26, mean 12.7, Fenchihu.

The ramicolous specimens have the lateral macroducts not particularly numerous and the gland spines even tending to be fewer than in the foliicolous specimens. Lateral macroducts on abd II and III, total on one side: 1–10, mean 5.1 in the specimens from Kanazawa; 6–13, mean 9.9, Tasiro; 3–14, mean 8.0, Kenting; 2–10, mean 6.2, Fenchihu. Lateral gland spines on abd II and III, total on one side: 10–27, mean 17.2, Kanazawa; 19–34, mean 25.8, Tasiro; 8–19, mean 14.1, Kenting; 7–16, mean 11.1, Fenchihu. Marginal gland spines on abd IV: 4–7, mean 5.8, Kanazawa; 5–10, mean 7.5, Tasiro; 2–5, mean 3.6, Kenting; 1–4, mean 2.6, Fenchichu.

Recognition characters (foliicolous and ramicolous adult females). Body variable in shape at full growth, with cephalothorax swollen in various degrees; at the extreme of development, the body is nearly as broad as long, flat on the frontal margin, broadest across the mesothorax, and gradually narrowing caudad. Anterior spiracles each with a compact cluster of many disc pores; posterior spiracles each with a much smaller cluster anterolaterally. Submedian macroducts occurring on abd III–V and usually also on VI (0–5), those on III and IV tending to be divided into segmental and infrasgmental series. Submarginal macroducts on abd III–V. Median trullae large, with a robust basal zygosis; tending to be sunken into apex of pgydium and divergent in foliicolous specimens, broader and more or less produced in ramicolous specimens. Second trullae with lateral lobule smaller than the mesal; third trullae less developed than the second, with lateral lobule much reduced in size and sometimes merged into pygidial margin.

Remarks. This species was originally described from near Taipei (‘Taihoku’), northern Taiwan, and referred to *Diaspis* probably because of one of the body shapes it shows at full growth. This body shape, shown in Fig. 17, is similar to that in *Diaspis* and thus rather strange among the species of *Aulacaspis*. However, adult females presumed to be fully grown are various in body shape, often with the cephalothorax broadened not so much as in the females of the *Diaspis*-type. *Phenacaspis obovata* was described from Japan on the basis of obovate females. Females with various body shapes have been observed within the same samples in both Taiwan and Japan, falling under the category of individual variation, and there is no doubt that they belong to the same species. (See also 6.2.)

2.8. *Aulacaspis digitifera*, n. sp. (Fig. 18)

Material. Collected at Maasin Forest, Brooke's Point, Palawan, Philippines, on *Litsea garciae* (Lauraceae), 24.VIII.1993 [lot no.: 93PL-137]. Females occurring on the lower surface of leaves and burrowing under the thin upper epidermis. Seventeen mounted adult females are available. Holotype: UPLB.

Adult females. Body, when fully grown, of the *vitis*-type, but peculiar in abd I much produced laterally to form a digitiform lobe on each side; attaining 1430μm in length; pygidium broadly triangular in outline, 230–260μm long. Anterior spiracles each accompanied with a cluster of 5–13, mean 8.0 (n=34), disc pores; posterior spiracles each accompanied with 1 or 2 disc pores anteriorly. Perivulvar disc pores 6–21 in median, 16–34 in each anterolateral, and 13–22 in each posterolateral group, total 77–115, mean 100.0 (n=17). Abd II with 4–9 macroducts and 4–10 gland spines on lateral lobe; III with 4–6 macroducts and 3–9 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 8–14, mean 11.8 (n=30). Total of lateral gland spines on each side 9–19, mean 14.2 (n=31). Abd IV with 2–4 (usually 3) gland spines marginally. Submedian macroducts on abd III–V, 1 or 2 on each of III and IV, and 1 on V. Submarginal macroducts on abd III–V, 1–5 on III, 2–4 on IV, and 1 or 2 on V. Total of dorsal macroducts 16–31, mean 23.7 (n=15). Median trullae much larger than lateral trullae, robust, with basal halves sunken into apex of pygidium, detached from each other, and with mesal margins divergent, roundish, and minutely serrate; basal zygosis represented by a pair of crooked slender scleroses united together by their apices. Second and third trullae well represented, inner lobule of second trulla with a pair of short linear scleroses basally. Abd IV and V flattish marginally, without prominent processes.

Recognition characters (foliicolous adult female). Body of the *vitis*-type; abd I much produced laterally to form a digitiform process on each side. Posterior spiracles each with 1 or 2 disc pores anteriorly. Dorsal macroducts few, occurring on Abd III–V. Median trullae much larger than lateral trullae, robust, with bases sunken into apex of pygidium, and with mesal margins divergent, roundish, and minutely serrate; basal zygosis represented by crooked slender scleroses united together at their mesal ends.

Remarks. This species is peculiarly characterized by the first abdominal segment produced laterally to form eminent digitiform processes on both sides. This character may be associated with the burrowing habit of the species, though such a digitiform growth has not been known in other burrowing diaspidids. The few dorsal macroducts and the serrate robust median trullae, of which the apical halves are produced at the apex of the pygidium, are probably adaptive to burrowing. This species is also unusual in the basal zygosis of the median trullae represented by a pair of crooked scleroses.

2.9. *Aulacaspis pellucida* (Figs 2, 19–23)

Phenacaspis pellucida Robinson, 1917: 22 ['Luzon, Laguna, Los Baños (Baker), October, 1915, on *Macaranga tanarius*.'].

Phenacaspis pellucida: Ferris, 1955: 51 ['Of this species there have been available specimens bearing the data of the type lot, although not necessarily type material.'].

Aulacaspis pellucida: Takagi, 1985: 48.

Material. Collected in Luzón, Palawan, Sabah, Singapore, and Malaya on plants of *Macaranga* (Euphorbiaceae) except for a lot collected on *Campnosperma auriculatum*

(Anacardiaceae) in Singapore. The sample from *C. auriculatum* is referred to this species only tentatively (see *Remarks for Group V*).

Group I. Grounds of the University of the Philippines at Los Baños, Luzón, Philippines, on *Macaranga tanarius*, 24.XI.1992 and 7.VIII.1994 [lot no.: 92PL-20, Sample 1; 94PL-15, Sample 2]. Robinson described the species from Los Baños, so that the samples of this group should belong to the same local population as her material and represent the type form of the species. One specimen mounted from the type material (labelled 'Los Baños, X.1915, C. F. Baker') is available for comparison.

Group II. Other localities in Luzón. Santa Lucia, Quezon, on *Macaranga tanarius*, 4.XII.1992 [lot no.: 92PL-86, Sample 3]. Puerto Azul, Ternate, on *Macaranga bicolor*, 8.XII.1992 [92PL-101, Sample 4]. Mt. Samat, Bataan, on *M. tanarius*, 18.VIII.1994 [94PL-65, Sample 5]. Mariveles, Bataan, on *M. tanarius*, 24.VIII.1994 [94PL-116, Sample 6].

Group III. Quezon, Palawan, Philippines, on *Macaranga hispida*, 21.VIII.1993 [lot no.: 93PL-112, Sample 7].

Group IV. Sabah (northeastern Borneo), Malaysia, on *Macaranga hypoleuca*. Sepilok, 20.X.1988 [lot no.: 88ML-180, Sample 8] and Danum Valley, 27.X.1988 [88ML-214, Sample 9].

Group V. Bukit Timah, Singapore, on *Macaranga conifera*, 5.VIII.1992 [lot no.: 92SP-9, Sample 10] and *Campnosperma auriculatum*, 6.VIII.1992 [92SP-20, Sample 11].

Group VI. Malaya, Malaysia. Cape Rachado, Negeri Sembilan, 10.XI.1986, on *Macaranga* sp. [lot no.: 86ML-439, Sample 12] and on *Macaranga gigantea* [86ML-451, Sample 13]. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, on *Macaranga hypoleuca*, 18.VI.1990 [90ML-31, Sample 14]. Bukit Nanas, Kuala Lumpur, on *Macaranga tanarius*, 31.VII.1990 [90ML-378, Sample 15] and on *M. gigantea*, 5.VIII.1990 [90ML-437, Sample 16].

Females and males occurring on the leaves and other parts of the host plants, sometimes causing shrinkage on the leaf surface. Female tests various in outline according to feeding sites, thin. Male tests tricarinate.

Female specimens were mounted from various parts of the plant body: leaf blade (abbreviated to *lb*), petiole (*pt*) (which is long in *Macaranga*), calyx (*cl*), shoot (*sh*), twig (*tw*), branch (*br*), and stem (*st*); in 10 samples, they were obtained from more than one part. These 10 samples are divided into subsamples according to the feeding sites: subsample *lb*, subsample *pt*, etc. The other six samples have specimens mounted only from the leaf blade.

Adult females, variation. This species belongs to the *vitis*-type in body shape. However, not all the examined adult females including apparently fully grown ones reveal the body shape of that type. All the examined specimens of Group III (Sample 7) are elongate fusiform.

There has been found in the subsamples from different feeding-sites little trace of ecophenotypic effect on the shape of the median trullae. *Macaranga*-associated samples from widely separated localities are also very similar in the median trullae, and it is practically impossible to recognize local forms on the basis of this feature. The sample collected on *Campnosperma auriculatum* in Singapore is somewhat different from the *Macaranga*-associated samples in the shape of the median trullae (see *Remarks for Group V*).

The subsamples in each of the 10 samples occurring on more than one part of the plant body are more or less different in the total number of the dorsal macroducts and that of the perivulvar disc pores. There is a tendency in the subsamples *lb* to have the dorsal macroducts and, especially, the perivulvar disc pores less numerous than in

the subsamples associated with the other plant parts, but this is not always the case. The differences in the mean values have been analysed statistically in six samples with subsamples each represented by more than a dozen (up to 22) individuals. The differences are definitely significant between the subsamples *lb* and *pt* of Sample 6. This sample has, in addition, subsamples *sh* and *st*, but these subsamples as well as some subsamples of other samples are too small for making reliable comparisons. Although reliable data are, therefore, much limited, it may be reasonable to assume from the larger subsamples that the ecophenotypic effect on the numbers of the dorsal macroducts and perivulvar disc pores is not always remarkable in this species.

Geographically, however, this species is considerably variable in the total number of the dorsal macroducts and also in that of the perivulvar disc pores. A scatter diagram is prepared for the correlation between the mean values of these numbers in all the samples, which are represented by their subsamples when these are available (Fig. 2). The diagram shows the occurrence of geographical differentiation in this species. The samples from Luzón are situated in a lower right area in the field of the scatter diagram, forming their own group or 'geogroup'. The samples from Malaya and Sabah (northeastern Borneo) are scattered in a broad upper middle area of the field, and comprised in a large indivisible group. The two samples from Singapore are not found in the midst of the Malaya-Borneo geogroup in spite of the geographical position of the island, but situated on the left side of the domain of the latter. The single sample available from Palawan is found in the lower left corner of the field, thus being isolated from the Luzón geogroup and also from the Malaya-Borneo geogroup. Thus the samples from Singapore and Palawan are puzzling. They may be too few to represent the populations on these islands. It seems, however, that they are extensions from the Malaya-Borneo geogroup. After all, the examined samples of *A. pellucida* may be roughly divided into the Luzón geogroup and the other geogroups. (As to the sample from Palawan and the samples from Singapore, see also *Remarks for Group III* and *Remarks for Group V*.)

In the ranges of the numbers of these macroducts and disc pores, every sample overlaps with a few or many others and all the samples are connected to form one large group.

Adult females, Group I (Sample 1 and 2). Body growing into the *vitis*-type, but often remaining fusiform or with meso- and metathorax expanded not remarkably; 680–1260μm (usually less than 1000μm) long; pygidium broadly triangular in outline, 195–245μm (usually about 210–230μm) long. Antennal tubercles often bearing 1 or 2 spiny processes; interantennal tubercle rudimentary or more often not discernible. Anterior spiracles each accompanied with 2–9 disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 9–18 in median, 13–29 in each anterolateral, and 8–24 in each posterolateral group, total 61–111. Abd II with 4–12 macroducts and 1–8 gland spines on lateral lobe; abd III with 3–8 macroducts and 4–10 gland spines along margin of lateral lobe; abd IV with 2–5 (usually 3 or 4) marginal gland spines. Submedian macroducts on abd III–VI, often divided into segmental and infrasegmental series on III–V, 1–7 (often 4) on III, 3–7 (often 4) on IV, 3–7 on V, and 1–4 (usually 2 or 3) on VI. Submarginal macroducts on abd III–V, usually in an irregularly double row on III, 5–12 on III, 2–8 on IV, and 1–5 on V. Total of dorsal macroducts on both sides 49–83. Median trullae very large relative to lateral trullae, sunken into apex of pygidium, detached from each other basally, gently divergent, with mesal margins roundish and roughly serrate; basal zygosis often represented by a pair of sclerotized pieces separated from each other by a narrow

space and extending anteriorly in a pair of slender sclerotized bands on ventral surface, but sometimes these sclerotized pieces set close or fused together to form a rather large zygosis. Second and third trullae well represented; mesal lobule of second trulla oblong, slightly dilated, with a pair of linear basal scleroses; lateral lobule smaller; third trullae smaller than the second. Pygidial margin on abd IV and V straight, finely serrate.

Sample 1, subsample *lb*. Disc pores associated with each anterior spiracle 4–9, mean 6.2 (n=39); total of perivulvar disc pores 69–101, mean 89.1 (n=20); total of lateral macroducts on each side 9–15, mean 12.2 (n=40); total of lateral gland spines on each side 10–17, mean 12.8 (n=40); total of dorsal macroducts on both sides 53–81, mean 66.6 (n=20).

Sample 1, subsample *pt*. Disc pores associated with each anterior spiracle 5–9, mean 7.6 (n=43); total of perivulvar disc pores 81–111, mean 91.7 (n=22); total of lateral macroducts on each side 9–20, mean 12.7 (n=36); total of lateral gland spines on each side 7–17, mean 11.4 (n=40); total of dorsal macroducts on both sides 61–83, mean 70.0 (n=22).

Sample 2 (*lb*). Disc pores associated with each anterior spiracle 2–9, mean 5.4 (n=33); total of perivulvar disc pores 70–94, mean 81.0 (n=17); total of lateral macroducts on each side 7–16, mean 10.3 (n=32); total of lateral gland spines on each side 8–14, mean 10.2 (n=32); total of dorsal macroducts on both sides 49–66, mean 56.8 (n=17).

Specimen mounted from the type material ('T' on Fig. 2). Disc pores associated with each anterior spiracle 4; total of perivulvar disc pores 72; total of lateral macroducts on each side 11; total of lateral gland spines on each side 11, 12; total of dorsal macroducts on both side 53. Dr D. J. Williams figured another specimen mounted from the type material (Fig. 5); it has the perivulvar disc pores and dorsal macroducts somewhat more numerous (estimated to be about 92 and 64, respectively).

Adult females, Group II (Sample 3–6). The adult females of this group are characterized substantially the same as those of Group I, though they are, as a whole, more broadly variable than the latter especially in the number of the perivulvar disc pores. The samples of Group I and II largely overlap in the ranges of the numbers of the disc pores, macroducts, and gland spines, forming an indivisible geogroup.

Sample 3 (*lb*). Disc pores associated with each anterior spiracle 3–10, mean 5.3 (n=38); total of perivulvar disc pores 68–91, mean 77.0 (n=20); total of lateral macroducts on each side 8–15, mean 11.5 (n=40); total of lateral gland spines on each side 8–16, mean 11.0 (n=40); total of dorsal macroducts on both sides 52–75, mean 61.6 (n=20).

Sample 4, subsample *lb*. Disc pores associated with each anterior spiracle 3–7, mean 4.9 (n=16); total of perivulvar disc pores 69–85, mean 76.6 (n=9); total of lateral macroducts on each side 7–14, mean 9.9 (n=17); total of lateral gland spines on each side 9–13, mean 11.0 (n=17); total of dorsal macroducts 49–67, mean 57.2 (n=9).

Sample 4, subsample *sh*. Disc pores associated with each anterior spiracle 6–11, mean 8.0 (n=19); total of perivulvar disc pores 82–105, mean 96.5 (n=10); total of lateral macroducts on each side 9–18, mean 13.6 (n=20); total of lateral gland spines on each side 8–15, mean 12.2 (n=19); total of dorsal macroducts on both sides 40–81, mean 64.5 (n=10).

Sample 5, subsample *lb*. Disc pores associated with each anterior spiracle 3–7, mean 5.3 (n=6); total of perivulvar disc pores 73–100, mean 88.7 (n=3); total of lateral macroducts on each side 8–12, mean 10.0 (n=6); total of lateral gland spines on each side

8–13, mean 10.5 (n=6); total of dorsal macroducts on both sides 55–64, mean 60.0 (n=3).

Sample 5, subsample *pt*. Disc pores associated with each anterior spiracle 4–13, mean 7.7 (n=38); total of perivulvar disc pores 83–110, mean 101.6 (n=20); total of lateral macroducts on each side 11–17, mean 13.3 (n=34); total of lateral gland spines on each side 9–18, mean 13.9 (n=34); total of dorsal macroducts on both sides 59–89, mean 74.9 (n=20).

Sample 6, subsample *lb*. Disc pores associated with each anterior spiracle 4–8, mean 6.3 (n=43); total of perivulvar disc pores 74–98, mean 88.2 (n=22); total of lateral macroducts on each side 7–15, mean 10.7 (n=43); total of lateral gland spines on each side 5–16, mean 11.8 (n=44); total of dorsal macroducts on both sides 41–72, mean 55.1 (n=22).

Sample 6, subsample *pt*. Disc pores associated with each anterior spiracle 5–11, mean 8.3 (n=31); total of perivulvar disc pores 89–115, mean 101.5 (n=17); total of lateral macroducts on each side 10–18, mean 13.4 (n=34); total of lateral gland spines on each side 10–19, mean 14.9 (n=34); total of dorsal macroducts on both sides 51–85, mean 69.3 (n=17).

Sample 6, subsample *sh*. Disc pores associated with each anterior spiracle 5–10, mean 8.1 (n=11); total of perivulvar disc pores 85–105, mean 95.8 (n=6); total of lateral macroducts on each side 9–17, mean 12.9 (n=12); total of lateral gland spines on each side 9–15, mean 12.0 (n=10); total of dorsal macroducts on both sides 40–80, mean 61.5 (n=6).

Sample 6, subsample *st*. Disc pores associated with each anterior spiracle 7–11, mean 9.4 (n=8); total of perivulvar disc pores 92–121, mean 110.2 (n=5); total of lateral macroducts on each side 14–16, mean 15.0 (n=8); total of lateral gland spines on each side 12–18, mean 14.8 (n=8); total of dorsal macroducts on both sides 67–88, mean 78.4 (n=5).

Adult females, Group III (Sample 7). Nine specimens from the leaf blade are available for study. They may be nearly fully grown, being 750–940μm long, but are elongate fusiform and about 2.3–2.5 times as long as wide. They are characterized by the perivulvar disc pores and the dorsal macroducts much fewer than in most of the other samples, but are not particularly different in other features, especially in the pygidial margin. Perivulvar disc pores 9–12 in median, 10–21 in each anterolateral, and 8–13 in each posterolateral group. Abd II with 2–8 macroducts and 2–6 gland spines on lateral lobe; III with 3–7 macroducts and 3–8 gland spines along margin of lateral lobe; abd IV with 2 or rarely 3 marginal gland spines. Submedian macroducts: 1 or 2 on each of abd III–V, 1 or rarely 2 on VI. Submarginal macroducts: 1–3 on III, 1 or 2 on IV and also on V.

Sample 7 (*lb*). Disc pores associated with each anterior spiracle 4–8, mean 6.0 (n=15); total of perivulvar disc pores 54–72, mean 64.3 (n=9); total of lateral macroducts on each side 6–15, mean 9.5 (n=13); total of lateral gland spines on each side 5–14, mean 10.2 (n=13); total of dorsal macroducts on both sides 21–29, mean 24.7 (n=6).

Remarks for Group III. The nine specimens from Palawan may be too few to represent the island population. However, they form a homogeneous group in having the dorsal macroducts and perivulvar disc pores very few as compared with most of the other samples, so that they should represent the Palawan geogroup. In its position relative to the other samples on the scatter diagram (Fig. 2), this geogroup may be interpreted to be an extension from the Malaya-Borneo geogroup rather than from the Luzón geogroup and to represent an extreme variation of the Bornean population. This interpretation finds

support in mammal biogeography, in which 'the Palawan region is part of the Sunda zoogeographic province, not part of the Philippine faunal province' (Heaney, 1986).

Adult females, Group IV (Sample 8, 9). Characterized by having the dorsal macroducts tending to be fewer and the spiracular and perivulvar disc pores and the lateral macroducts and gland spines more numerous than in Group I. Different from the Luzón geogroup in abd VI having only 1 submedian macroduct on each side (exceptionally 2 on one side alone); interantennal tubercle often present, sometimes with 1 derm pocket on one side alone or 2 pockets on both sides.

Sample 8, subsample *lb*. Disc pores associated with each anterior spiracle 8–13, mean 10.5 (n=17); total of perivulvar disc pores 92–104, mean 95.3 (n=10); total of lateral macroducts on each side 10–20, mean 14.9 (n=20); total of lateral gland spines on each side 12–21, mean 15.4 (n=20); total of dorsal macroducts on both sides 31–54, mean 44.2 (n=10).

Sample 8, subsample *tw*. Disc pores associated with each anterior spiracle 7–14, mean 10.6 (n=5); total of perivulvar disc pores 102–110, mean 105.0 (n=3); total of lateral macroducts on each side 13–17, mean 15.0 (n=6); total of lateral gland spines on each side 12–23, mean 18.2 (n=6); total of dorsal macroducts on both sides 38–50, mean 42.0 (n=3).

Sample 9, subsample *lb*. Disc pores associated with each anterior spiracle 8–14, mean 9.7 (n=18); total of perivulvar disc pores 89–122, mean 101.4 (n=10); total of lateral macroducts on each side 12–19, mean 14.9 (n=19); total of lateral gland spines on each side 13–23, mean 17.5 (n=19); total of dorsal macroducts on both sides 32–69, mean 53.2 (n=10).

Sample 9, subsample *br*. Disc pores associated with each anterior spiracle 7–12, mean 9.7 (n=32); total of perivulvar disc pores 95–135, mean 117.9 (n=18); total of lateral macroducts on each side 11–20, mean 14.9 (n=36); total of lateral gland spines on each side 13–23, mean 17.5 (n=35); total of dorsal macroducts on both sides 39–55, mean 45.5 (n=18).

Adult females, Group V (Sample 10, 11). Perivulvar disc pores and dorsal macroducts tending to be fewer than in Group IV and VI. Abd VI with 1 submedian macroduct on each side in Sample 10 (occurring on *Macaranga*); with 1, often (64–67%) with none, in Sample 11 (on *Campnosperma*).

Sample 10 (*lb*). Disc pores associated with each anterior spiracle 7–10, mean 8.6 (n=10); total of perivulvar disc pores 67–86, mean 81.3 (n=6); total of lateral macroducts on each side 8–13, mean 10.1 (n=12); total of lateral gland spines on each side 11–15, mean 13.6 (n=10); total of dorsal macroducts on both sides 29–35, mean 31.5 (n=6). Median trullae as in the other samples from *Macaranga*.

Sample 11, subsample *lb*. Disc pores associated with each anterior spiracle 7–29, mean 13.6 (n=40); total of perivulvar disc pores 77–110, mean 98.5 (n=20); total of lateral macroducts on each side 6–13, mean 10.1 (n=39); total of lateral gland spines on each side 8–21, mean 14.7 (n=37); total of dorsal macroducts on both sides 23–35, mean 32.0 (n=20). Median trullae narrow, nearly of the same width throughout except basally, dentate rather than serrate on mesal margins.

Sample 11, subsample *br*. Disc pores associated with each anterior spiracle 7–22, mean 13.5 (n=29); total of perivulvar disc pores 88–115, mean 99.2 (n=18); total of lateral macroducts on each side 5–16, mean 9.8 (n=35); total of lateral gland spines on each side 11–20, mean 14.5 (n=35); total of dorsal macroducts on both sides 26–40,

mean 33.3 (n=18). Median trullae as in subsample *lb*.

Remarks for Group V. This group contains two samples collected at the same locality, Bukit Timah, Singapore, and on the different host plants belonging to the different families: Sample 10 from *Macaranga conifera* and Sample 11 from *Campnosperma auriculatum*. Sample 11 differs from Sample 10 in the median trullae nearly evenly narrow throughout and dentate rather than serrate (Figs 22, 23), in the perivulvar disc pores tending to be more numerous (Fig. 2), and in the sixth abdominal segment often having no submedian macroduct. The latter two characters, however, are concerned with tendency in number or frequency in occurrence, and the first character alone affords a constant difference.

All the *Macaranga*-associated samples of this species are considerably stable in the shape of the median trullae in spite of the fact that they are broadly variable geographically and sometimes also ecophenotypically in the numbers of the perivulvar disc pores and dorsal macroducts (see *Adult females, variation*). This observation may afford a good basis for the view that the *Campnosperma*-associated sample represents another species, which is distinguishable from *A. pellucida* in the shape of the median trullae.

However, the difference in the median trullae, though clear, is not great, and may not suffice for regarding the sample from *Campnosperma* as representing a distinct species. In fact, Sample 11 is very close to or substantially agrees with Sample 10 in the total numbers of the spiracular disc pores, lateral macroducts, lateral gland spines, and dorsal macroducts. When combined together and not attributed to chance coincidence, these agreements strongly suggest a close relationship between the samples. These samples are indeed remarkably different from each other in the number of the perivulvar disc pores (the difference between Sample 10 (*lb*) and Sample 11, subsample *lb*, is statistically significant), but these disc pores are especially variable in number among the samples from the Luzón geogroup and also from the Malaya-Borneo geogroup. All this supports the view that Sample 10 and 11 belong to the same local population of *A. pellucida* and that the observed differences between them are due to ecophenotypic effect on the different host plants.

The available material is not sufficient to show which view is correct, so that Sample 11 is referred to *A. pellucida* in this study only tentatively.

Adult females, Group VI (Sample 12–16). Not distinguishable from Group IV but, as a whole, more broadly variable in the numbers of the perivulvar disc pores and the dorsal macroducts. Abd VI with 1 submedian macroduct on each side, occasionally with 2 or 3. Interantennal tubercle and derm pockets sometimes well represented.

Sample 12 (*lb*). Disc pores associated with each anterior spiracle 5–16, mean 10.7 (n=32); total of perivulvar disc pores 84–134, mean 106.8 (n=20); total of lateral macroducts on each side 8–19, mean 14.1 (n=40); total of lateral gland spines on each side 10–25, mean 16.2 (n=40); total of dorsal macroducts on both sides 32–91, mean 62.3 (n=20).

Sample 13, subsample *lb*. Disc pores associated with each anterior spiracle 5–18, mean 12.1 (n=32); total of perivulvar disc pores 76–127, mean 98.6 (n=20); total of lateral macroducts on each side 9–19, mean 14.2 (n=40); total of lateral gland spines on each side 7–24, mean 16.4 (n=40); total of dorsal macroducts on both sides 29–81, mean 55.8 (n=20).

Sample 13, subsample *tw*. Disc pores associated with each anterior spiracle 6–16,

mean 11.0 (n=23); total of perivulvar disc pores 81–121, mean 98.7 (n=15); total of lateral macroducts on each side 10–15, mean 12.8 (n=30); total of lateral gland spines on each side 7–17, mean 12.7 (n=29); total of dorsal macroducts on both sides 30–62, mean 45.3 (n=15).

Sample 14 (*lb*). Disc pores associated with each anterior spiracle 7–11, mean 8.8 (n=6); total of perivulvar disc pores 90, 102, 110 (n=3); total of lateral macroducts on each side 11–15, mean 13.7 (n=6); total of lateral gland spines on each side 12–18, mean 15.2 (n=6); total of dorsal macroducts on both sides 30, 35, 41 (n=3).

Sample 15, subsample *lb*. Disc pores associated with each anterior spiracle 9–19, mean 13.7 (n=16); total of perivulvar disc pores 98–122, mean 106.5 (n=8); total of lateral macroducts on each side 12–17, mean 14.9 (n=16); total of lateral gland spines on each side 11–19, mean 15.5 (n=15); total of dorsal macroducts on both sides 37–58, mean 46.0 (n=8).

Sample 15, subsample *cl*. Disc pores associated with each anterior spiracle 9–22, mean 14.2 (n=12); total of perivulvar disc pores 74–132, mean 105.5 (n=6); total of lateral macroducts on each side 12–17, mean 13.6 (n=12); total of lateral gland spines on each side 10–22, mean 13.8 (n=12); total of dorsal macroducts on both sides 28–86, mean 50.0 (n=6).

Sample 15, subsample *br*. Disc pores associated with each anterior spiracle 9–28, mean 15.6 (n=12); total of perivulvar disc pores 104–176, mean 130.9 (n=7); total of lateral macroducts on each side 11–19, mean 14.9 (n=11); total of lateral gland spines on each side 12–21, mean 15.7 (n=11); total of dorsal macroducts on both sides 46–76, mean 57.9 (n=7).

Sample 16 (*lb*). Disc pores associated with each anterior spiracle 6–24, mean 14.6 (n=37); total of perivulvar disc pores 96–150, mean 122.7 (n=20); total of lateral macroducts on each side 14–25, mean 18.3 (n=38); total of lateral gland spines on each side 12–27, mean 20.5 (n=37); total of dorsal macroducts on both sides 40–79, mean 60.3 (n=20).

Recognition characters (adult female). Body growing to the *vitis*-type, but often remaining fusiform or with meso- and metathorax not remarkably expanded laterally. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Submedian macroducts on abd III–VI (often no submedian macroducts on VI in the sample from *Campnosperma*); submarginal macroducts on abd III–V. Median trullae much larger than lateral trullae, sunken into apex of pygidium, with mesal margins divergent, roundish, and roughly serrate (or evenly narrow and dentate in the sample from *Campnosperma*); basal zygosis represented by a pair of sclerotized pieces, which are sometimes fused together to form a rather large zygosis. Lateral trullae with oblong lobules.

Remarks. This species and three other species described in this paper are associated with plants of *Macaranga* (except for the *Campnosperma*-associated form in Singapore). *Aulacaspis pellucida* may be closely related to one of the latter three, *Aulacaspis binunga* (2.10.), from which it is easily distinguishable in having no dorsal macroducts on the second abdominal segment. It appears to be more closely related to *Aulacaspis guioae*, which occurs on *Guioa*, family Sapindaceae (see *Remarks* under 2.19.).

2.10. *Aulacaspis binunga*, n. sp. (Fig. 24)

Material. Collected at Sabang, Pinamalayan, Mindoro, Philippines, on *Macaranga tanarius* (local name: Binunga) (Euphorbiaceae), 11.VIII.1994 [lot no.: 94PL-17]. Females and males occurring on the lower surface of leaves and on petioles, causing shrinkage on the leaf surface, females also on shoots. Female test not so thin as to be transparent. Male test tricarinate. Holotype: UPLB.

Adult females were mounted from the leaf blade (abbreviated to *lb*), petiole (*pt*), and shoot (*sh*), and the sample is divided into subsamples according to the feeding sites: subsample *lb* (with 11 specimens), subsample *pt* (14), and subsample *sh* (11). Holotype, from the subsample *pt*.

Adult females, subsample lb, pt, and sh. Body growing to the *vitis*-type, with meso- and metathorax expanded laterally; about 1450μm long at maximum, but usually not exceeding 1000μm; pygidium broadly triangular in outline, about 235–300μm long. Interantennal tubercle and derm pockets sometimes well developed. Anterior spiracles each accompanied with about 14–30 disc pores (not always counted exactly). Posterior spiracles each with 1–6 disc pores anteriorly; 1–6, mean 3.1 (n=22) in subsample *lb*, 1–4, mean 2.2 (n=23) in *pt*, 1–4, mean 2.3 (n=22) in *sh*. Perivulvar disc pores 5–21 in median, 24–43 in each anterolateral, and 12–30 in each posterolateral group; total 89–149, mean 127.8 (n=11) in subsample *lb*, 127–164, mean 145.2 (n=13) in *pt*, 120–134, mean 125.6 (n=11) in *sh*. Abd II with 5–18 macroducts and 4–12 gland spines on lateral lobe; III with 3–11 macroducts and 5–13 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 8–23, mean 15.4 (n=18) in subsample *lb*, 11–27, mean 18.9 (n=24) in *pt*, and 14–25, mean 18.5 (n=22) in *sh*. Total of lateral gland spines on each side 9–18, mean 14.6 (n=18) in subsample *lb*, 11–24, mean 17.3 (n=22) in *pt*, 10–19, mean 15.1 (n=22) in *sh*. Abd IV with 2–4, usually 2 or 3, gland spines marginally. Abd I with 1–5 submedian dorsal microducts. Submedian macroducts occurring on abd II–V and usually also on VI, often divided into segmental and infrasegmental series on II and III; 3–7 on II, 4–8 on III, 4–7 on IV, 2–5 on V, usually 1, at times 0 or 2, on VI. Submarginal macroducts on abd II–V, row on II and sometimes also on III irregularly double; 3–14 on II, 5–13 on III, 2–8 on IV, 2– 5 on V. Total of dorsal macroducts on both sides 60–94, mean 77.3 (n=9) in subsample *lb*, 82–115, mean 101.8 (n=12) in *pt*, 75–96, mean 79.8 (n=11) in *sh*. Median trullae very large as compared with lateral trullae, sunken into apex of pygidium, detached from each other basally, with mesal margins divergent, roundish, and roughly serrate; basal zygosis represented by a pair of sclerotized pieces separated from each other by a narrow space. Second trullae with lobules well represented and oblong, mesal lobule with a pair of linear basal scleroses, lateral lobule a little smaller. Third trullae similar to but somewhat smaller than the second. Pygidial margin on abd IV and V straight, serrate.

Recognition characters (adult female). Body growing to the *vitis*-type. Posterior spiracles each with a few to several disc pores anteriorly. Submedian macroducts on abd II–V, usually 1 on VI. Submarginal macroducts on II–V. Median trullae very large as compared with lateral trullae, sunken into apex of pygidium, with mesal margins divergent, roundish, and roughly serrate; basal zygosis represented by a pair of sclerotized pieces separated from each other by a narrow space.

Remarks. This species is very similar to *A. pellucida* (2.9.), another *Macaranga*-associated species, in the pygidial margin, especially in the shape of the median trullae, and it is probably closely related to the latter. It is easily distinguishable from the latter

in having dorsal macroducts on the second abdominal segment in addition to the third to sixth and in having disc pores at both pairs of spiracles.

This species was collected in the island of Mindoro, which is situated just south of Luzón and between Luzón and Palawan. No material of *Aulacaspis pellucida* was obtained in this island in spite of the occurrence of *A. pellucida* in the latter two islands, on which *A. binunga* was not collected.

2.11. *Aulacaspis macarangae*, n. sp. (Figs 25, 26)

Material. Collected in Malaya, Malaysia, on *Macaranga* spp. (Euphorbiaceae). Cameron Highlands, alt. ca. 1400m, Pahang, on *Macaranga* sp. (probably *M. hullettii*), 1.XII.1985 [lot no.: 85ML-76]; on *Macaranga curtisii*, 14.X.1986 and 17.X.1986 [86ML-189, -235]; on *Macaranga* sp., 20.X.1986 [86ML-256]. Bukit Tapah, near the Cameron Highlands, alt. 650m, on *Macaranga tanarius*, 19.X.1986 [86ML-251]. Female and male tests occurring on the lower surface of leaves. The female insect induces a rather deep, irregular depression, or an irregularly shaped pit gall, on the lower leaf surface, the depression producing on the upper leaf surface a dark coloured, rounded prominence. The full-grown adult female has the body swollen ventrally, thus fitting into the pit gall, and is covered with the test dorsally. Male test with a faint median carina. Holotype, from [86ML-256]: FRIM.

Adult females from the Cameron Highlands. Body growing broadened especially in thoracic region and swollen ventrally. (In slide-mounted full-grown females the mouth-parts and antennae are pushed forward, with the frontal area anterior to them rolled onto the dorsal side, owing to the swollen ventral side of the body pressed and made flat). Body length about 550–780μm; pygidium triangular in outline, about 160–190μm long. Anterior spiracles each accompanied with 3–13 disc pores; 5–8, mean 6.5 (n=4) in sample from [85ML-76], 4–9, mean 6.1 (n=18) in [86ML-189], 3–9, mean 5.7 (n=39) in [86ML-235], 3–13, mean 6.3 (n=40) in [86ML-256]. Posterior spiracles with no disc pores. Perivulvar disc pores 7–15 in median, 13–27 in each anterolateral, and 9–17 in each posterolateral group; total 53 and 54 (n=2) in sample from [85ML-76], 56–72, mean 65.6 (n=9) in [86ML-189], 61–85, mean 71.1 (n=20) in [86ML-235], 51–84, mean 70.9 (n=20) in [86ML-256]. Abd II with 2–7 macroducts and 2–7 gland spines on lateral lobe; III with 2–7 macroducts and 3–8 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 4–10, mean 7.0 (n=3) in sample from [85ML-76], 6–12, mean 10.1 (n=18) in [86ML-189], 6–13, mean 10.1 (n=40) in [86NK-235], 8–13, mean 9.9 (n=40) in [86ML-256]. Total of lateral gland spines on each side 7–9, mean 8.3 (n=3) in sample from [85ML-76], 7–12, mean 9.1 (n=18) in [86ML-189], 6–12, mean 9.8 (n=39) in [86ML-235], 5–12, mean 8.3 (n=40) in [86ML-256]. Abd IV with 1–4, usually 2 or 3, gland spines marginally. Submedian macroducts on abd III–VI, 1–3 on III, 1–4 on IV, 1–3 on V, 1–3 on VI. Submarginal macroducts on abd III–V, 1–4 on each segment. Total of dorsal macroducts 22 and 28 (n=2) in sample from [85ML-76], 24–36, mean 29.9 (n=9) in [86ML-189], 16–41, mean 29.8 (n=20) in [86ML-235], 20–37, mean 30.6 (n=20) in [86ML-256]. Median trullae much longer than lateral trullae, sunken into apex of pygidium, separated from each other by a good space basally, divergent, slender, with mesal margins slightly depressed subapically and obscurely serrate basally to the depression; basal zygosis shaped nearly like an inverted V. Lateral trullae well represented; second trullae with lobules oblong, the third a little smaller; a pair of linear basal scleroses well represented on mesal lobule of second trulla. Pygidial margin on abd

IV and V little rugged, minutely serrate.

Adult females from Bukit Tapah. Three adult females are available. They tend to have the spiracular and perivulvar disc pores, lateral and submarginal macroducts, and lateral gland spines more numerous than in the females from the Cameron Highlands, but the available sample is too small for comparison. Disc pores associated with each anterior spiracle 8 or 9, mean 8.3 (n=4); total of perivulvar disc pores 81–87, mean 84.7 (n=3); total of lateral macroducts on each side 14–16, mean 14.6 (n=5); total of lateral gland spines on each side 15–19, mean 16.6 (n=5); submarginal macroducts 4 or 5 on abd III, 3–5 on IV, 2 or 3 on VI; total of dorsal macroducts on both sides 31 or 40 (n=2).

Recognition characters (foliicolous adult female). Body growing broadened especially in thoracic region. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Submedian macroducts on abd III–VI; submarginal macroducts on III–V; total of dorsal macroducts on both sides rarely exceeding 40. Median trullae much longer than lateral trullae, sunken into apex of pygidium, divergent, slender, with mesal margins slightly depressed subapically and obscurely serrate basally to the depression; basal zygosis shaped nearly like an inverted V.

Remarks. This species lives in a leaf pit gall, but it shows no remarkable morphological modification in association with this habit except for the broadened body, which is swollen on the ventral side at full growth. It is rather unique in having the median trullae slightly depressed subapically on the mesal margins.

2.12. *Aulacaspis mahangena*, n. sp. (Fig. 27)

Material. Collected in Malaya, Malaysia, on *Macaranga curtisii* (local name for *Macaranga* spp.: Mahang) (Euphorbiaceae). Bukit Larut, 950m, Perak, 9.X.1986 [lot no.: 86ML-138]. Bukit Fraser, 1250m, Pahang, 30.X.1986 [86ML-365]. Females occurring on the lower surface of the leaves. Female tests very small, thin, transparent. Holotype, from [86ML-365]: FRIM.

Adult females from Bukit Fraser. Body fusiform or, at full growth, rhombic with thoracic region expanded laterally; small, about 420–525μm long; pygidium triangular in outline, 135–150μm long. Anterior spiracles each accompanied with 2–4, mean 2.9 (n=14), disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 5–8 in median, 8–13 in each anterolateral, and 7–11 in each posterolateral group; total 42–49, mean 44.6 (n=10). Abd II at times with 1 macroduct and 1–3 gland spines on lateral lobe; III with 2–4 macroducts and 3–6 gland spines along margin of lateral lobe; IV with 2 marginal gland spines. Submedian macroducts usually absent, at times 1 present on abd V. Submarginal macroducts 1 or 2 at times present on abd III, usually 1, at times 2, on IV, and 1 on V. Median trullae somewhat larger than lobules of lateral trullae, sunken into apex of pygidium, gently divergent, spatulate, with mesal margins obscurely serrate; basal zyosis represented by a pair of small sclerotized pieces. Lateral trullae with lobules well developed; mesal lobule of the second with a pair of well-developed linear basal scleroses.

Adult female from Bukit Larut. Body about 560–720μm long; pygidium about 140–150μm long. Anterior spiracles each with 1–5, mean 2.5 (n=22), disc pores. Perivulvar disc pores 3–8 in median, 9–15 in each anterolateral, and 4–9 in each posterolateral group; total 38–52, mean 47.2 (n=11). Abd II with 1–4 macroducts and 1–4 gland spines on lateral lobe; III with 2–4 macroducts and 3–6 gland spines on margin of lateral lobe.

Total of lateral macroducts on each side 4–7, mean 6.0 (n=22). Total of lateral gland spines on each side 5–8, mean 7.7 (n=21). Abd IV with 1 or 2, usually 2, gland spines marginally. Submedian macroducts absent. Submarginal macroducts usually 1, at time 2 or absent, on abd III, 1, at times 2, on IV, and 1 on V. Total of submarginal ducts on both sides 5–8, mean 6.3 (n=11).

Recognition characters (foliicolous adult female). Body small, fusiform or, when fully grown, rhombic with thoracic region expanded laterally. Anterior spiracles each with a few to several disc pores; posterior spiracles with no disc pores. Perivulvar disc pores not numerous, total about 50 at maximum. Lateral macroducts few, at times lacking on abd II. Lateral gland spines also at times lacking on abd II. Submedian macroducts usually absent on abdominal segments, 1 at times present on abd V. Submarginal macroducts few, absent or 1 or 2 present on abd III, usually 1 on each of IV and V. Median trullae somewhat larger than lobules of lateral trullae, sunken into apex of pygidium, gently divergent, spatulate, with mesal margins obscurely serrate; basal zygosis represented by a pair of small sclerotized pieces.

Remarks. Among the species associated with *Macaranga*, this species is characterized and recognized by the body smaller and the spiracular and perivulvar disc pores and the dorsal macroducts all few. (For comparisons with other species, see *Remarks* under 2.14.)

2.13. *Aulacaspis canarii*, n. sp. (Figs 28, 29)

Material. Collected in Malaysia on plants of *Canarium* (Burseraceae). Sandakan, Sabah (northeastern Borneo), on *Canarium* sp., 15.XI.1988 [lot no.: 88ML-359]. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, on *Canarium pilosum*, 22.VI.1990 [90ML-59]. Bukit Bauk, Terengganu, Malaya, on C. *pilosum*, 15.VII.1990 [90ML-227]. Bukit Nanas, Kuala Lumpur, on *C. pilosum*, 5.VIII.1990 and 23.VIII.1990 [90ML-438, -602]. Females and males occurring on the lower surface of leaves, females along veins. Female tests flat, very thin, transparent. Male tests tricarinate. Holotype, from [90ML-602]: FRIM.

Adult females from Kuala Lumpur. Body growing to the *vitis*-type, but often remaining fusiform at full growth, about 570–960µm long; pygidium triangular in outline, about 135–165µm long. Disc pores associated with each anterior spiracles 1–4, mean 2.5 (n=4) in sample from [90ML-59], 1–8, mean 4.6 (n=18) in [90ML-438], 3–8, mean 5.2 (n=33) in [90ML-602]. Posterior spiracles with no disc pores. Perivulvar disc pores 6–12 in median, 10–17 in each anterolateral, and 3–11 in each posterolateral group; total 49–59, mean 54.7 (n=3) in sample from [90ML-59], 44–58, mean 50.0 (n=9) in [90ML-438], 42–61, mean 52.7 (n=20) in [90ML-602]. Abd II with 1–5 macroducts, sometimes without macroducts, and 1–4 gland spines on lateral lobe; III with 1–4 macroducts and 2–8 gland spines on margin of lateral lobe. Total of lateral macroducts on each side 3–8, mean 5.7 (n=6) in sample from [90ML-59], 1–6, mean 3.1 (n=18) in [90ML-438], 1–8, mean 3.9 (n=32) in [90ML-602]. Total of lateral gland spines on each side 4–10, mean 6.5 (n=6) in sample from [90ML-59], 4–9, mean 6.7 (n=18) in [90ML-438], 3–10, mean 6.8 (n=28) in [90ML-602]. Abd IV with 2 or 3, usually 2, marginal gland spines. Submedian macroducts usually absent but rarely 1 present on abd III, 1 or sometimes 2 on IV, usually 1 and rarely 2 on V. Submarginal macroducts 1 or 2, rarely none, on each of abd III–V. Total of dorsal macroducts on both sides 10–17, mean 14.0 (n=3) in sample from [90ML-59], 10–14, mean 12.8 (n=9) in [90ML-438], 11–15, mean

13.6 (n=20) in [90ML-602]. Median trullae much longer than lateral trullae, sunken into apex of pygidium, separated from each other by a good space basally, then divergent, elongate, with mesal margins dentate or roughly serrate; basal zygosis represented by a pair of small sclerotized pieces separated from each other by a narrow but distinct space and extending into a pair of linear scleroses on ventral surface of pygidium. Lateral trullae with lobules well represented, mesal lobule of second trulla with a pair of linear basal scleroses. Pygidial margin on abd IV and V straight or nearly so, finely serrate.

Adult females from Bukit Bauk. Characterized substantially the same as the samples from Kuala Lumpur. Disc pores associated with each anterior spiracle 2–7, mean 4.9 (n=37); total of perivulvar disc pores 37–60, mean 53.7 (n=21); total of lateral macroducts on each side 1–6, mean 3.9 (n=37); total of lateral gland spines on each side 3–8, mean 6.0 (n=36); total of dorsal macroducts on both sides 9–18, mean 11.9 (n=20).

Adult females from Sandakan. Characterized substantially the same as the samples from Malaya. Disc pores associated with each anterior spiracle 3–7, mean 4.5 (n=39); total of perivulvar disc pores 39–50, mean 45.0 (n=21); total of lateral macroducts on each side 3–8, mean 5.5 (n=42); total of lateral gland spines on each side 9–15, mean 11.0 (n=42); submedian macroducts always lacking on abd III; total of dorsal macroducts on both sides 8–13, mean 11.0 (n=21).

Recognition characters (foliicolous adult female). Body growing to the *vitis*-type, but often remaining fusiform. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Total of perivulvar disc pores around 50. Lateral macroducts at times lacking on abd II. Submedian macroducts few, rarely 1 occurring on abd III, usually 1 or 2 present on each of IV and V. Submarginal macroducts also few, usually present on abd III–V, but rarely absent on III or IV. Median trullae much longer than lateral trullae, sunken into pygidium, divergent, elongate, with mesal margins dentate or roughly serrate; basal zygosis represented by a pair of small sclerotized pieces extending into elongate scleroses on ventral surface of pygidium. Pygidial margin on abd IV and V straight, finely serrate.

Remarks. The examined samples were collected on the western and eastern sides of the Malay Peninsula and in Sabah, northeastern Borneo. They show little variation in spite of the widely separated localities. (For comparisons with similar species, see *Remarks* under 2.14.)

2.14. *Aulacaspis canariicola*, n. sp. (Fig. 30)

Material. Collected at the Pasoh Forest Reserve, Negeri Sembilan, Malaya, Malaysia, on *Canarium littorale* f. *tomentosum* (Burseraceae), 27.IX.1986 [lot no.: 86ML-34]. Females and males occurring on the lower surface of leaves, females along veins. Female tests oblong, very inconspicuous. Male tests tricarinate. Holotype: FRIM.

Adult females. Body fusiform, at times with thoracic region more or less expanded laterally; about 500–700μm long; pygidium triangular in outline, about 125–145μm long. Interantennal tubercle and derm pockets at times present but rudimentary. Anterior spiracles each accompanied with 2–5, mean 3.1 (n=30), disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 6–8 in median, 8–14 in each anterolateral, and 3–9 in each posterolateral group; total 38–48, mean 45.2 (n=13). Abd II with no macroducts and no gland spines on lateral lobe; III with 1 or 2 macroducts and 1–3, usually 1 or 2, gland spines on margin of lateral lobe; IV with 2 gland spines marginally.

Submedian macroducts absent. Submarginal macroducts on abd III–V, usually 1 on each segment, at times absent on III, sometimes 2 on IV; total on both sides 5–8, mean 6.5 (n=15). Median trullae much longer than lateral trullae, sunken into apex of pygidium, separated from each other by a good space basally, then divergent, elongate, with mesal margins dentate or roughly serrate; basal zygosis small, shaped like an inverted V. Second trullae well represented; mesal lobule with a pair of linear scleroses basally. Third trullae with lateral lobule much shortened, notched or serrate. Pygidial margin on abd IV and V straight or slightly concave, rather roughly serrate.

Recognition characters (foliicolous adult female). Body fusiform, sometimes with thoracic region expanded laterally. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Perivulvar disc pores scarcely amounting to 50 in total. Abd II without macroducts and gland spines on lateral lobe; III with 1 or 2 macroducts and 1–3 gland spines along margin of lateral lobe. Submedian macroducts absent. Submarginal macroducts present on abd III–V, usually 1 on each segment, sometimes 2 on IV. Median trullae much longer than lateral trullae, sunken into pygidium, elongate, divergent, with mesal margins dentate or roughly serrate; basal zygosis shaped like an inverted V. Third trullae with lateral lobule much shortened.

Remarks. This species is apparently closely related to *Aulacaspis canarii* (2.13.). In *A. canarii*, the basal zygosis of the median trullae is represented by a pair of pieces detached from each other, whereas in *A. canariicola* these pieces are fused at their anterior ends to form an inverted V. *A. canarii* usually has a few submedian macroducts on the fourth and fifth abdominal segments, whereas *A. canariicola* has no submedian macroducts. *A. canarii* usually has a few macroducts and always possesses a few gland spines on the lateral lobe of the second abdominal segment, whereas *A. canariicola* has no macroducts and no gland spines on the lateral lobe of this segment. *A. canarii* has the lateral lobule of the third trulla well developed, whereas *A. canriicola* has a much shortened one. These two *Canarium*-associated scale insects are similar to the *Macaranga*-associated *Aulacaspis mahangena* (2.12.) in body shape and in having the macroducts much decreased in number, but are remarkably different from the latter in having dentate or roughly serrate median trullae.

2.15. *Aulacaspis canariiphila* (Fig. 31)

Material. Collected on Gunong Jerai (altitude not recorded), Kedah, Malaya, Malaysia, on *Canarium littorale* (Burseraceae), 8.XI.1991 [lot no.: 91ML-370]. Females occurring on the lower surface of leaves; tests thin, but not transparent, irregular in outline. (Specimens of *Aulacaspis calcarata* were also mounted from this lot of material.) Holotype: FRIM.

Adult females. Body of the *vitis*-type, about 600–800μm long; pygidium broadly triangular in outline, about 170–210μm long. Interantennal tubercle and derm pockets sometimes present, but tending to be rudimentary. Anterior spiracles each accompanied with 2–7, mean 3.1 (n=31), disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 2–10 in median, 15–22 in each anterolateral, and 9–15 in each posterolateral group; median group sometimes divided medially into 2 subgroups; total 60–81, mean 67.7 (n=17). Abd II often lacking macroducts and gland spines on lateral lobe, sometimes (20%, n=34) with 1 macroduct and sometimes (about 30%, n=34) with 1 gland spine or rarely with 2 or 3; III with 2 or 3, usually 2, macroducts and 2–4, usually 2 or 3, gland spines on margin of lateral lobe; IV with 2 marginal gland spines. Submedian macroducts

absent. Submarginal macroducts present on abd III–V, 1 or more often (79%, n=33) 2 on III, 1 or usually (85%, n=34) 2 on IV, and always 1 on V; total on both sides 7–10, mean 9.3 (n=16). Median trullae very large relative to lateral trullae, sunken into apex of pygidium, gently divergent, elongate, with mesal margins roughly serrate; basal zygosis well developed, shaped like an inverted V, anteriorly with an elongate triangular sclerotic patch of derm on ventral surface of pygidium. Lateral trullae well represented, with lobules robust and dilated; mesal lobule of second trulla with a pair of linear scleroses basally; lateral lobule of third trulla much shortened. Margin of abd V rather roughly serrate; pore prominence on abd IV low and broad, with a small but distinct triangular process or spur at middle; a similar but smaller process on pore prominence associated with mesal marginal macroduct of V.

Recognition characters (foliicolous adult female). Body of the *vitis*-type. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Abd II often with no macroducts and no gland spines on lateral lobe; III with a few macroducts and a few gland spines on margin of lateral lobe. Submedian macroducts absent. Submarginal macroducts present on abd III–V, few on each segment. Median trullae very large relative to lateral trullae, sunken into apex of pygidium, gently divergent, with mesal margins roughly serrate; basal zygosis shaped like an inverted V, anteriorly with an elongate triangular sclerotic patch of derm. Lateral trullae with lobules robust and dilated. Pygidial margin of abd IV and also of V with a spur-like process.

Remarks. This species has a small but distinct triangular process or spur on each of the pore prominences of the fourth and fifth abdominal segments as in the *calcarata* species group of *Aulacaspis* (see 6.1.). *Aulacaspis canariiphila* is readily distinguishable from the other two *Canarium*-associated species, *A. canarii* (2.13.) and *A. canariicola* (2.14.), in having the calcarate pore prominences and in the state of the median trullae.

2.16. *Aulacaspis elongata*, n. sp. (Fig. 32)

Material. Collected in the grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, Malaysia, on *Scaphocalyx spathacea* (Flacourtiaceae), 17.VI.1990, 27.VI.1990, and 30.X.1991 [lot no.: 90ML-24, -72; 91ML-301]. Females and males occurring on both surfaces of leaves, females mainly along veins, sometimes on margin. Female tests very slender, thin, fragile, with nymphal exuvial casts terminal (second-instar exuvial cast about 2.2–2.5 times as long as wide). Male tests tricarinate. The examined samples apparently belong to the same local population, and are united together in the description. Holotype, from [90ML-72]: FRIM.

Adult females. Body at full growth elongate, about thrice or a little more as long as wide, with lateral sides almost parallel through thorax and prepygidial abdomen; exceeding 1000μm in length; prosoma about as long as postsoma, with a pair of round prominences bearing eyes caudad of frontal margin; metathorax and abd I–III gently lobed laterally; pygidium nearly triangular in outline, slightly roundish, usually about 200–240μm long. Interantennal tubercle usually present, often divided medially into a pair of swellings; interantennal derm pockets absent. Anterior spiracles each accompanied with 2–8, mean 4.9 (n=95), disc pores; posterior spiracles each with 1 (81.6%, n=98) or 2 disc pores anteriorly. Perivulvar disc pores 4–16 in median, 12–23 in each anterolateral, and 9–19 in each posterolateral group; total 58–87, mean 69.7 (n=54). Abd II with 6–15 macroducts and 2–7 gland spines on lateral lobe; III with 3–9 macroducts and 3–8 gland spines on margin of lateral lobe. Total of lateral macroducts on

each side 11–22, mean 16.5 (n=97). Total of lateral gland spines on each side 7–14, mean 10.5 (n=79). Abd IV with 2, rarely 3, gland spines marginally. Submedian macroducs usually (80.6%, n=108) absent, at times 1, on abd III; usually (83.3%, n=108) 1, at times 2 or 0, on IV; usually (89.8%, n=108) 1, at times 2 or rarely 0, on V; usually (89.8%, n=108) absent, at times 1, on VI. Submarginal macroducts 1–4 on each of abd III–V, usually 3 or 4 on each of III and IV and 2 or 3 on V. Total of dorsal macroducts on both sides 15–31, mean 21.3 (n=54). Median trullae much longer than lateral trullae, sunken into apex of pygidium, separated from each other by a good space, then divergent, with mesal margins serrate; basal zygosis shaped like an arch, sometimes appearing to be divided into a pair of pieces. Lateral trullae well represented; mesal lobule of second trulla with a pair of linear scleroses basally. Pore prominence of abd IV low and broad, usually with a spur-like process or a few small triangular processes; a similar process on pore prominence associated with mesal marginal macroduct of V.

Recognition characters (foliicolous adult female). Body elongate, with lateral sides nearly parallel. Eyes on a pair of round prominences. Interantennal tubercle usually present, often divided medially. Anterior spiracles each with a small cluster of disc pores; posterior spiracles each usually with 1 disc pore anteriorly. Submedian macroducts usually absent on abd III, usually present but very few on IV and V, usually absent on VI. Submarginal macroducts on abd III–V, few on each segment. Median trullae much longer than lateral trullae, sunken into apex of pygidium, divergent, with mesal margins serrate; basal zygosis shaped like an arch, sometimes divided into a pair of pieces. Pygidial margin of abd IV and V with small triangular processes.

Remarks. The adult females of this species and another form (*Aulacaspis* 91BP-*Dg*, 4.1.2., tentatively united with *Aulacaspis calcarata*, 4.1.) have the body much elongated at full growth quite unusually in *Aulacaspis*. They occur along the veins, or sometimes on the margin, of the leaves. Their elongate bodies are apparently adaptive to these feeding sites (and possibly ecophenotypic on these sites to some degree). There is in the other features no good reason for excluding them from the genus. Moreover, these two forms are similar to the *calcarata* species group of *Aulacaspis* in having spur-like processes on the pygidial margin of the fourth and fifth abdominal segments, and *A.* 91BP-*Dg* is especially close to *Aulacaspis calcarata* except for the slender body (see 6.1.).

A. elongata is distinguishable from *A.* 91BD-*Dg* in the posterior spiracles usually accompanied with one or two disc pores and the median trullae much larger than the lateral trullae. It may be similar also to *Aulacaspis hedyotidis* (=*Chionaspis hedyotidis*, 5.5.) except for the fact that it is unusually elongate and provided with spur-like processes on the pygidium (see *Remarks* under 5.5.).

2.17. *Aulacaspis katus*, n. sp. (Fig. 33)

Material. Collected in Nepal, on *Castanopsis tribuloides* (local name: Katus) (Fagaceae) or an undetermined species of *Castanopsis*. Sheopuri [Sivapuri], alt. ca. 2000m, near Kathmandu, Bagmati, on *Castanopsis* sp., 31.VIII.1975 [lot no.: 75NPL-122]. Nagarjun, alt. 1470m, Kathmandu Valley, Bagmati, on *Castanopsis tribuloides*, 12.X.1983 [83NPL-20]. Dhankuta, alt. 1100m, Kosi, on *C. tribuloides*, 22.XI.1983 [83NPL-236]. Chotepatan, alt. 900m, Pokhara District, Gandaki, on *C. tribuloides*, 6.XII.1983 and 10.XII.1983 [83NPL-294, -324]. Females and males occurring on the lower surface of leaves. Female tests irregular in outline, flat, very thin, nearly transparent. Male tests tricarinate. Holotype, from [83NPL-324]: SEHU.

Adult females from Chotepatan. Samples from [83NPL-294] and [83NPL-324] are united together. Body fusiform, with metathorax and abd I moderately and abd II and III strongly lobed laterally; when fully grown, a little constricted on abd I, with meso- and metathorax tending to be expanded laterally but not much; attaining about 1260–1300μm in length; pygidium nearly triangular in outline, about 205–235μm long. Anterior spiracles each accompanied with 4–10, mean 6.4 (n=37), disc pores; posterior spiracles each with 1–3, mean 1.8 (n=42), disc pores anteriorly. Perivulvar disc pores 2–9 in median, 8–28 in each anterolateral, and 6–18 in each posterolateral group; median group often divided medially into 2 subgroups; total 37–85, mean 73.8 (n=21). Abd II with 2–4 macroducts and 1–4 gland spines (rarely and probably abnormally with no gland spines) on lateral lobe; III with 3–4 macroducts and 3–7 gland spines along margin of lateral lobe. Total of lateral macroducts on each side 5–8, mean 6.2 (n=42). Total of lateral gland spines on each side 3–10, mean 5.9 (n=42). Abd IV with 1–5, mean 3.0 (n=42), gland spines marginally. Submedian macroducts absent on all abdominal segments. Submarginal macroducts present on abd III and IV only; 1–5 on III, 2–4 on IV; total on both sides 8–16, mean 11.7 (n=21). Median trullae very large relative to lateral trullae, sunken into apex of pygidium, separated from each other by a good space, then divergent, with mesal margins curved and serrate; basal zygosis shaped like an inverted V, thick. Second trullae with lobules oblong; mesal lobule with a pair of short linear scleroses basally. Third trullae with lateral lobule shortened and broadened, serrate on lateral side. Pygidial margin on abd IV and V nearly straight, pore prominences a litte produced.

Adult females from Sheopuri. Characterized substantially the same as the females from Chotepatan. Anterior spiracles each with 4–8, mean 5.7 (n=10), disc pores; posterior spiracles each with 1–3, mean 1.9 (n=12), disc pores. Total of perivulvar disc pores 67–83, mean 77.3 (n=6). Total of lateral macroducts on each side 5–8, mean 6.5 (n=12). Total of lateral gland spines on each side 5–10, mean 7.4 (n=12). Total of submarginal macroducts on both sides 11–20, mean 16.2 (n=6).

Two adult females are available from Nagarjun. They have the wax-secreting organs somewhat less numerous than in the specimens from Sheopuri.

Adult females from Dhankuta. Characterized substantially the same as the females from Chotepatan. Anterior spiracles each with 1–6, mean 4.0, disc pores (n=8): posterior spiracles each with 1 or 2, mean 1.3, disc pores (n=8). Total of perivulvar disc pores 74 or 82, mean 76.7 (n=3). Total of lateral macroducts on each side 6 or 7, mean 6.2 (n=6). Total of lateral gland spines on each side 3–9, mean 6.7 (n=6). Total of submarginal macroducts on both sides 11–14, mean 12.7 (n=3).

Recognition characters (foliicolous adult female). Body fusiform, with abd I and II well lobed laterally; meso- and metathorax somewhat expanded laterally at full growth. Anterior spiracles each with a small cluster of disc pores; posterior spiracles each with 1–3 disc pores anteriorly. Submedian macroducts absent. Submarginal macroducts present only on abd III and IV, not numerous. Median trullae very large relative to lateral trullae, sunken into apex of pygidium, divergent, with mesal margins curved and serrate; basal zygosis shaped like an inverted V, thick. Mesal lobule of second trulla with a pair of short linear scleroses basally. Lateral lobule of third trulla shortened and broadened, serrate on lateral side.

Remarks. This species is peculiar and easily distinguishable from the other species described in this paper in having dorsal macroducts only submarginally on the third and

fourth abdominal segments.

The possibility that this species belongs to *Chionaspis* is not excluded in consideration of the host association. Many species of *Chionaspis* occurring in Asia are associated with fagaceous plants, which are in principle not among the host plants of *Aulacaspis*. (See also 5.9. and 6.2.)

2.18. *Aulacaspis dilleniae,* n. sp. (Fig. 34)

Material. Collected on Mt. Kinabalu, alt. 2750m, Sabah (northeastern Borneo), Malaysia, on *Dillenia* sp. (Dilleniaceae), 2.X.1988 [lot no.: 88ML-29]. Females occurring on the upper and lower surfaces, and males on the lower surface, of leaves. Female tests ovate in outline. Holotype: FRIM.

Adult females. Body, when fully grown, nearly of the *vitis*-type, about 1500μm long at maximum. Pygidium broadly rounded on free margin, about 270–325μm long. Anterior spiracles each with 16–37, mean 25.1 (n=32), disc pores; posterior spiracles each with 9–28, mean 17.1 (n=36), disc pores anterolaterally. Perivulvar disc pores 15–26 in median, 15–47 in each anterolateral, and 30–48 in each posterolateral group; total 148–192, mean 170.0 (n=20). Abd II with 9–26 macroducts and 6–15 gland spines on lateral lobe; III with 6–20 macroducts and 9–19 gland spines on margin of lateral lobe. Total of lateral macroducts on each side 19–46, mean 26.0 (n=33). Total of lateral gland spines on each side 19–33, mean 24.8 (n=36). Abd IV with 5–12, mean 7.2 (n=36), gland spines marginally. Submedian macroducts on abd III–V and usually also on VI, divided into segmental and infrasegmental series on III and IV and at times also on V; 5–10 on III, 4–11 on IV, 3–11 on V, 1–5, at times (10%, n=40) absent, on VI. Submarginal macroducts on abd III–V, at times (25%, n=40) present also on II, arranged in an irregularly double row on III and also on II when present; 6–15 on III, 7–14 on IV, 6–15 on V; 4–14 on II when present. Total of dorsal macroducts 82–135, mean 111.0 (n=20), when the macroducts occurring on abd II are excluded; 106–141, mean 115.1 (n=20), when included. Usually (82.5%, n=40) microducts occurring on dorsal surface of postsoma in a somewhat variable extent anterior to submedian and submarginal rows of macroducts of abd III; very variable in number, usually abundant submedially and less numerous submarginally; in a few cases a number of microducts strewn on metathorax to abd III across the segments, estimated at about 200 in total. Median trullae large relative to lateral trullae, sunken into apex of pygidium, divergent, elongate, same in width for most length, gently curved, with mesal margins obscurely serrate; basal zygosis small but distinct, sometimes appearing to be divided into a pair of pieces. Lateral trullae well represented; second trullae with lobules oblong, mesal lobule with a pair of slender linear scleroses basally; third trullae with lobules a little broader than those of the second. Margin of abd V with 3 broad low prominences.

Recognition characters (foliicolous adult female). Body of the *vitis*-type, with pygidium rounded along free margin. Posterior spiracles each with a good number of disc pores anterolaterally. Lateral macroducts and lateral gland spines on abd II and III and marginal gland spines on IV numerous. Submedian macroducts occurring on abd III–V and usually also on VI; submarginal macroducts on III–V and at times also on II. Usually a number of dorsal microducts strewn on abd I–III and at times also on metathorax. Median trullae large relative to lateral trullae, sunken into apex of pygidium, divergent, elongate, gently curved, with mesal margins obscurely serrate; basal zygosis

small but distinct.

Remarks. Most of the examined specimens have a number of dorsal microducts on anterior postsomatic segments, but this character is not stable and not adoptable as a diagnostic one of the species. Among the species of the *vitis*-type described in this paper, *A. dilleniae* is well characterized by having the disc pores associated with both pairs of spiracles, the dorsal macroducts, and the gland spines all abundant. It may be compared with *Aulacaspis anaimala* (2.5.), from which it is readily distinguishable in having elongate median trullae. (See also 6.2.)

2.19. *Aulacaspis guioae*, n. sp. (Figs 35, 36)

Material. Collected in Malaysia on plants of *Guioa* (Sapindaceae) and an undetermined plant of the family Sapindaceae. Sepilok, Sabah (northeastern Borneo), on a tree of the Sapindaceae [lot no.: 88ML-346]. Beserah Forest Reserve, Kuantan, Pahang, Malaya, on *Guioa pleuropteris*, 6.VII.1990 [90ML-112, -123]. Bako National Park, Sarawak (northwestern Borneo), on *Guioa* sp., 14.X.1991 [91ML-162]. Females and males occurring on the lower surface of leaves, females also on twigs. Female tests narrow when occurring along veins. Holotype, from [90ML-123]: FRIM.

Foliicolous adult females from the Beserah Forest Reserve. The samples from [90ML-112] and [90ML-123] are united together. Body growing to the *vitis*-type (many specimens, however, are elongate fusiform), about 1220μm in length at maximum; pygidium nearly triangular in outline, about 190–225μm long. Interantennal tubercle sometimes well developed; derm pockets sometimes present. Anterior spiracles each accompanied with 5–14, mean 8.0 (n=56), disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 8–14 in median, 14–22 in each anterolateral, and 7–15 in each posterolateral group; total 55–84, mean 69.9 (n=28). Abd II with 3–6 macroducts and 1–6 gland spines on lateral lobe; III with 2–5 macroducts and 3–8 gland spines on margin of lateral lobe; IV with 1 or usually (95%, n=55) 2 gland spines marginally. Total of lateral macroducts on each side 5–10, mean 7.4 (n=56). Total of lateral gland spines on each side 4–12, mean 8.4 (n=56). Submedian macroducts at times (11%, n=56) 1 present on abd III, often 1 (about 60%, n=56) and at times 2 present on each of IV and V, always absent on VI. Submarginal macrdocuts 2–5 on abd III, 1–4 on IV, usually (92%, n=56) 1 or 2, at times 3, rarely absent, on V. Total of dorsal macroducts on both sides 10–28, mean 18.3 (n=28). Median trullae very large relative to lateral trullae, sunken into apex of pygidium, separated from each other by a good space basally, then divergent, elongate, with mesal margins dentate or roughly serrate; basal zygosis well developed. Second trullae with lobules oblong, mesal lobule with a pair of short linear scleroses basally. Third trullae with lateral lobule short and broad. Pygidial margin of abd IV and V straight.

Foliicolous adult females from the Bako National Park. Characterized substantially the same as the adult females from the Beserah Forest Reserve. Anterior spiracles each with 7–16, mean 11.2 (n=13), disc pores. Perivulvar disc pores, total 51–83, mean 64.3 (n=7). Abd II with 1–4 macroducts and 1–3 gland spines on lateral lobe; III with 3–5 macroducts and 4–9 gland spines on margin of lateral lobe; IV with 2 gland spines marginally. Total of lateral macroducts on each side 4–8, mean 5.6 (n=14). Total of lateral gland spines on each side 5–12, mean 7.8 (n=14). Submedian macroducts usually (93%, n= 14) 1 present on each of abd IV and V, at times (21%, n=14) 1 on V. Total of dorsal macroducts 11–24, mean 16.3 (n=7).

Two ramicolous adult females are available from the same sample, but they are not in good condition. They have the lateral macroducts and lateral gland spines fewer than in the foliicolous specimens, but they do not differ much from the latter in the numbers of the other wax-secreting organs. They have the median trullae more robust than in the foliicolous specimens, divergent from their bases, and more or less produced at the apex of the pygidium.

Foliicolous adult females from Sepilok. Anterior spiracles each with 6–8, mean 6.7 (n=6), disc pores. Perivulvar disc pores 11–14 in median, 20–24 in each anterolateral, and 12–16 in each posterolateral group; total 79–87, mean 84.0 (n=3). Abd II with 3 or 4 macroducts and 2–6 gland spines on lateral lobe; III with 4 macroducts and 5–8 gland spines on margin of lateral lobe. Total of lateral macroducts on each side 7 or 8, mean 7.8 (n=4). Total of lateral gland spines on each side 8–13, mean 10.3 (n=4). Total of dorsal macroducts 14 or 18 (n=2).

Recognition characters (foliicolous adult female). Body growing to the *vitis*-type. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Submedian macroducts lacking on abd III and VI almost always, very few when occurring on IV and V. Submarginal macroducts on abd III–V, few especially on V. Median trullae very large relative to lateral trullae, sunken into apex of pygidium, divergent, with mesal margins dentate or roughly serrate; basal zygosis distinct. Third trullae with lateral lobule short and broad.

Remarks. This species is very similar to *Aulacaspis pellucida* (2.9.), which is associated with *Macaranga* and broadly distributed in eastern tropical Asia. It is distinguishable from the latter in the submedian dorsal macroducts few and usually absent on the third and sixth abdominal segments, in the median trullae united by a well-developed basal zygosis, and in the lobules of the third trulla short and broad. It should be distinct from *A. pellucida* on account of its host association.

2.20. *Aulacaspis enkleiae*, n. sp. (Figs 37, 38)

Material. Collected in Malaysia on *Enkleia malaccensis* (Thymelaeaceae). Cape Rachado, Negeri Sembilan, Malaya, 10.XI.1986 [lot no.: 86ML-442]. Kabili-Sepilok Forest Reserve, Sabah (northeastern Borneo), 16.XI.1988 [88ML-366]. Bako National Park, Sarawak (northwestern Borneo), 10.XI.1991 [91ML-106]. Females occurring on twigs [88ML-366]; females and males occurring on the lower surface of leaves [86ML-442, 91ML-106]. Holotype, from [88ML-366]: FRIM.

Ramicolous adult females from the Kabili-Sepilok Forest Reserve. Body of the *vitis*-type at full growth, attaining about 1250μ in length, pygidium nearly triangular in outline, slightly roundish marginally, about 255–285μm long. Interantennal tubercle usually present, often divided into a pair of swellings; interantennal derm pockets often present. Anterior spiracles each with 6–35, mean 16.3 (n=39), disc pores; posterior spiracles each with 1–4, mean 1.6 (n=40), disc pores anteriorly. Perivulvar disc pores 7–24 in median, 21–34 in each anterolateral, and 14–30 in each posterolateral group; total 86–135, mean 114.0 (n=20). Abd II with 4–8 macroducts and 2–7 gland spines on lateral lobe; III with 3–6 macroducts and 3–10 gland spines on margin of lateral lobe; IV with 2–4, usually (83%, n=40) 2, gland spines. Total of lateral macroducts on each side 7–13, mean 10.6 (n=40). Total of lateral gland spines on each side 6–14, mean 10.1 (n=39). Submedian macroducts 1 or 2 on III, 1–4 on IV, usually (95%, n=40) 1, rarely 2 or

absent, on V, and usually (85%, n=40) absent, at times 1, on VI. Submarginal macroducts 3–7 on abd III, 2–5 on IV, 1 or 2, usually (85%, n=40) 2, on V. Total of dorsal macroducts on both sides 20–35, mean 26.4 (n=20). Median trullae very large relative to lateral trullae, forming a notch at apex of pygidium, with apical half produced; separated from each other by a narrow space basally; each nearly triangular, blunt apically, minutely serrate on mesal and lateral margins; basal zygosis strongly developed. Lateral trullae well represented, but with lobules rather short and broad, minutely serrate; mesal lobule of second trulla without distinct linear scleroses basally. Pygidial margin of abd IV and V with no prominent processes.

Foliicolous adult females from the Bako National Park. Four specimens are available, all in poor condition. Anterior spiracles each with about 6–12 disc pores (not always counted exactly); posterior spiracles with 1 or 2 disc pores. Perivulvar disc pores 8–12 in median, 7–23 in each anterolateral, and 9–17 in each posterolateral group; total 63–80, mean 69.5 (n=4). Lateral macroducts and lateral gland spines on abd II and III not exactly countable; abd IV with 2 or 3 gland spines marginally. Submedian macroducts 1 on abd III, 1 or 2 on each of IV and V, and 1 on VI. Submarginal macroducts 2 or 3 on each of abd III and IV, 2 (in 6 out of 8 cases), or 1 or absent, on VI. Total of dorsal macroducts 20–26, mean 23.5 (n=4). Trullae characterized nearly the same as those in the ramicolous specimens from the Kabili-Sepilok Forest Reserve.

A single foliicolous specimen of the adult female was mounted from the material collected at Cape Rachado, Malaya. It is characterized substantially the same as the foliicolous specimens from the Bako National Park.

Ramicolous and foliicolous forms. The foliicolous specimens have the perivulvar disc pores apparently fewer than in the ramicolous specimens, but it is not certain whether this difference is due to the feeding sites or to the collection localities, because none of the samples has both ramicolous and foliicolous forms. In other characters, these forms are not appreciably different.

Recognition characters (foliicolous and ramicolous adult females). Body of the *vitis*-type. Posterior spiracles each with 1 or a few disc pores anteriorly. Submedian macroducts occurring on abd III–V and at times on VI, very few on each segment. Submarginal macroducts on abd III–V. Median and lateral trullae minutely serrate. Median trullae very large relative to lateral trullae, robust, nearly triangular, with apical half produced; basal zygosis strongly developed. Lateral trullae with lobules rather short and broad.

Remarks. Among the species of the *vitis*-type, this species is well characterized by the median trullae, which are robust and shaped nearly triangular, with the apical half produced beyond the apex of the pygidium.

2.21. *Aulacaspis artocarpi*, n. sp. (Fig. 39)

Material. Collected in the grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaya, Malaysia, on *Artocarpus elasticus* (Moraceae), 1.XI.1986 and 2.XI.1986 [lot no.: 86ML-382 and –390]. Females and males on the upper and lower surfaces of leaves. Female tests small, oblong, irregular in outline; male tests tricarinate. Twenty specimens of the adult female mounted from the lot [86ML-382] and five from [86ML-390] have been examined. They apparently belong to the same local population, so that they are united together in the description. Holotype, from [86ML-382]: FRIM.

Adult females. Body fusiform, with meso- and metathorax tending to be irregularly expanded laterally at full growth, attaining about 1000μm in length; pygidium triangular in outline, about 160–170μm long. Interantennal tubercle well represented, complete or divided into a pair of swellings; interantennal derm pockets often present. Anterior spiracles each accompanied with 3–6, mean 4.4 (n=45), disc pores; posterior spiracles with no disc pores. Perivulvar disc pores 5–12 in median, 8–16 in each anterolateral, and 4–11 in each posterolateral group; total 42–52, mean 47.0 (n=25). Abd II usually (94%, n=49) with no macroducts, at times with 1, and usually (75%, n=48) with no gland spines, at times with 1–3, on lateral lobe; III with 1–5, mean 2.7 (n=49), macroducts and 2–5, mean 3.0 (n=48), gland spines on margin of lateral lobe. Abd IV with 1–3, usually 2 or 3, gland spines marginally. Submedian macroducts 1 present (50%, n=48) or none on abd III, 1 (90%, n=48) or 2 on IV, 1 (86%, n=48) or 2 on V, absent on VI. Submarginal macroducts 1–3 on each of III and IV, 1 or 2 on V. Total of dorsal macroducts on both sides 10–20, mean 14.3 (n=24). Median trullae a little larger than lobules of lateral trullae, sunken into apex of pygidium, forming a small notch on the latter, separated from each other by a good space basally, then gently divergent, dilated apicad, rounded apically, notched several times on mesal margin and once on lateral side; basal zygosis represented by a pair of small sclerites separated from each other and united with a pair of linear scleroses extending anteriorly on ventral surface of pygidium. Second trullae with lobules blunt apically, notched once on mesal side and several times on lateral side, each with a pair of linear scleroses basally. Third trullae with lobules similar to those of the second in size and shape. Pygidial margin of abd V with 3 low serrate prominences.

Recognition characters (foliicolous adult female). Body nearly fusiform, with meso- and metathorax tending to be irregularly expanded laterally at full growth. Interantennal tubercle well represented, often accompanied with interantennal derm pockets. Anterior spiracles each with a small cluster of disc pores; posterior spiracles with no disc pores. Abd II usually with no macroducts and no gland spines on lateral lobe. Dorsal macroducts occurring on abd III–V, very few, often lacking submedially on III. Median trullae a little larger than lobules of lateral trullae, separated from each other by a good space basally, dilated apicad, rounded apically, notched several times on mesal margin and once on lateral side; basal zygosis represented by a pair of small sclerites separated from each other and united with a pair of linear scleroses extending anteriorly. Lateral trullae with lobules notched several times on lateral side.

Remarks. This species is similar to *Aulacaspis mahangena* (2.11.), *Aulacaspis canarii* (2.13.), and *Aulacaspis canariicola* (2.14.) in body shape, in lacking macroducts and gland spines always or frequently on the lateral lobes of the second abdominal segment, and in having very few dorsal macroducts. It is easily distinguishable from the latter three in the median trullae small, being only a little larger than the lobules of the lateral trullae, and, in this respect, it may be closely related to none of them

3. Undetermined atypical species of *Aulacaspis*

One of the following three species may be identical with a certain named species but is not determined. The other two are probably new species, but the specimens are too poor in condition.

3.1. *Aulacaspis* 88Kn-*Ap* (Fig. 40)

Material. Collected on Mt. Kinabalu, alt. 1780m, Sabah (northeastern Borneo), Malaysia, on *Actinodaphne pruinosa* (Lauraceae), 12.X.1988 [lot no.: 88ML-142]. Three foliicolous specimens of the adult female are available, but they are not in good condition.

Remarks. One of the specimens, better in condition, is elongate, 1420μm long, broadest and 580μm wide across the mesothorax, a little constricted on the first abdominal segment (460μm wide), and membranous in the prepygidial region. It appears to represent a full-grown adult female. It is similar to the specimens of *Aulacaspis loranthi* (2.2.) in the outline of the body, in the arrangement of the dorsal macroducts, and in the median trullae and other pygidial margin, but differs from the latter in the prepygidial derm wholly membranous, without sclerotic patches and spots, in the segmental boundaries including those of the mesothorax not distinct, in having a pair of interantennal derm pockets, and in having more numerous disc pores associated with the posterior spiracles. It is distinct from *A. loranthi* in the first instar, in which it has five-segmented antennae and *A. loranthi* six-segmented antennae (see 6.2.).

3.2. *Aulacaspis* 65FCH-*Be* (Fig. 41)

Material. Collected at Fenchihu, Taiwan, on *Beilschmiedia erythrophloia* (Lauraceae), 12.IV.1965. A single foliicolous specimen of the adult female is available; its test was circular in outline, with the exuvial casts central. This specimen was described under '*Chionaspis* sp.' by Takagi (1970, p. 79), and was remounted for the present study.

Remarks. The available specimen has the cephalothorax somewhat expanded. It may be identified with *Diaspis machilicola* (5.6.) or *Diaspis machilicola* var. *cinnamomicola* (5.1.), both these forms having been described by Takahashi (1935) from Taiwan. It is noteworthy that *D. m*. var. *cinnamomicola* was described from '*Cinnamomum erythrophloia*' (=*Beilschmiedia erythrophloia*), the same plant species as the host of the present specimen.

3.3. *Aulacaspis* 85Ps-*N* (Fig. 42)

Material. Collected at the Pasoh Forest Reserve, Negeri Sembilan, Malaya, Malaysia, on *Neoscortechinia* sp. (Euphorbiaceae), 26.XI.1985 [lot no.: 85ML-35]. Females on the upper and males on the lower surface of leaves. Two mounted adult females are available for study. They are very poor in condition, apparently having been collected at some time after their death on the host plant.

Remarks. This species is characterized by having the cephalothorax swollen into a nearly round mass. The swollen region includes the metathorax, thus differing from the swollen prosoma in the typical species of *Aulacaspis*. One of the specimens has submedian macroducts on the first to sixth abdominal segments and submarginal macroducts on the second to fifth. It seems that the other specimen has no macroducts on the first segment. These specimens probably represent an undescribed species.

4. Other Atypical Species of *Aulacaspis*

I described the following seven species in previous papers, so that they are noted

here only briefly. My study on one of them, *Aulacaspis vitis*, was incomplete, leaving many specimens not definitely identified with it. Two other species, *Aulacaspis kuzunoi* and *Aulacaspis uenoi*, are referred to the genus rather tentatively. (As to *A. uenoi*, see 6.2.)

4.1. *Aulacaspis calcarata*

Aulacaspis vitis: Williams and Watson, 1988: 76 [Papua New Guinea, on *Durio zibethinus*].

Aulacaspis calcarata Takagi, 1999: 137 [Malaya, Sarawak, Sabah, and Luzón, on plants belonging to 12 families].

Material. Specimens newly mounted in the present study from the following material collected in Malaysia are referable to *Aulacaspis calcarata.*

Malaya. Gunong Jerai (altitude not recorded), Kedah, on *Canarium littorale* (Burseraceae), 8.XI.1991 [lot no.: 91ML-370]. Grounds of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, on *Litsea spathacea* (Lauraceae), 30.VII.1990 [90ML-362]. Bukit Nanas, Kuala Lumpur, on *Litsea umbellata*, 31.VII.1990 and 5.VIII.1990 [90ML-391, -392, -425]. Kuantan, Pahang, on *Linostoma pauciflorum* (Thymelaeaceae), 6.VII.1990 [90ML-107]; on *Canarium patentinervium*, 6.VII.1990 and 10.VII.1990 [90ML-111, -176]; on *Dacryodes rostrata* (Burseraceae), 6.VII.1990 [90ML-118]; on *Rourea rugosa* (Connaraceae), 15.VIII.1990 [90ML-518].

Sarawak. Santubong, on *Rourea minor*, 24.X.1991 [91ML-267].

Sabah. Sepilok, on *Archidendron* sp. (Fabaceae), 2.XI.1988 [88ML-244].

Remarks. This species as originally described belongs to the *vitis*-type in body shape. In the present study, two forms (4.1.1. and 4.1.2.) having other body shapes should be treated under *A. calcarata*.

4.1.1. *Aulacaspis* 90KD-*Lp* (Fig. 43)

Material. Kuala Dungun, Terengganu, Malaya, Malaysia, on *Linostoma pauciflorum* (Thymelaeaceae), 18.VII.1990 [lot no.: 90ML-258]. Female and male tests occurring on the upper surface of leaves (male tests on the lower surface, too); female tests narrow, somewhat variable in width, gently convex dorsally, with exuvial casts terminal.

Remarks. Eight specimens of the adult female have been examined. They are apparently fully grown, being about 1100μm long at maximum, but elongate fusiform and about 2.6–3.0 times as long as wide. Their second-instar exuvial casts are also narrow, being about twice as long as wide. In the other characters this form is not distinguishable from *Aulacaspis calcarata.* (See also 4.1.2. and 6.1.)

It should be added that the sample from the lot [90ML-107] (see 4.1.; Kuantan, on *Linostoma pauciflorum*, the same plant species as the host of *A.* 90KD-*Lp*) is definitely referable to *A. calcarata*, the adult females growing to the *vitis*-type and the second-instar exuvial casts being about 1.5–1.7 times as long as wide.

4.1.2. *Aulacaspis* 91BP-*Dg* (Fig. 44)

Material. Bukit Perangin, Sik, Kedah, Malaya, Malaysia, on *Durio griffithii* (Bombacaceae), 9.XI.1991 [lot no.: 91ML-375]. Females and males occurring on the upper surface of leaves; female tests occurring exclusively along the leaf margin, slender, with the exuvial casts terminal and brownish to blackish.

Remarks. About a dozen of full-grown adult females were mounted, but they are not in good condition, having been collected probably at some time after their death on the host plant. They are much elongated and slender, being 910–1330μm long and about 3.3–4.7 times as long as wide. Their second-instar exuvual casts are also very narrow, being about 2.6–2.8 times as long as wide. This elongation of the body, not only in the adult female but also in the second-instar female, may be due to ecophenotypic effect at least to some degree, because the individuals occurred on the leaf margin. If this supposition is correct, it is possible that *A.* 91BP-*Dg* is an ecophenotypic form of *Aulacaspis* 90KD-*Lp* (4.1.1.). Except for the body elongation in the adult and second-instar female stages, both these forms are not distinguishable from *Aulacaspis calcarata* (4.1.), and may be referred to the latter tentatively. (See also 6.1.)

4.2. *Aulacaspis kuzunoi*

Aulacaspis kuzunoi Kuwana and Muramatsu, 1932: 99 [‘On *Miscanthus*, Moji.’ Japan].

Phenacaspis susukicola Siraiwa, 1939: 17 [‘Host: On under surface of leaf sheaths of *Miscanthus sinensis* Anders (Susuki). Locality: Kôyô-yen, Mt. Rokko, Hyôgo-ken …’ Japan].

Miscanthaspis kuzunoi: Takagi, 1961: 70 [‘Amami- Ôsima, on *Miscanthus* sp.; Hatizyô-zima, on *Miscanthus* sp.’ Japan; type species of *Miscanthaspis*].

Remarks. This species has a slender body, which is a little broadened towards the caudal angles of the prosoma and slightly constricted across the first abdominal segment. It may represent an attenuated form of the *rosae*-type. It is not only noticeably different from the typical species of *Aulacaspis* in the body shape of the adult female but also peculiar in the first instar in having the basal antennal segment produced anteriorly to form a conical process.

4.3. *Aulacaspis marginata*

Aulacaspis marginata Takagi, 1999: 140 [Malaya and Palawan, on *Litsea castanea* and other various plants].

Remarks. This species belongs to the *calcarata* species group, and the body of the full-grown adult female is of the *vitis*-type. This species is probably broadly distributed in eastern tropical Asia, occurring on diverse plants including durian.

4.4. *Aulacaspis marina*

Aulacaspis marina Takagi and Williams, 1998: 53 [Bali, Palawan, and Malaya, on *Rhizophora apiculata* and *R. mucronata*].

Aulacaspis marina: Takagi, in Takagi and De Faveri, 2009 [Bali, Java, and Sulawesi, on *Xylocarpus granatum* and *Rhizophora mucronata*].

Remarks. This species is of the *vitis*-type in body shape, and is very similar to *Aulacaspis vitis* in the adult female but easily distinguishable in the second-instar male. It is associated with mangroves.

4.5. *Aulacaspis schizosoma*

Chionaspis schizosoma Takagi, 1970: 77 [Taiwan, on *Machilus japonica* and *M. kusanoi*].

Superturmaspis schizosoma: Chen, 1983: 86 [Continental China: Sichuan, Yunnan, Guizhou, Guangxi, and Fujian, on *Phoebe nanmu*, *Cinnamomum camphora*, and *Elaeagnus pungens*; type species of *Superturmaspis*].

Semichionaspis schizosoma: Tang, 1985: 170 [Continental China; type species of *Semichionaspis*].

Aulacaspis schizosoma: Takagi, 1999: 145 [Nepal, on *Dodecadenia grandiflora*].

Remarks. The adult female grows to the *vitis*-type. The exuvial cast of the second-instar female has a pair of deep notches on the thoracic margin. It seems that this species is distributed in a broad subtropical region of Asia from Taiwan to the Himalayas.

4.6. *Aulacaspis uenoi*

Chionaspis uenoi Takagi, 1970: 74 [‘Fen-chi-hu, on *Lindera communis*.’ Taiwan].

Aulacaspis uenoi: Takagi, 1985: 50.

Aulacaspis uenoi: Takagi, 1999: 146 [‘… it has six-segmented antennae in the first instar.’].

Remarks. This species was described on the basis of a few specimens, which suggest that it grows to the *vitis*-type in body shape. It may be closely related to *Aulacaspis machili*. (See also 6.2.)

4.7. *Aulacaspis vitis*

Chionaspis vitis Green, 1896: 3.

Chionaspis vitis: Green, 1899: 140 [Sri Lanka, on *Vitis lanceolaria*, *Elaeagnus latifolia*, and *Loranthus* sp.].

Aulacaspis vitis: Takagi, 1985: 50.

Aulacaspis vitis: Takagi and Williams, 1998: 57 [Sri Lanka, on *Vitis* sp. and *Elaeagnus latifolia*; Nilgiri Hills, Tamil Nadu, India, on a species of the Vitaceae and *Elaeagnus conferta* (=*E. latifolia*)].

Remarks. Chionaspis vitis or *Phenacaspis vitis* were recorded by authors from many localities in tropical Asia and from various plants, but many of these records may not be acceptable without critical re-examinations of specimens. A large number of specimens collected in tropical Asia on diverse plants were once examined on the supposition that they are referable or closely related to *Aulacaspis vitis*, but were left undetermined (for a summary of the examination, see Takagi and Williams, 1998).

5. Other Published Names Combinable with *Aulacaspis*

Ten names are mentioned in this section, but the species these names indicate are not clear to me. Some of them are combined with *Aulacaspis* only tentatively.

5.1. *Aulacaspis cinnamomicola*

Diaspis machilicola var. *cinnamomicola* Takahashi, 1935: 15 [‘Host.–*Cinnamomum erythrophloia*, attacking leaf and branch. Hab.–Kussha near Shikikun (Taihoku Prefecture).’ Taiwan].

Remarks. It is possible that *Aulacaspis* 65FCH-*Be* (3.2.; Fig. 42) is identical with *Diaspis machilicola* var. *cinnamomicola.* So far as based on the description, however,

var. *cinnamomicola* does not appear to be clearly distinguishable from *Diaspis machilicola* (5.6.).

5.2. *Aulacaspis depressa*

Chionaspis depressa Zehntner, 1897: 20 [East Java, on *Saccharum ciliare*].

Aulacaspis depressa: Takagi, 1985: 45.

Remarks. If this species is correctly referred to *Aulacaspis*, it should represent an attenuated form of the *rosae*-type.

5.3. *Aulacaspis elaeagni*

Chionaspis elaeagni Green, 1896: 3.

Chionaspis elaeagni: Green, 1899: 138 [‘Habitat on under surface of leaves of *Elaeagnus latifolia*; Pundaluoya.’ Sri Lanka].

Phenacaspis elaeagni: Ferris, 1955: 48 [‘There are available two specimens of this species from Ceylon, these in the Koebele Collection, which may have come from Green’].

Aulacaspis elaeagni: Takagi, 1985: 45.

Remarks. Pl. XLVI, Fig. 3 (‘Adult female, after oviposition’) and Fig. 6 (‘Adult female, before oviposition’) in Green (1899) suggest that this species grows to the *vitis*-type in body shape. The specimens Ferris (1955) examined should be immature adult females, because his figure shows only a sligtht expansion of the mesothorax.

5.4. *Aulacaspis formosana*

Phenacaspis formosana Takahashi, 1934: 7 [‘Host.–*Wikstroemia* sp., attacking the lower side of leaf. Hab.–Ikenohata (Rato-Gun).’ Taiwan].

Aulacaspis formosana: Takagi, 1985: 46.

Remarks. This species is referable to *Aulacaspis*, ‘the basal abdominal segment lacking lateral glands as large as those on the posterior segments’. The body is ‘Oblong’, with the ‘Cephalothorax a little wider than the abdomen’.

5.5. *Aulacaspis hedyotidis*

Chionaspis hedyotidis Green, 1899: 142 [‘Habitat on *Hedyotis auricularia* and other allied species. … Pundaluoya. Specimens of *Hedyotis Lawsoniae* have been received from Nuwara Eliya, …’ Sri Lanka].

Aulacaspis hedyotidis: Takagi, 1985: 46.

Remarks. Chionaspis hedyotidis may be very similar to *Aulacaspis* 90KD-*Lp* (4.1.1.), which is tentatively united with *Aulacaspis calcarata* (4.1.) in this study. According to Green (1899), *C. hedyotidis* has disc pores associated with both pairs of spiracles (‘Parastigmatic glands at each spiracle.’), whereas *A.* 90KD-*Lp* has no disc pores associated with the posterior spiracles. If this difference is real, these forms should not belong to the same species, because the presence or absence of disc pores at the posterior spiracles is considerably stable in general. By the same reason, *Aulacaspis* 91BP-*Dg* (4.1.2.; united with *A. calcarata*, 4.1.) also should be different from *C. hedyotidis* specifically.

C. hedyotidis may also be compared with *Aulacaspis elongata* (2.16.) on the supposition that the latter represents an ecophenotypically elongated form of the former. The figure given by Green (1899) does not show any spur-like processes on the pygidium of *C. hedyotidis*. If this state is real, *C. hedyotidis* should have no close relationship to *A. elongata.*

'*Phenacaspis hedyotidis* Green' was recorded 'on a tree of the Lauraceae ?' in Thailand (Takahashi, 1942), and as occurring on durian, *Durio zibethinus*, in Malaya (Yunus and Ho, 1980). The record from durian is noteworthy, because *A. calcarata*, a polyphagous species, occurs on durian and *A.* 91BP-*Dg* is known from a plant of the durian genus.

C. hedyotidis is undoubtedly an atypical species of *Aulacaspis*. The relationships among *A. hedyotidis*, *A.* 91BP-*Dg*, *A.* 90KD-*Lp*, and *A. calcarata* remain to be examined.

5.6. *Aulacaspis machilicola*

Diaspis machilicola Takahashi, 1935: 13 ['Host.–*Machilus* sp., attacking the basal part of stem. Hab.–Chipponsan (Taito Province).' Taiwan].

Remarks. This species is referable to *Aulacaspis*, the 'Basal abdominal segment … lacking lateral glands and spines'. The body is 'Oblong, broadest on the meso- or metathorax, gradually narrowed towards the pygidium'. *Diaspis machilicola* was distinguished from *Diaspis machili* (*Aulacaspis machili* in the present study; 2.7.) in having many dorsal macroducts on the second abdominal segment and in other characters. It is possible that *Aulacaspis* 65HCF-*Be* (3.2.; Fig. 42) is identical with *A. machilicola* or *A. cinnamomicola* (5.1.).

5.7. *Aulacaspis oblonga*

Duplachionaspis oblonga Chen, 1983: 60 [Yunnan, China, on an undetermined plant].

Aulacaspis oblonga: Takagi, in Takagi and De Faveri, 2009: 114.

Remarks. The host plant of this species is unknown, but it is presumably not a grass. The exclusion of the species from *Duplachionaspis* is based on the view that the species of that genus should be associated with monocotyledonous grasses and especially with Poaceae. Fig. 39 in Chen (1983) apparently shows a teneral adult female, and the body shape of the full-grown female is unknown.

5.8. *Aulacaspis polygoni* (Fig. 6)

Chionaspis polygoni Green, 1899: 134 ['Habitat on stems on *Polygonum chinense*. Pundaluoya.' Sri Lanka].

Pseudaulacaspis polygoni: Takagi, 1985: 48.

Remarks. I once referred this species to *Pseudaulacaspis*. Dr D. J. Williams figured this species apparently on the basis of a specimen from Green's material. Looking into his figure (Fig. 6), I have been convinced that this species is more probably a member of *Aulacaspis*. It has a few macroducts and many long gland spines on the lateral lobes of the second and third abdominal segments, while having none on the preceding segments. The body of the adult female is broadly fusiform (Green, 1899, Pl. XLIV) or narrowly ovate (Fig. 6).

5.9. *Aulacaspis pudica*

Phenacaspis pudica Ferris, 1953; 65 [‘From *Quercus sinensis*, at Si-shan, Kunming, Yunnan Province, China, … Occurring on the underside of the leaves, the adult female buried beneath the very thick tomentum’].

Aulacaspis pudica: Takagi, 1985: 48.

Remarks. This species is peculiar, being very small in body size and having no lateral macroducts and no lateral gland spines on all the prepygidial segments. It represents a simplified dwarf form apparently adapted to cryptic living under the leaf tomentum. *Phenacaspis* being no longer a taxon, the species needs a genus that may harbour it. It apparently belongs to the Chionaspidina. I once supposed that it was referable to *Aulacaspis*. In fact, a few species referred to *Aulacaspis* in the present study come near this species in the lateral macroducts and gland spines obsolete except those remaining on the third abdominal segment. However, it is also possible that this species belongs to *Chionaspis*, because there are many oak-associated species of *Chionaspis* in Asia. (See 2.17. and 6.3.)

5.10. *Aulacaspis yunnanensis*

Duplachionaspis yunnanensis Feng et al., 2004: 21 [‘Dawei mountain, Hekou, Yunnan Province, China, … Host: *Ficus carica* L. …’].

Aulacaspis yunnanensis: Takagi, in Takagi and De Faveri, 2009: 115.

Remarks. This species apparently belongs to the *vitis*-type in body shape, and may be close to *Aulacaspis marginata* (4.3.).

6. Concluding Remarks

6.1. Emergence of different body shapes in *Aulacaspis*

In the diaspidids except the pupillarial ones, the body of the adult female starts its growth under the second-instar exuvial cast, conforming with the latter in outline at that time. It grows outside the exuvial cast, increasing in size and changing in shape, and ultimately assumes the shape characteristic of the species concerned. This process is not always completed for some reason or other, and the body may fail to assume the ultimate shape. In the *Aulacaspis* species of the *vitis*-type, apparently fully grown adult females sometimes remain obovate, oblong, or even fusiform. In the species of the *rosae*-type, endoparasitic wasps sometimes suppress the enlargement of the prosoma. The different body shapes in the adult females of *Aulacaspis* are largely formed during this stage through the developmental process, which should be plastic in the evolutionary course, too.

The *calcarata* species group of *Aulacaspis* was composed of seven species; five of them belong to the *rosae*-type and the other two, *Aulacaspis calcarata* (4.1.) and *Aulacaspis marginata* (4.3.), to the *vitis*-type, the adult females being mushroom-shaped in the *rosae*-type and roughly rhombic in the *vitis*-type in the outline of the body at full growth (Takagi, 1999). In spite of the different body shapes, all these species agree in having an unusual character, the occurrence of a small but distinct spur-like marginal process (sometimes replaced with a few small triangular processes) on each of the fourth

and fifth abdominal segments. They are similar to each other also in the characters of the median trullae in the foliicolous forms.

Among the species described in this paper, two species, *Aulacaspis canariiphila* (2.15.) and *Aulacaspis elongata* (2.16.), are similar to the species of the *calcarata* group in having spur-like processes on the pygidial margin. Both these species are represented by the foliicolous forms, which differ from the foliicolous forms of the species of the group in having the median trullae usually well zygotic basally. However, because the occurrence of the spur-like processes is not a usual character in the genus, these two species should tentatively be referred to the *calcarata* species group. Furthermore, in the ramicolous individuals of *A. calcarata* the median trullae are strongly zygotic basally (Takagi, 1999, Fig. 4, Ea). *A. canariiphila* belongs to the *vitis*-type, whereas the full-grown adult female of *A. elongata* is elongate and slender.

If the *calcarata* species group as composed above is really a natural one and the species of the group are, therefore, related to each other more closely than to species outside the group, the diversity in body shape should have emerged within the group. The supposition may be adopted that the ancestral form of the group was fusiform in body shape and provided with spur-like processes on the pygidial margin. This supposition may be reasonable, because the fusiform body is common in the Diaspidinae, and also because the apparently fully grown and yet elongate fusiform adult females of the sample *Aulacaspis* 90KD-*Lp* (4.1.1.) are very similar to *A. calcarata* and have tentatively been referred to the latter. (The form *A.* 90KD-*Lp* may substitute for the supposed ancestral form.) Each of the mushroom-shaped and rhombic bodies is derivable from the ancestral form by enhancing or accelerating the growth of the prosoma or of the meso- and metathorax. The body shape of the *rosae*-type is also derivable from the *vitis*-type by combining partial acceleration with partial suppression in somatic growth (Takagi, 1999, p. 152). The elongate and slender body is producible simply by accelerating the growth of the prepygidial region along the longitudinal axis of the body, and such elongated bodies are observed in various Diaspidinae. In *A. elongata* and *A.* 91BP-*Dg* (4.1.2.) the elongation takes its start in the second-instar nymphal stage (of which the exuvial casts are elongate fusiform) and continues during the growth of the adult female.

In the *calcarata* species group, the five species of the *rosae*-type are probably closely related to each other, all occurring on *Calophyllum* or *Mesua*, Clusiaceae. None of the other species of the *calcarata* group are associated with these plant genera, two species of the *vitis*-type occurring on other diverse plants. This fact suggests that, once the different body shapes were established in this species group, further speciation took place in each of the *rosae*- and *vitis*-type subgroups. It suggests also that there are in the genus other species groups that are composed of two or more body shape subgroups.

The species of the *rosae*- and *vitis*-type occupy a great part of the genus. The full-grown adult females of some atypical species are fusiform, oblong, or obovate, and such individuals are found also in the species of the *vitis*-type. The elongate and slender body, which is not rare in the Diaspidinae, is known also in *Aulacaspis* (*A. elongata* and *A.* 91BP-*Dg*) and is associated with the leaf veins or the leaf margin. *Aulacaspis gracilis* (2.1.) is apparently an extraordinarily slender form of the *rosae*-type, and *Aulacaspis kuzunoi* (4.2.) and *Aulacaspis depressa* (5.2.) may also be attenuated forms of that type. *Aulacaspis loranthi* (2.2.) is peculiar in the body nearly parallel-sided and in having a complete mesothorax. *Aulacaspis machili* (2.7.) and *Aulacaspis* 85Ps-*N* (3.3.) have the

cephalothorax swollen into a prominent mass, which is transversely oblong in the former and round in the latter at full growth and suggests accelerated growth in all of the head and the thoracic segments. *Aulacaspis digitifera* (2.8.) belongs to the *vitis*-type, but is unique in having the first abdominal segment produced to form prominent digitiform processes on both sides of the body; the adult females burrow under the leaf epidermis, and the view may be adopted that the digitiferous body represents a unique adaptation to burrowing. In *Aulacaspis macarangae* (2.11.) the body grows broadened especially in the thoracic region and swollen on the ventral side apparently in adaptation to living in a pit gall.

The typical species are much more numerous than the atypical species (see 6.4.), probably having ecological superiority over the species of the other body shapes. The *vitis*-type is common among the atypical species. The body shapes of the *rosae*- and *vitis*-type should have emerged many times in *Aulacaspis*. All the body shapes in the genus must have adaptive significance in association with the movement of the body in constructing the protective test, but we have only a poor knowledge about the movement of the body beneath the test under construction in various armoured scale insects.

It should be added that some of the atypical species are often provided with the interantennal tubercle or swellings and the interantennal derm pockets. These features occur also in *Myrtaspis*, which can be taken for a generalized relative of *Aulacaspis*, having a fusiform body with lateral macroducts and gland spines occurring on all the prepygidial abdominal segments. (For *Myrtaspis*, see Takagi, 1999, p. 147.)

6.2. Number of antennal segments in the first instar

Aulacaspis is closely related to *Myrtaspis*, whereas *Chionaspis* is supposed to have some relationship to *Narayanaspis*. In the first instar, the genera of the former pair have five-segmented antennae, whereas those of the latter pair agree in having six-segmented antennae (Takagi, 1999, p. 147).

The statement above about the number of the antennal segments in the first instar was a generalization based on my observations on many species but, of course, not on all species known at that time. In the present study, I have examined first-instar exuvial casts for the number of the antennal segments in 20 species. (Among the species 2.1.–2.21. and 3.1.–3.3., the four species 2.1., 2.6., 2.8., and 3.2. have no mounted exuvial casts or no exuvial casts in good condition.) The antennae are five-segmented in 15 species, but apparently six-segmented in the other five, *Aulacaspis loranthi* (2.2.), *A. litzeae* (2.3.), *A. machili* (2.7.), *A. katus* (2.17.), and *A. dilleniae* (2.18.). *A. uenoi* (4.6.) also has six-segmented antennae (Takagi, 1999, p. 146). *A. machili* and *A. uenoi* may be closely related to each other, but the six species as a whole do not seem to form a close group so far as based on their adult females. It is open to question whether all these species are correctly referred to *Aulacaspis*. There may be three ways to cope with this situation.

First, these species with six-segmented antennae may be returned or transferred to *Chionaspis*. The main difficulty encountered here is that these species more or less deviate from the usual species of *Chionaspis* in their body shapes. *A. loranthi* (apart from the possibility that it is conspecific with *A. peresnathae*; see *Remarks* for 2.2.) is unusual for a species of *Chionaspis* as well as of *Aulacaspis* in having a parallel-sided elongate body and a complete mesothoracic segment. *A. dilleniae* and *A. uenoi* belong to the *vitis*-type in body shape, and this type of body is not unusual among the atypical

species of *Aulacaspis*. *A. machili* often grows to a broad body with a transversely oblong cephalothorax. *A. litzeae* and *A. katus* are oblong or fusiform but, when fully grown, they have the mesothorax or the meso- and metathorax somewhat expanded laterally.

There is another matter. As stated above, these six species do not form their own group. If they are really members of *Chionaspis*, it follows that the localization of the lateral macroducts and gland spines, an unusual character adopted as a dignostic one of *Aulacaspis*, was acquired also in *Chionaspis* and more than once among the species, but this consequence may not readily be accepted. Furthermore, when the six species are referred to *Chionaspis*, there is available no clue for distinguishing between *Aulacaspis* and *Chionaspis* in the stage of the adult female.

Secondly, the six species may be referred neither to *Aulacaspis* nor to *Chionaspis*. If *A. loranthi* has nothing to do with *A. peresnathae* (*Remarks* for 2.2.), it may be supposed to have its own genus especially on account of the complete mesothoracic segment. However, it is practically impossible to imagine any particular genera for the acceptance of the other species, of which the adult females are not so uniquely characterized as *A. loranthi*.

Thirdly, all the six species may be retained in *Aulacaspis*, with some reason adduced in support of the retainment. The *calcarata* species group, when accepted as a natural one, shows that the genus is remarkably variable in the body shape of the full-grown adult female. There is no pre-existing principle that the species of a genus should be highly uniform in the nymphal stages as well as in the adult female. *Aulacaspis* 88Kn-*Ap* (3.1.) is similar to *A. loranthi* (2.2.) so far as compared with the latter in the adult female, but differs from the latter in having five-segmented antennae in the first instar. If they are closely related to each other, they suggest that the number of the antennal segments sometimes changes between related species. Similar cases are needed, including other genera (for example, *Rutherfordia*; see Takagi et al., 1989), in order to admit this possibility.

I once had the view that the antennae of the first instar nymphs should be five-segmented in the Diaspidini (in contrast with the six-segmented antennae of the Lepidosaphidini), and that they may sometimes appear to have six or more segments owing to the presence of one or more deep infrasegmental constrictions. Later, by the use of a more powerful microscope, I was convinced that the antennae were definitely six-segmented in some Diaspidini. However, to determine the number of the antennal segments in Diaspidini is still not always easy when mounted specimens (often exuvial casts) are not in good condition. I do not think that all published figures of the antennae of the first-instar nymphs of Diaspidini, drawn by authors, are exact and reliable in showing the number of the segments.

A plausible evolutionary change in the number of the antennal segments may be a reduction, from six to five. However, the occasional occurrence of the reverse change, from five to six, may also reasonably be supposed, because reversals in individual characters are not rare in plants and animals. (Moreover, the concept of modular gene expression is congruent with the supposition that atavistic forms reflecting ancestral character patterns sometimes emerge abruptly. The second-instar males of some diaspidids exhibit quite different character patterns within the same genera, and this phenomenon should involve atavism.)

In diaspidid taxonomy, nymphal characters have positively been adopted not long enough except for those of the second-instar females (usually their exuvial casts)

especially in pupillarial forms. In general, our knowledge on them is still fragmentary and not well built up for taxonomic evaluation. In this situation, the purpose of this section of the paper is to explain the debatable point, not to give any definite conclusion for it.

6.3. Host plants

The typical species of *Aulacaspis* as a whole occur on diverse plants, but are restricted to angiosperms except for one species associated with cycads exclusively (and occasional records of a few species from cycads). A considerable part of them are associated with lauraceous plants exclusively, frequently, or occasionally. Some species are associated with poaceous grasses.

The same holds true for the atypical species dealt with in this paper. All these species occur on angiosperms, one-third of them are associated with lauraceous plants exclusively so far as known, and two species with poaceous plants. This is harmonious with the view that the atypical species are part of *Aulacaspis* and related to the typical species in various ways to form an indivisible taxon.

However, two atypical species are especially noteworthy for their association with the family Fagaceae, from which many species of *Chionaspis* occurring in Asia but no typical *Aulacaspis* species have been recorded (see 2.17. and 5.9.).

6.4. A summary

The total of the known species of *Aulacaspis* is calculated, as a trial, at 117, including the 17 new species and the three undetermined ones dealt with in this paper and two new species described in another paper, Takagi (2012). (It remains debatable whether the six species mentioned in the section 6.2. really belong to *Aulacaspis*. Possibly conspecific but indetermined forms are counted as different species, but such cases are few. On the other hand, there may exist unknown sibling species. *Aulacaspis vitis* and *Aulacaspis marina* are known siblings, which are clearly distinguishable from each other in the second-instar male but not easily in the adult female.) The 41 species enumerated as atypical in the present paper constitute 35% of the total. When undescribed typical species in my collection are added to the total, the proportion of the atypical species decreases. However, it is meaningless at present to give any exact percentage. Above all, it is not knowable how many species really exist in the genus. The number of the known species suggests that *Aulacaspis* is a considerably large genus. They concentrate in tropical and subtropical Asia and warm-temperate eastern Asia. These parts of the world cover the Indian, Malesian, and Sino-Japanese plant biogeographical regions all with rich florae and luxuriant forests, and are complicated in topography, embracing coastal and inland plains, highlands and undulating hills, huge mountains and great mountain ranges, and a vast extent in the Asian continent and a tremendous number of islands in the Malesian region. Moreover, many of these islands repeated their union and separation in the glacial and interglacial times. In a rough and probably very conservative estimation, there should exist three hundred species in the genus, and it may safely be assumed that at least one-fourth of them are atypical. The actual numbers of typical and atypical species may be considerably large. If the atypical species are correctly referable to *Aulacaspis*, they are to be connected with the typical

species on evolutionary grounds, which should involve developmental factors (partial acceleration in somatic growth, atavism, etc.) as well as behavioural and ecological ones (test construction, host association, competition, etc.).

At the conclusion of this paper, it should be added that the diagnostic description of the genus I once gave (Takagi, 1999) no longer completely covers the genus as understood in the present study. First, the full-grown adult females of the atypical species are more broadly diverse in body shape. Even the species of the *rosae*-type are various not only in the enlargement of the prosoma but also in the broadening of the prepygidial metasomatic segments, so that they also are not uniform in the outline of the body. Different body shapes are sometimes exhibited by presumably closely related species or even within the same species, definitely having no generic value under the latter circumstances. Second, the localization of the lateral macroducts and gland spines, which are restricted to the second and third abdominal segments, is still a diagnostic character of central importance, but occasionally this character is modified by the loss of macroducts or gland spines or both on the second segment. (A certain species tentatively referred to the genus has no lateral macroducts and gland spines on all the prepygidial segments). Third, the genus should include species with six-segmented antennae in the first instar. Last, my statement on the median trullae in the generic diagnosis is partly inadequate and misleading. These trullae also are various especially in their basal parts, where they are separated by a very slender space or definitely united together usually through a distinct sclerite (zygosis), which is various in shape and size and may correspond to a pair of small sclerites occurring on the bases of separated median trullae. Sometimes zygotic and non-zygotic median trullae occur within the same species in ecophenotypic or fluctuating individual variation and, in this feature, too, the contrasting states do not warrant generic separation.

References

Borchsenius, N. S., 1965. Essay on the classification of the armored scale insects (Homoptera, Coccoidea, Diaspididae). Revue d'Entomologie de l'URSS 44: 362–376.

Borchsenius, N. S., 1966. A Catalogue of the Armoured Scale Insects (Diaspidoidea) of the World. Nauk, 450pp.

Chen F.-G., 1983. The Chionaspidini (Diaspididae, Coccoidea, Homoptera) from China. Chengdu, 175pp.

Cockerell, T. D. A., 1893. Museum notes. Coccidae. Journal of the Institute of Jamaica 1: 180.

Cockerell, T. D. A., 1902. The coccid genus *Aulacaspis*. The Entomologist 35: 58–59.

Feng J.-n., Wang P.-m., Li L.-m., and Chou I., 2004. Two new species of the family Diaspididae (Homoptera: Diaspididae) from China. Entomotaxonomia 26: 19–22.

Ferris, G. F., 1937. Atlas of the Scale Insects of North America, I. Stanford University Press, serial no. 1–135.

Ferris, G. F., 1955. The genus *Phenacaspis* Cooley and Cockerell. Part I. Microentomology 20: 41–82.

Ferris, G. F., 1956. The genus *Phenacaspis* Cooley and Cockerell. Part II. Microentomology 21: 67–83.

Green, E. E., 1896. Catalog of Coccidae collected in Ceylon. Indian Museum Notes 4: 2–10.

Green, E. E., 1899. The Coccidae of Ceylon. Part II. London: Dulau, p. xiii–xli, 105–169, Pls XXXI–LX.
Green, E. E., 1900. Supplementary notes on the Coccidae of Ceylon. Journal of the Bombay Natural History Society 13: 66–76, Pls A–D, 252–257, Pls E–G.
Green, E. E., 1919. Notes on Indian Coccidae of the sub-family Diaspidinae, with descriptions of new species. Records of the Indian Museum 16: 433–449, Pls XXVI–XXXI.
Green, E. E., 1922. Coccidae of Ceyon. Part V. London: Dulau, p. 345–472, Pls CXXXIII–CXCIa.
Green, E. E., 1937. An annotated list of the Coccidae of Ceylon, with emendations and additions to date. Ceylon Journal of Science, Section B, Zoology and Geology 20: 277–341.
Heaney, L. R., 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. Biological Journal of the Linnean Society 28: 127–165.
Knipscher, R. C., Miller, D. R., and Davidson, J. A., 1976. Biosystematics of *Chionaspis nyssae* Comstock (Homoptera: Diaspididae), with evidence supporting leaf and bark dimorphism of the scale. Melanderia 25, 30pp.
Kuwana, I., 1926. The diaspine Coccidae of Japan, IV. Department of Finance, Japan, Imperial Plant Quarantine Service, Technical Bulletin 4. 44pp., Pls I–XII.
Kuwana, I. and Muramatsu, K., 1932. Three new species of the diaspine coccids from Japan. Journal of Plant Protection (Byô-Chû-Gai Zasshi) 19: 95–100, pl.
Liu, T.-X., Kosztarab, M., and Rhoades, M., 1989. Biosystematics of the adult females of the genus *Chionaspis* (Homoptera: Coccoidea: Diaspididae) of North America, with emphasis on polymorphism. Virginia Agricultural Experiment Station, Virginia Polytechnic Institute and State University, Bulletin 88-2: vi+126pp.
MacGillivray, A. D., 1921. The Coccidae: Tables for the Identification of the Subfamilies and Some of the Most Important Genera and Species together with Discussions of their Anatomy and Life History. Scarab Company, Illinois, viii+502pp.
Newstead, R., 1901. Monograph of the Coccidae of the British Isles I. Ray Society, London, xii+220pp., Pls A–E, I–XXXIV.
Robinson, E., 1917. Coccidae of the Philippine Islands. The Philippine Journal of Science D 12: 1–47, Pls I–VI.
Scott, C. L., 1952. The scale insect genus *Aulacaspis* in eastern Asia. Microentomology 17: 33–60.
Siraiwa, H., 1939. Two new scale insects from Japan. Transactions of the Kansai Entomological Society 9: 16–18, Pls I and II.
Takagi, S., 1961. A contribution to the knowledge of the Diaspidini of Japan (Homoptera: Coccoidea) Part III. Insecta Matsumurana 24: 69–103.
Takagi, S., 1967. An additional note on dimorphism in *Chionaspis nyssae*. Insecta Matsumurana, 30: 55–56.
Takagi, S., 1970. Diaspididae of Taiwan based on material collected in connection with the Japan-U.S. Co-operative Science Programme, 1965 (Homoptera: Coccoidea), II. Insecta Matsumurana 33, 146pp.
Takagi, S., 1985. The scale insect genus *Chionaspis*: A revised concept (Homoptera: Coccoidea: Diaspididae). Insecta Matsumurana New Series 33: 1–77.
Takagi, S., 1999. For a better understanding of *Aulacaspis*: The *calcarata* species group (Homoptera: Coccoidea: Diaspididae). Insecta Matsumurana New Series 55: 133–180.
Takagi, S., 2012. Two new species of *Aulacaspis* from Japan, with notes on a strange organ and seasonal variation (Sternorrhyncha: Coccoidea: Diaspididae). Insecta

Matsumurana New Series 68: 117–132, 8 figs.
Takagi, S. and De Faveri, S., 2009. Notes on scale insects of *Aulacaspis* associated with mangroves and cycads (Sternorrhyncha: Coccoidea: Diaspididae). Insecta Matsumurana New Series 65: 101–129.
Takagi, S. and Kawai, S., 1966. Some Diaspididae of Japan (Homoptera: Coccoidea). Insecta Matsumurana 28(2): 93–120, Pls XVII–XXVIII.
Takagi, S. and Kawai, S., 1967. The genera *Chionaspis* and *Pseudaulacaspis* with criticism on *Phenacaspis* (Homoptera: Coccoidea). Insecta Matsumurana 30: 29–43.
Takagi, S., Tho Y. P., and Khoo S. G., 1989. Beginning with *Diaulacaspis* (Homoptera: Coccoidea: Diaspididae): Convergence or effect? Insecta Matsumurana New Series 42: 143–199.
Takagi, S. and Williams, D. J., 1998. A new mangrove-infesting species of *Aulacaspis* occurring in South-east Asia, with a revision of *A. vitis* (Homoptera: Coccoidea: Diaspididae). Insecta Matsumurana New Series 54: 51–76.
Takahashi, R., 1931. Some Coccidae of Formosa. Transactions of the Natural History Society of Formosa 21: 1–5.
Takahashi, R., 1934. Observations on the Coccidae of Formosa. Part IV. Department of Agriculture, Government Research Institute, Formosa, Japan, Report 63: 1–38.
Takahashi, R., 1935. Observations on the Coccidae of Formosa. V. Department of Agriculture, Government Research Institute, Formosa, Japan, Report 66: 1–37.
Takahashi, R., 1942. Some injurious insects of agricultural plants and forest trees in Thailand and Indo-China, II Coccidae. Government Agricultural Research Institute, Taiwan, Nippon (Japan), Report 81, 56pp.
Takahashi, R., 1952. Descriptions of five new species of Diaspididae from Japan, with notes on dimorphism in *Chionaspis* or *Phenacaspis* (Coccoidea, Homoptera). Miscellaneous Reports of the Research Institute for Natural Resources 27: 7–15.
Takahashi, R., 1953. Dimorphism in some species of *Chionaspis* or *Phenacaspis* (Diaspididae, Coccoidea, Homoptera). Bollettino del Laboratorio di Zoologia Generale e Agraria《Filippo Silvestri》, Portici 33: 48–56.
Tang F.-t., 1986. The Scale Insects of Horticulture and Forest of China. Shanxi Agricultural University Press, 305pp.
Williams, D. J. and Watson, G. W., 1988. The Scale Insects of the Tropical South Pacific Region, Part I, The Armoured Scales (Diaspididae). CAB International Institute of Entomology, 289pp.
Yunus, A. and Ho T. H., 1980. List of Economic Pests, Host Plants, Parasites and Predators in West Malaysia (1920–1978). Ministry of Agriculture, Malaysia, 538pp.
Zehntner, L., 1897. De Plantenluizen van het Suikerriet op Java. II. *Chionaspis saccharifolii* n. sp. III. *Chionaspis depressa* n. sp. Mededeelingen van het Proefstation Oost-Java, Nieuwe Serie 36: 1–26.

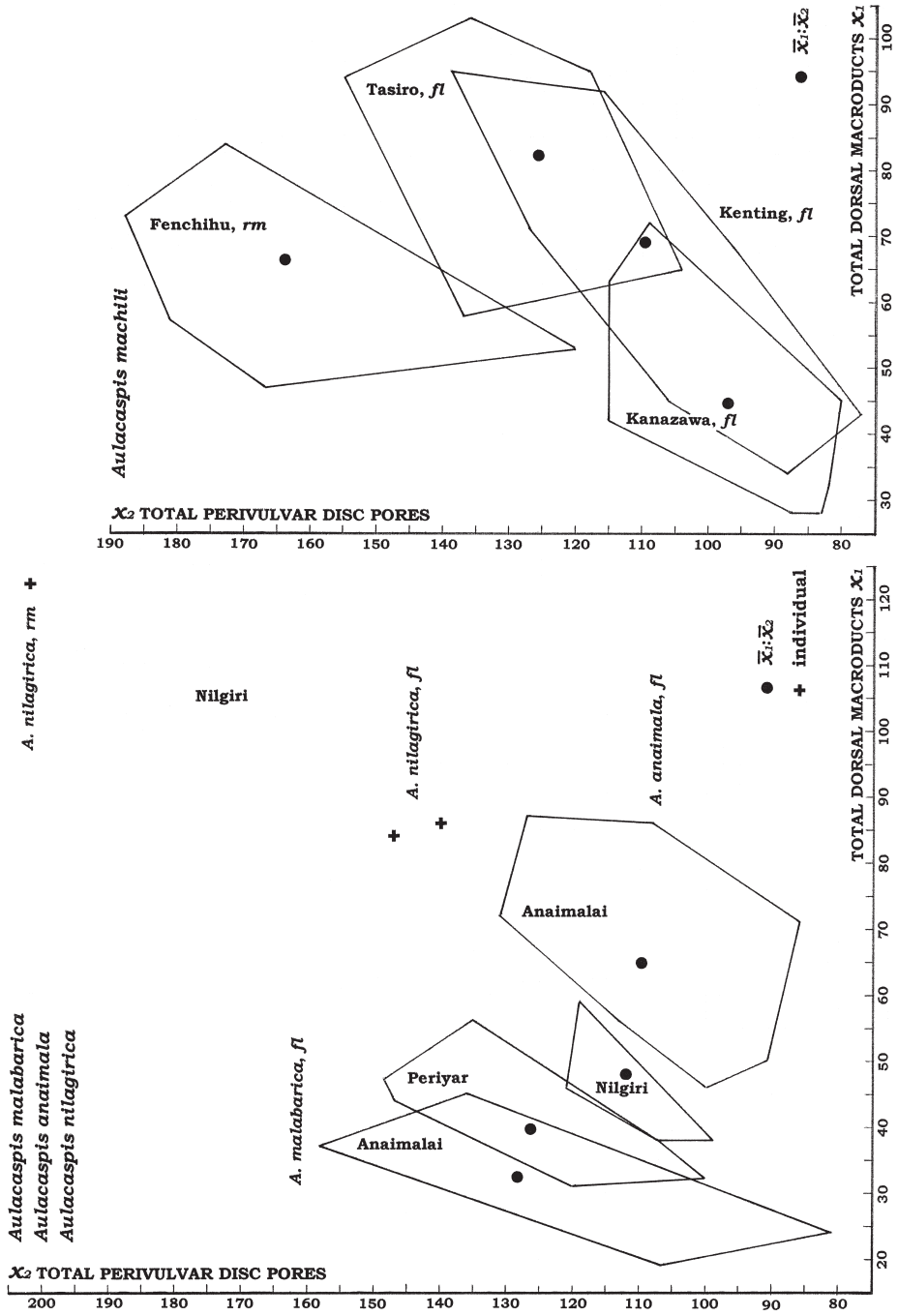

Fig. 1. *Aulacaspis malabarica* complex and *Aulacaspis machili*, adult females. Total number of perivulvar disc pores against total number of dorsal macroducts. Feeding sites: *fl*, leaf; *rm*, twig or branch.

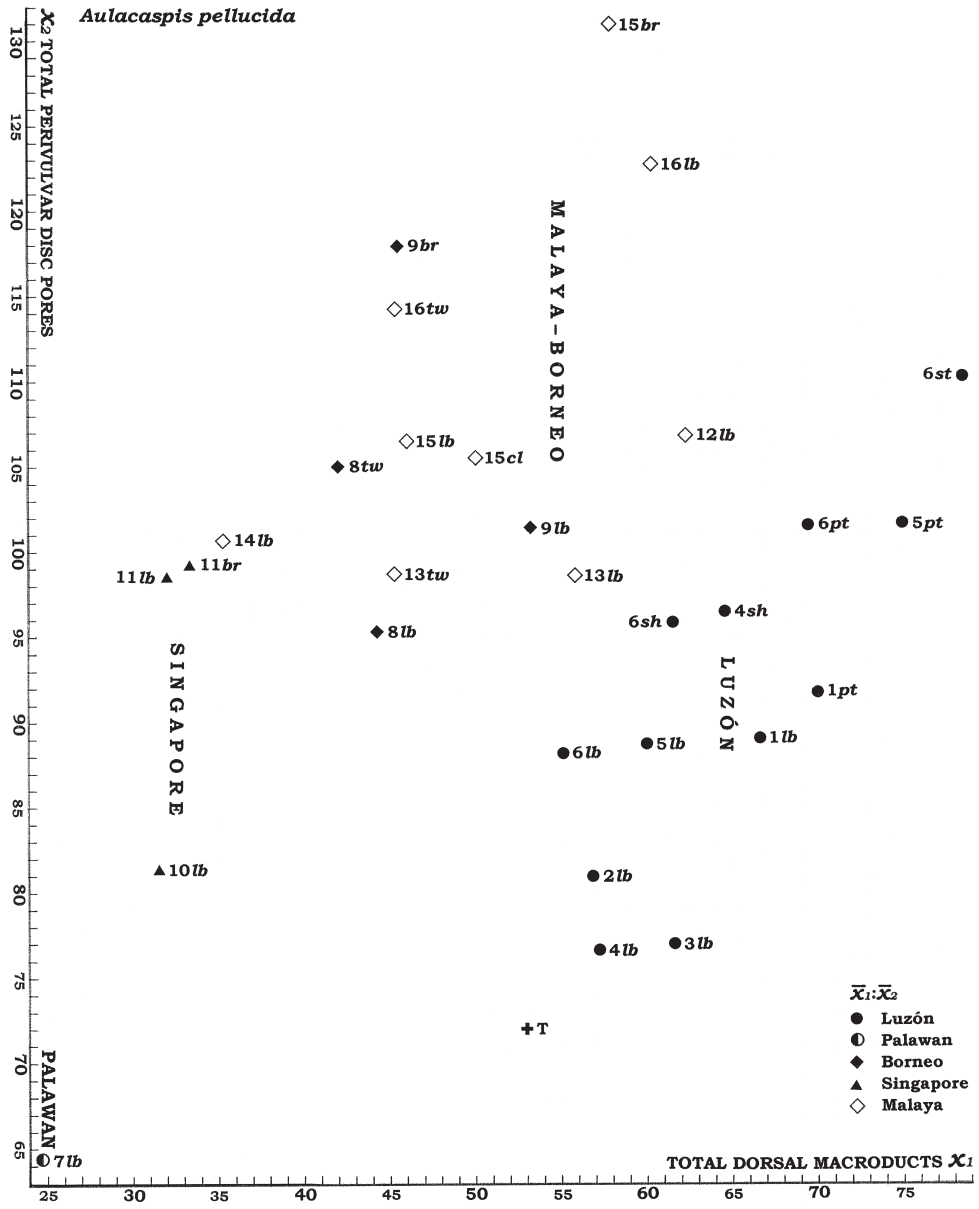

Fig. 2. *Aulacaspis pellucida*, adult females. Total number of perivulvar disc pores against total number of dorsal macroducts. Circular, quadrangular, and triangular marks representing sample or subsample means, each with a sample number and a feeding site. Feeding sites: *lb*, leaf blade; *pt*, petiole; *cl*, calyx; *sh*, shoot; *tw*, twig; *br*, branch; *st*, stem. Cross marked with T, specimen from the type material.

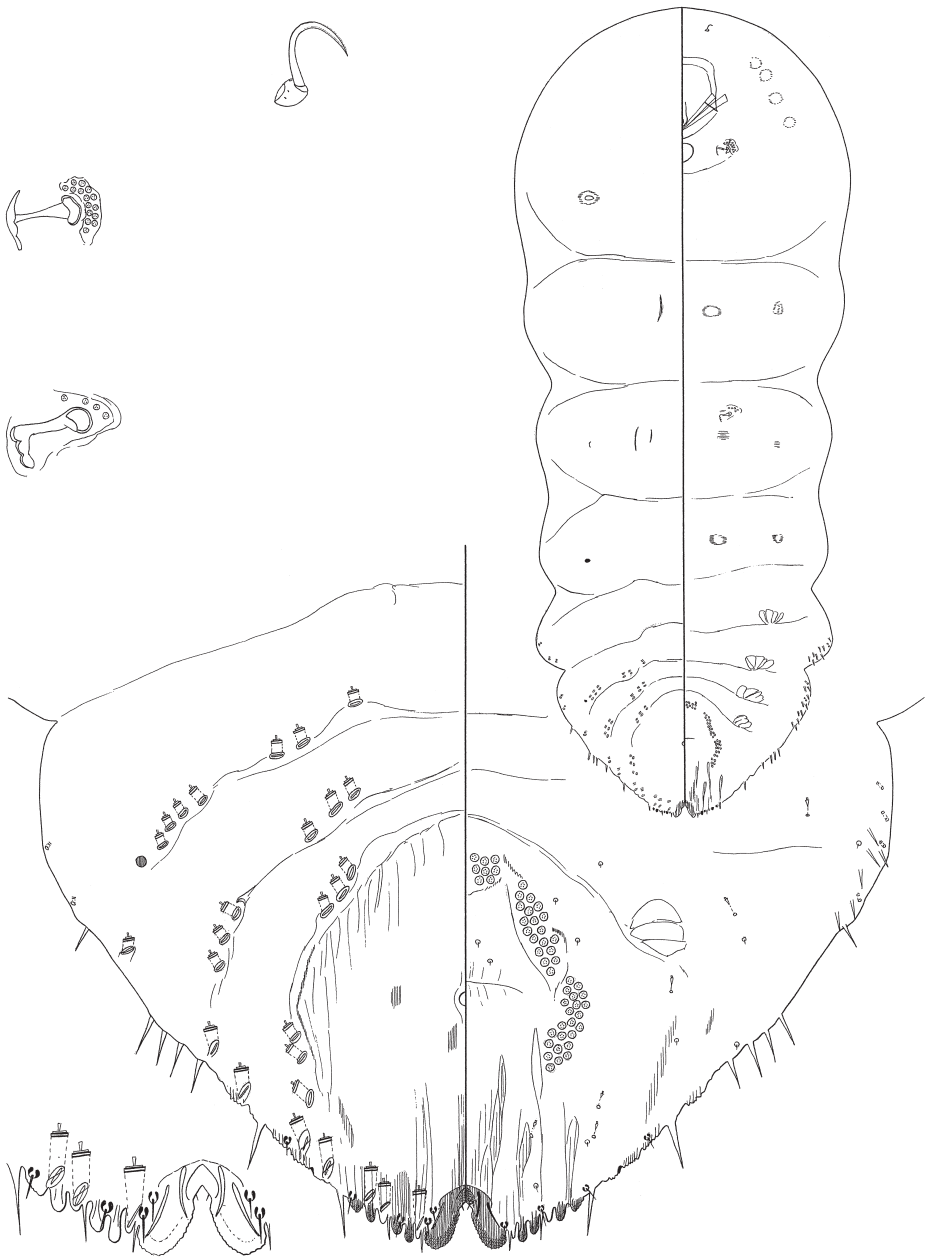

Fig. 3. '*Aulacaspis loranthi*, Ceylon, Pundaluoya, *Loranthus*, ii.1887, cotype' (D. J. Williams).

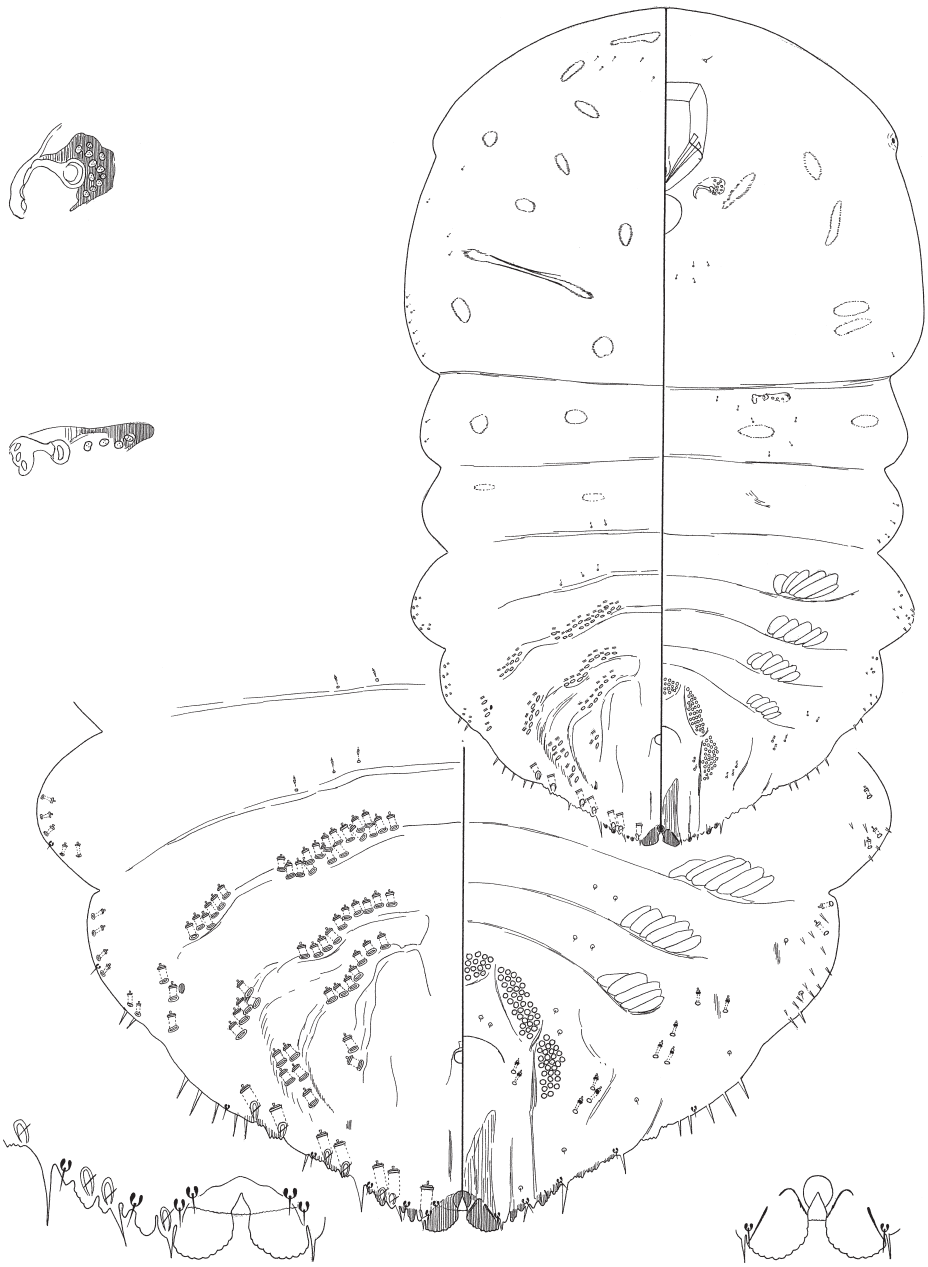

Fig. 4. '*Aulacaspis peresnathae* sp. n. m/s, (det. as *A. loranthi*), India, West Bengal, Peresnath, 9.IV.1909' (D. J. Williams). This form is undoubtedly identical with '*Diaspis loranthi*' recorded by Green (1919) from '*Loranthus cordifolius*: Paresnath, Bihar, 4000 ft.' (see *Remarks* under 2.2. *Aulacaspis loranthi*).

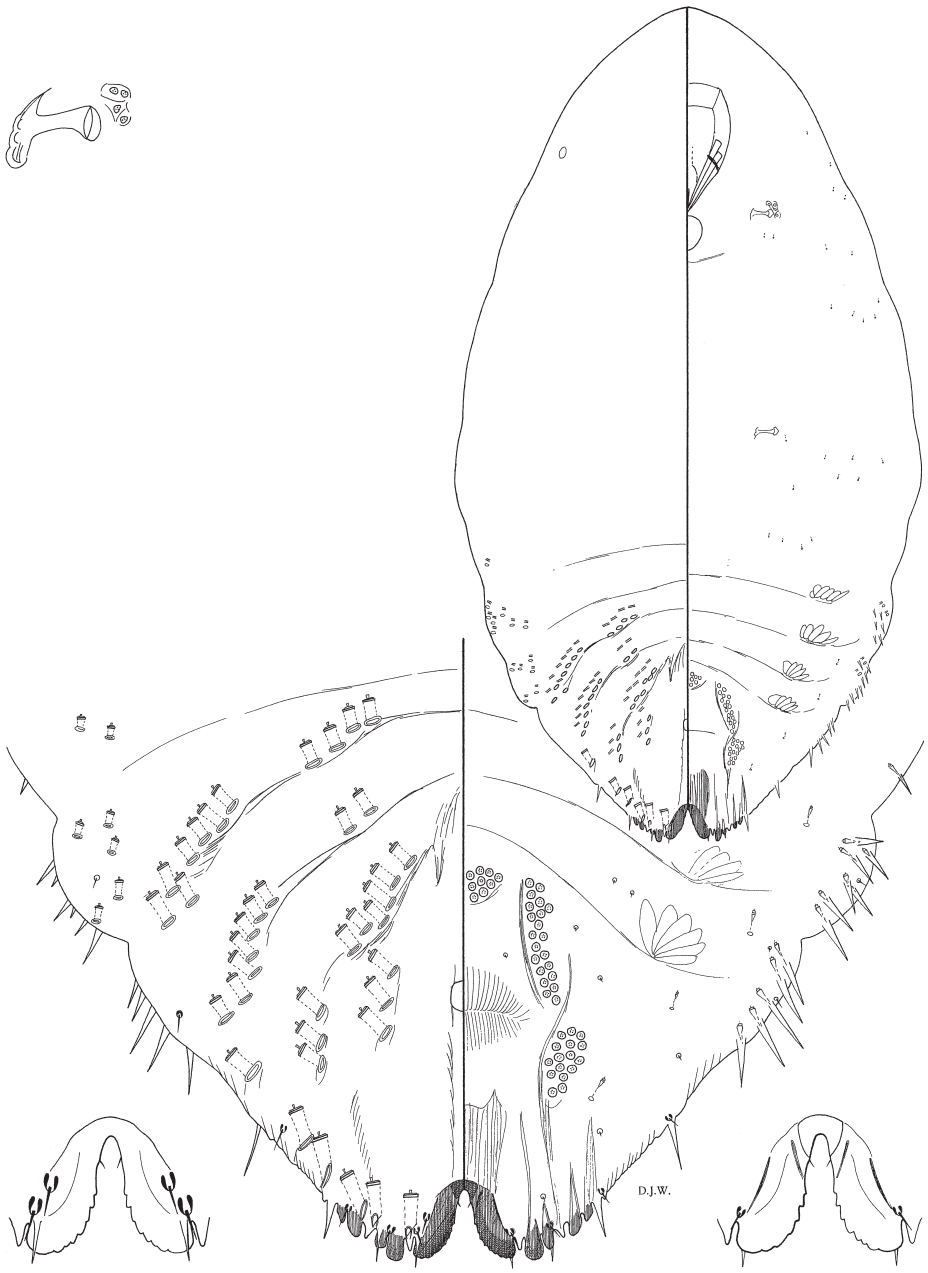

Fig. 5. '*Phenacaspis pellucida* (Robinson), Philippines, *Macaranga tanarius*, C. F. Baker.' (D. J. Williams).

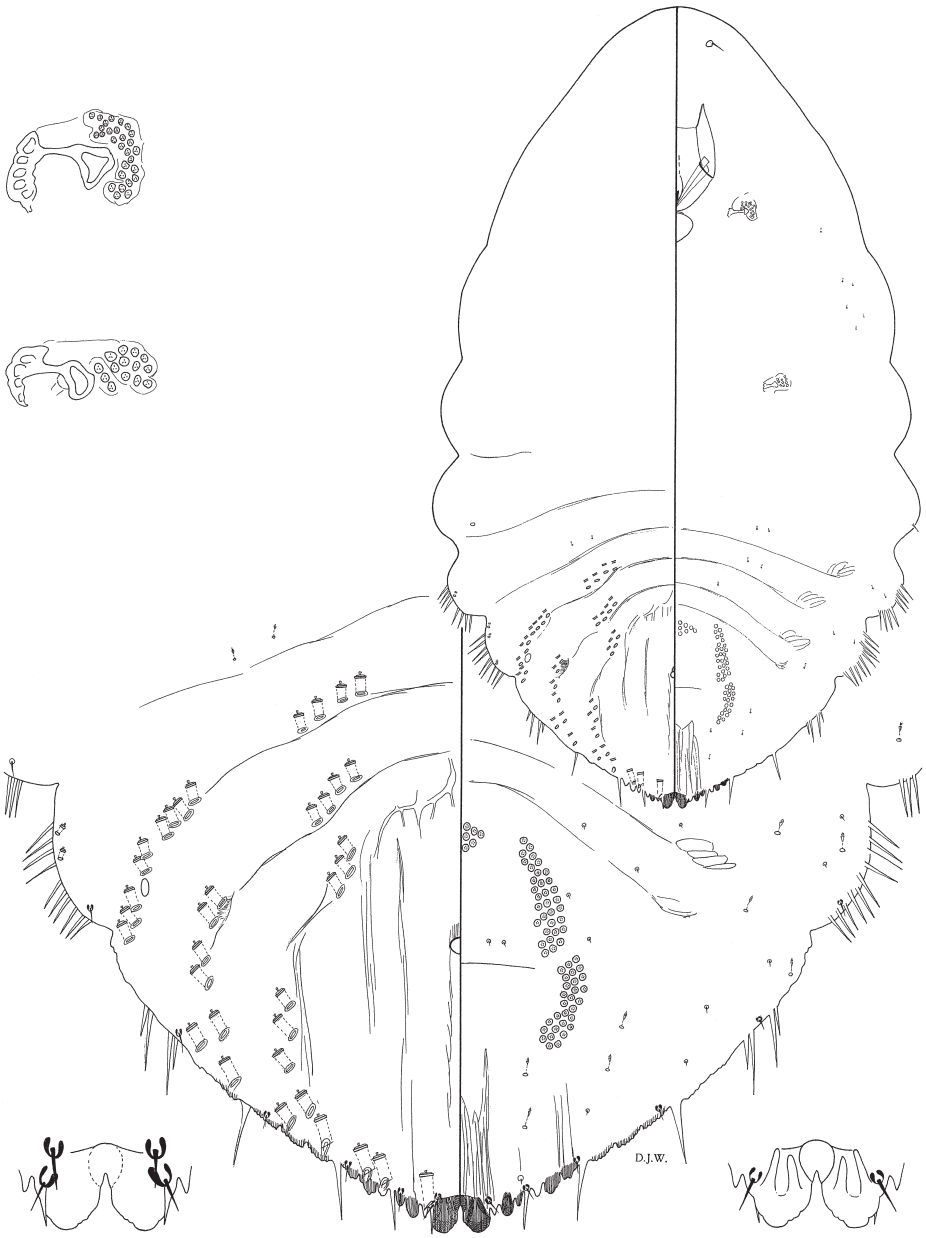

Fig. 6. '*Phenacaspis polygoni* Green, Ceylon, Pundaluoya, *Polygonum chinense*' (D. J. Williams).

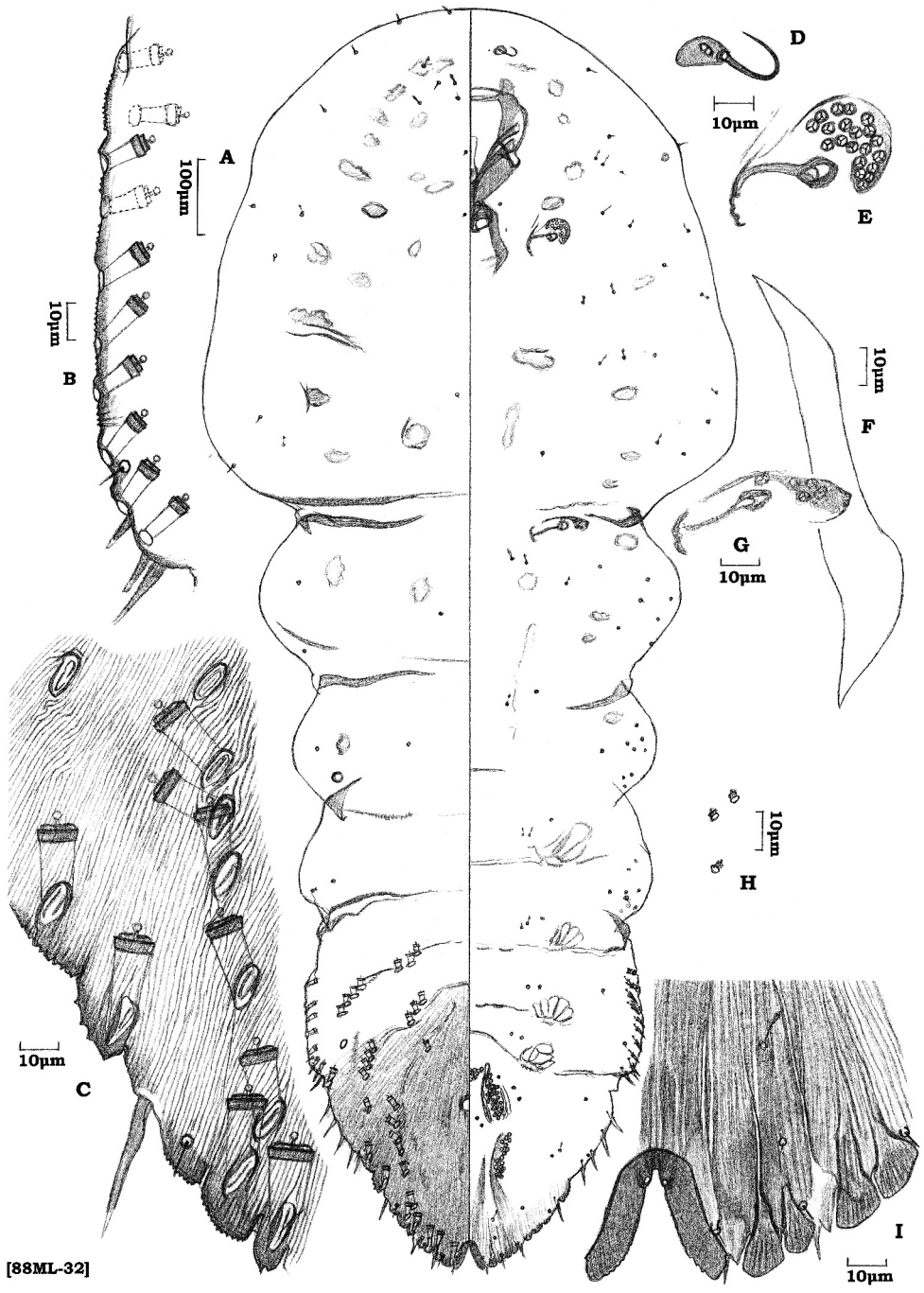

Fig. 7. *Aulacaspis gracilis* (2.1.), adult female, full-grown. Mt. Kinabalu, 2500m, Sabah, on *Actinodaphne pruinosa*, leaf [88ML-32]. B, lateral lobe of abd III, dorsal; C, pygidial margin, dorsal, abd IV and V; D, antenna; E, anterior spiracle; F, peribuccal sclerosis, outline; G, posterior spiracle; H, ventral microducts on posterolateral corner of abd I; I, trullae.

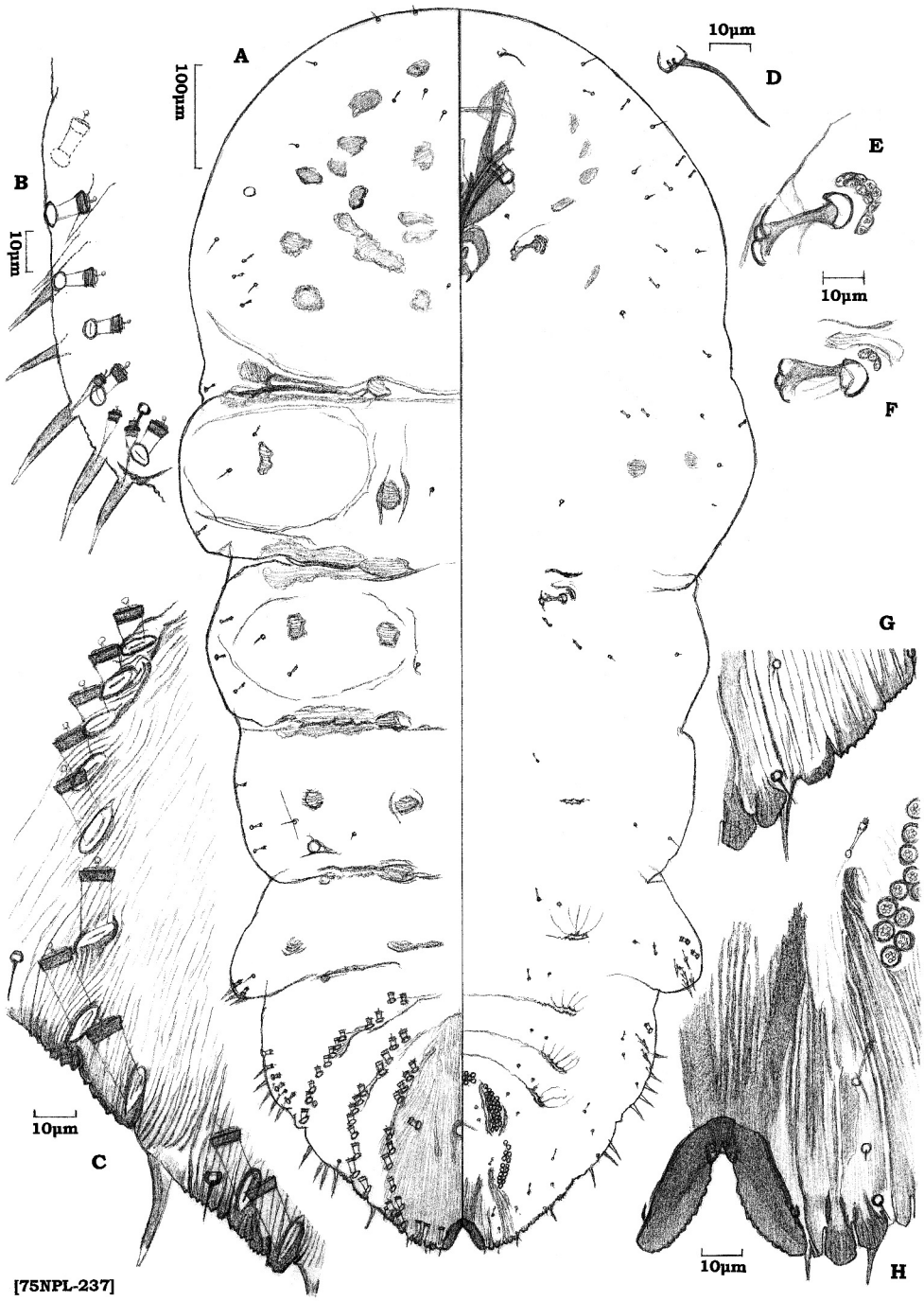

Fig. 8. *Aulacaspis loranthi* (2.2.), adult female, full-grown. Bagmati, 1770m, Nepal, on *Machilus duthiei*, leaf [75NPL-237]. B, lateral lobe of abd III, dorsal; C, pygidial margin, dorsal, abd IV and V; D, antennae; E, anterior spiracle; F, posterior spiracle; G, third trulla; H, median and second trullae.

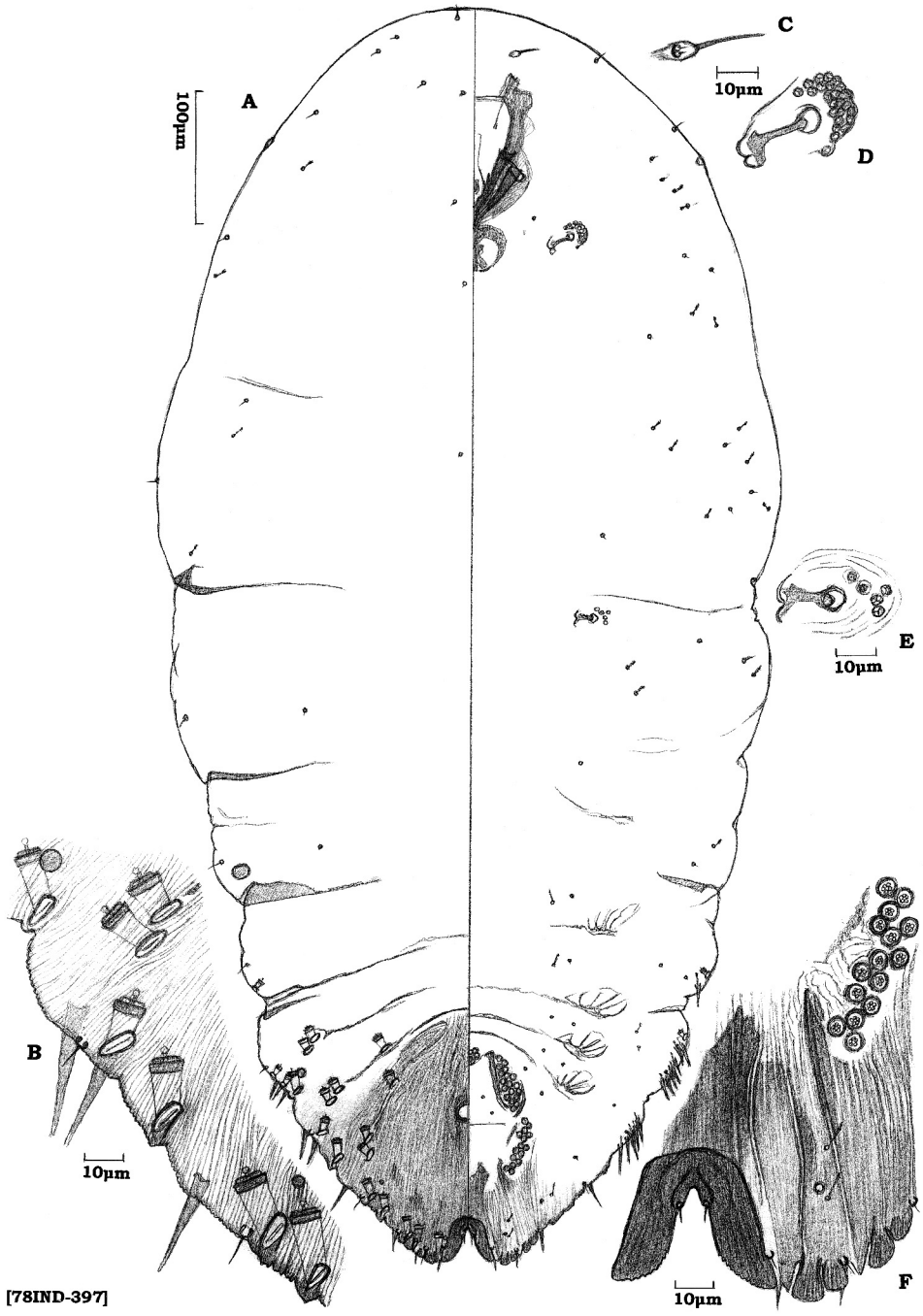

Fig. 9. *Aulacaspis litzeae* (2.3.), adult female, probably fully grown. Periyar Tiger Reserve, 900m, South India, on *Actinodaphne* sp., leaf [78IND-397]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D anterior spiracle; E, posterior spiracle; F, trullae.

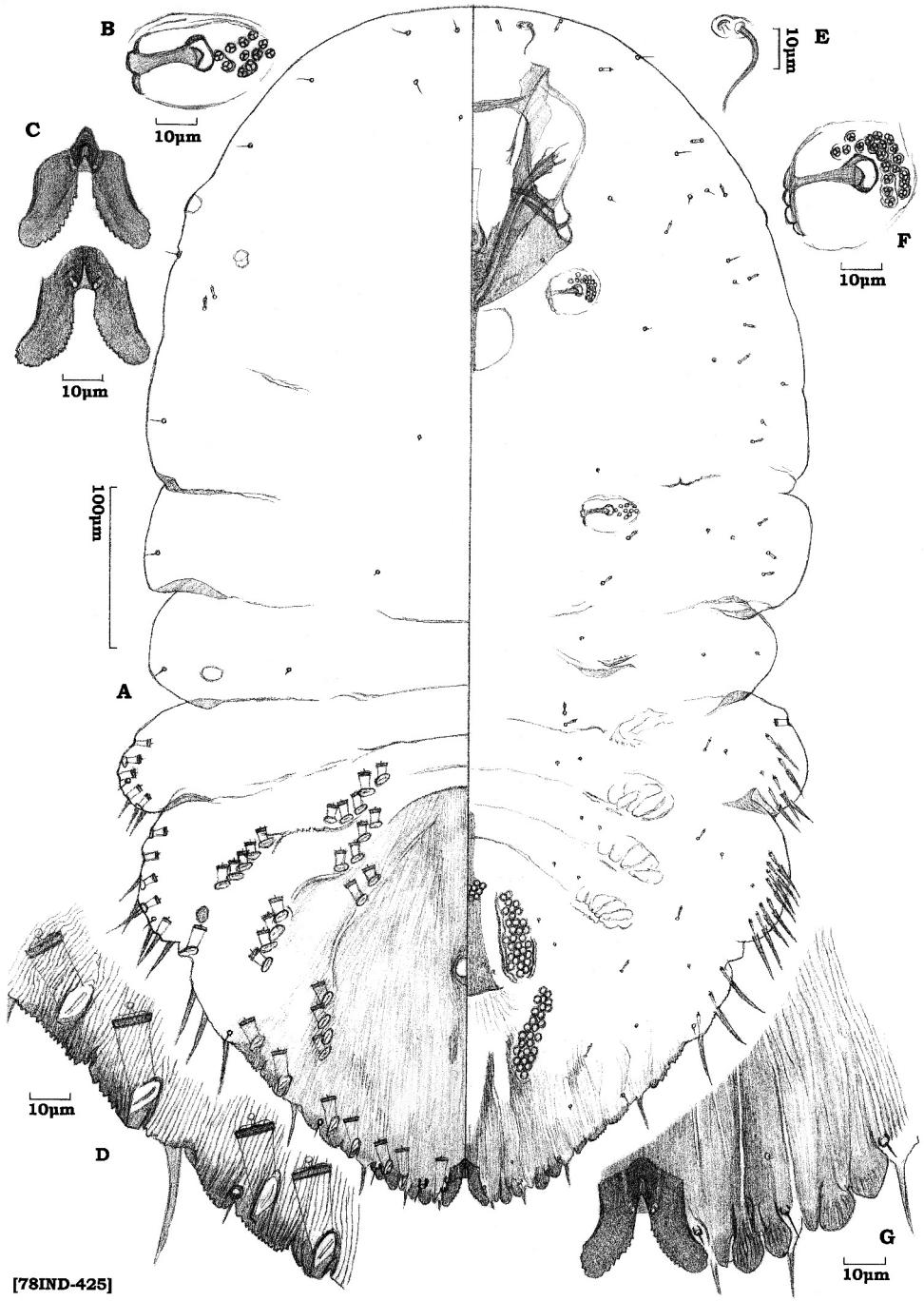

Fig. 10. *Aulacaspis malabarica* (2.4.), adult female, juvenile. Periyar Tiger Reserve, 900m, South India, on *Cinnamomum zeylanicum*, leaf [78IND-425]. B, posterior spiracle; C, median trullae; D, pygidial margin, dorsal, abd IV and V; E, antenna; F, anterior spiracle; G, trullae.

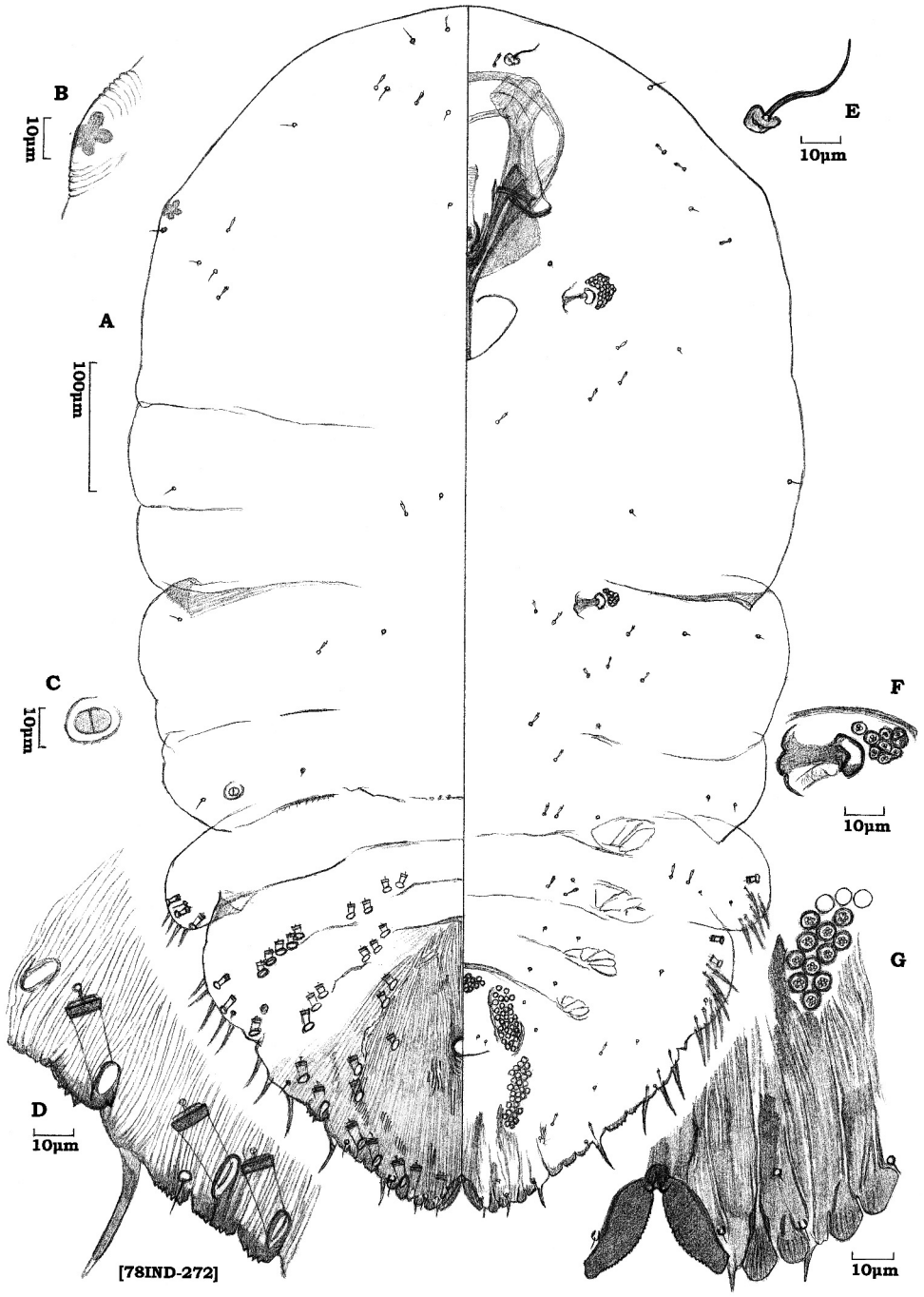

Fig. 11. *Aulacaspis malabarica* (2.4.), adult female, juvenile. Anaimalai, 750m, South India, on *Cinnamomum* sp., leaf [78IND-272]. B, eye spot; C, dorsal boss on abd I; D, pygidial margin, dorsal, abd IV and V; E, antenna; F, posterior spiracle; G, trullae.

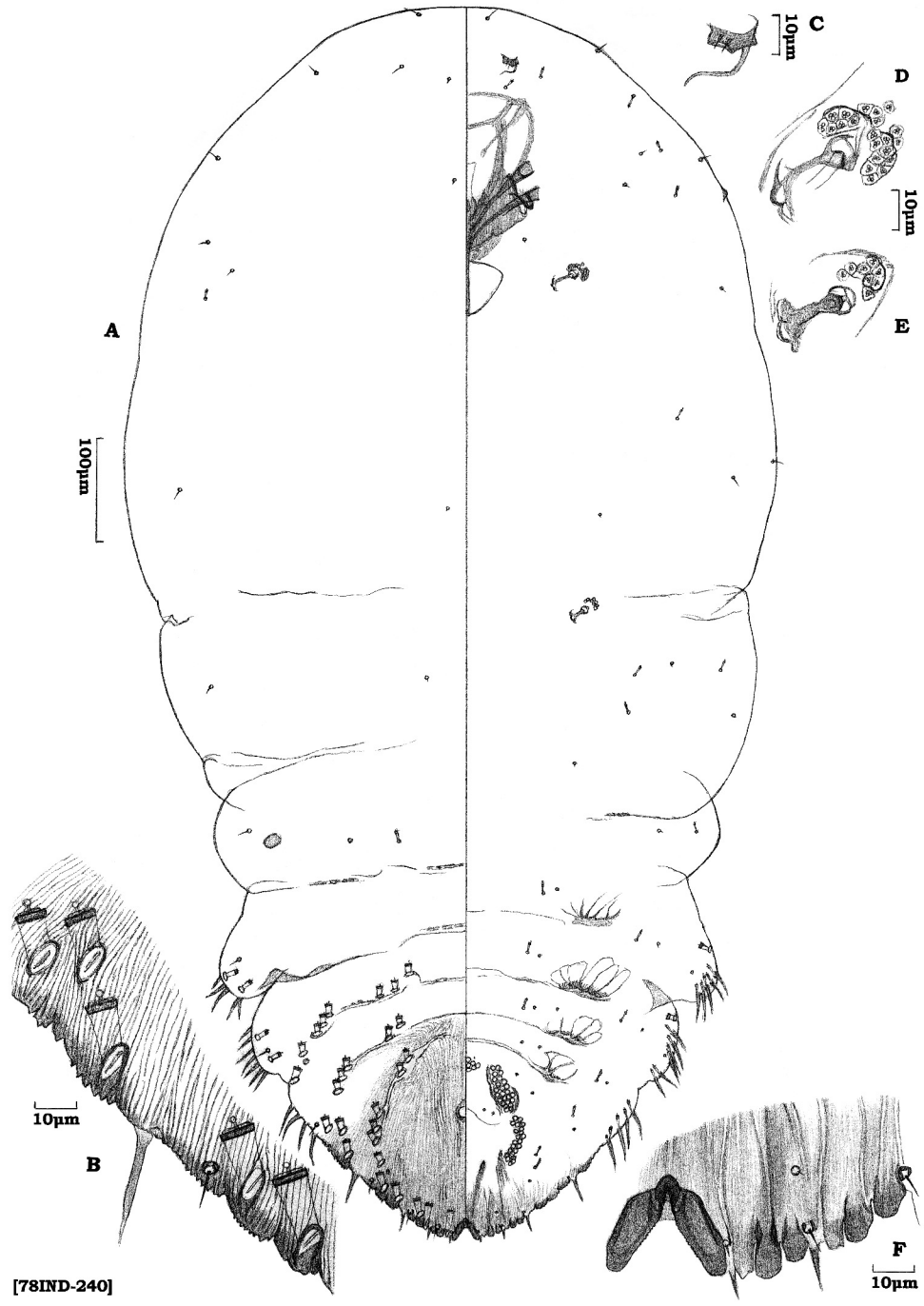

Fig. 12. *Aulacaspis malabarica* (2.4.), adult female, probably not fully grown. Nilgiri, 1600m, South India, on *Neolitsea* sp., leaf [78IND-240]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

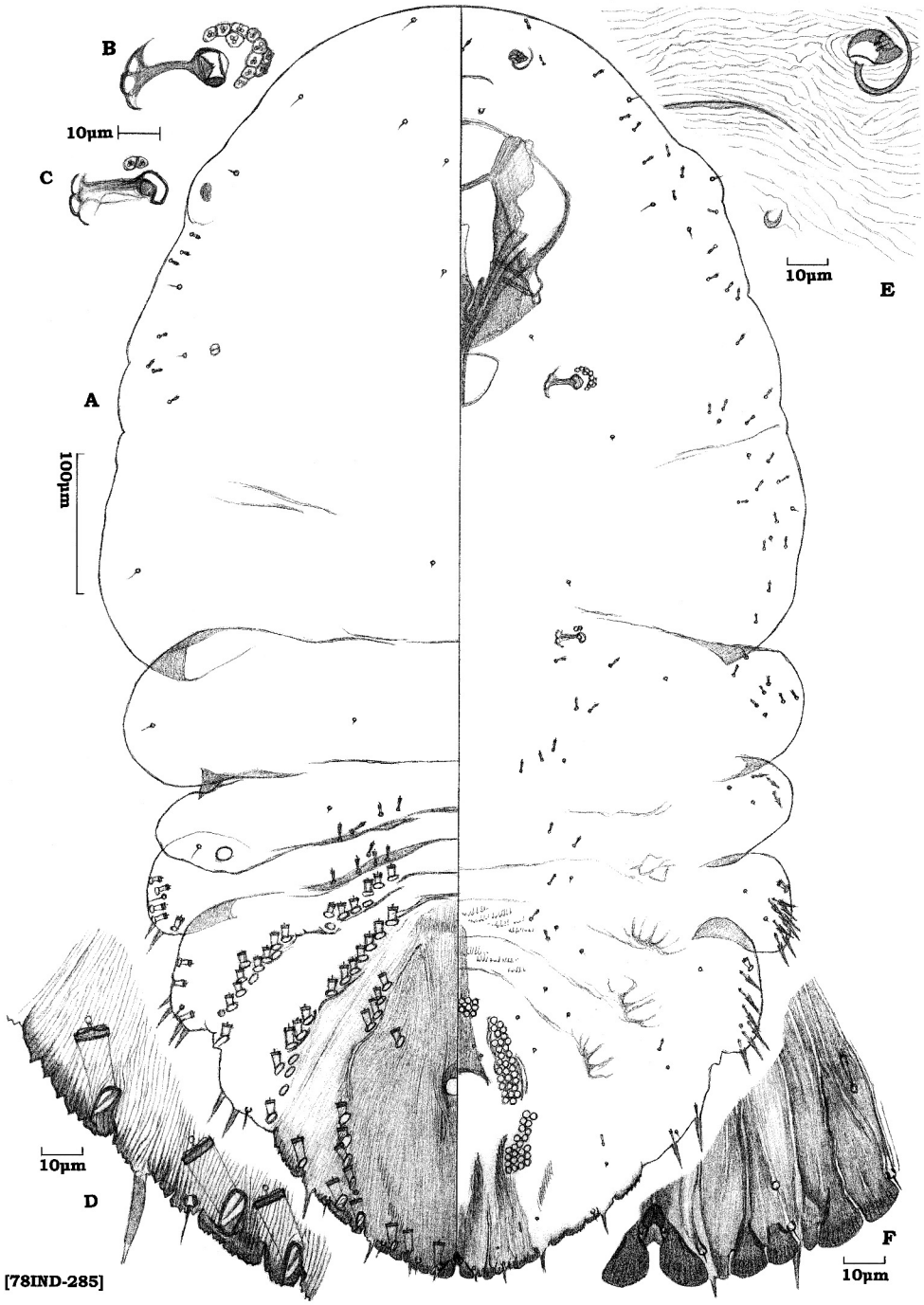

Fig. 13. *Aulacaspis anaimala* (2.5.), adult female, juvenile. Anaimalai, 750m, South India, on a lauraceous plant, leaf [78IND-285]. B, anterior spiracle; C, posterior spiracle; D, pygidial margin, dorsal, abd IV and V; E, antenna, interantennal tubercle (part), and interantennal derm pocket; F, trullae.

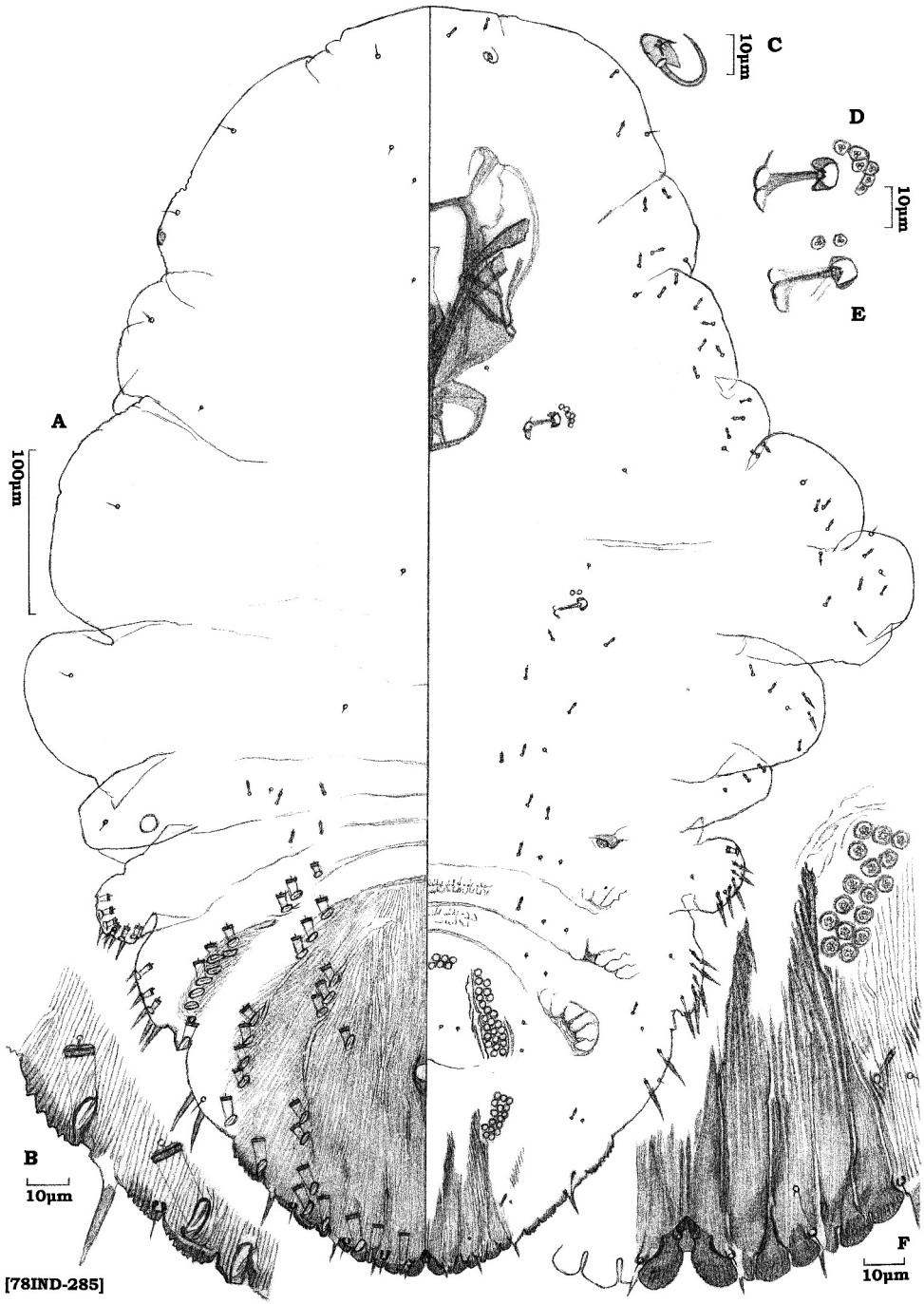

Fig. 14. *Aulacaspis anaimala* (2.5.), adult female, probably fully grown, but with mesothorax not much expanded on one side. Anaimalai, 750m, South India, on a lauraceous plant, leaf [78IND-285]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

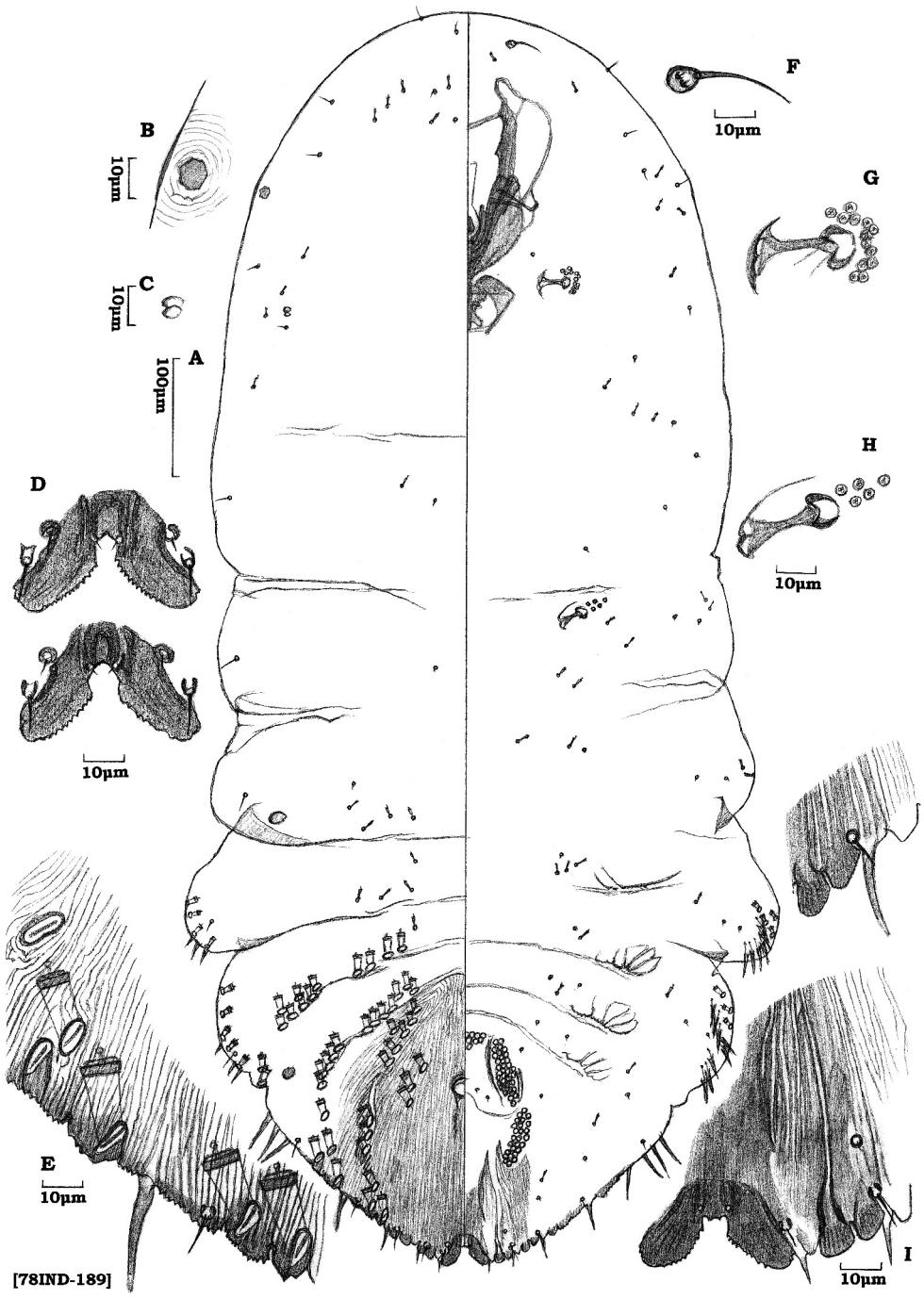

Fig. 15. *Aulacaspis nilagirica* (2.6.), adult female, juvenile. Nilgiri, 2600m, South India, on *Litsea* sp., leaf (D, other specimens from leaf and twig) [78IND-189]. B, eye spot; C, cicatrix on prosoma; D, median trullae, examples from leaf (upper) and twig (lower); E, pygidial margin, dorsal, abd IV and V; F, antenna; G, anterior spiracle; H, posterior spiracle; I, third trulla (upper), median and second trullae (lower).

Fig. 16. *Aulacaspis machili* (2.7.), adult female, probably fully grown (nearly representing the form *Phenacaspis obovata*). Kanazawa, Japan, on *Persea thunbergii*, leaf. B, antenna; C, pygidial margin, dorsal, abd IV and V; D, anterior spiracle; E, posterior spiracle; F, trullae.

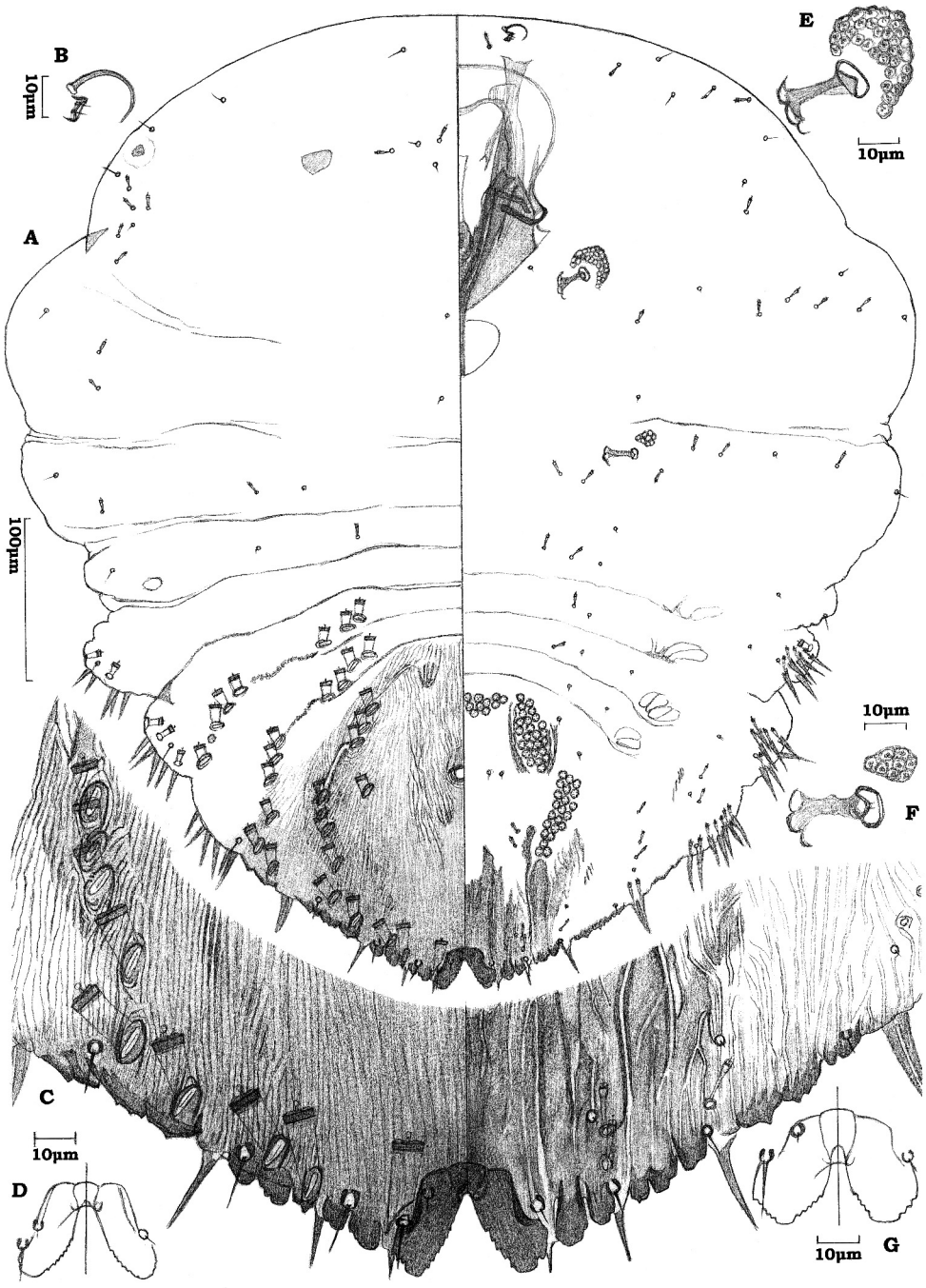

Fig. 17. *Aulacaspis machili* (2.7.), adult female, full-grown (representing the form *Diaspis machili*). Kanazawa, Japan, on *Persea thunbergii*, leaf. B, antenna; C, pygidial margin; D, median trullae, one extreme of variation; E, anterior spiracle; F, posterior spiracle; G, median trullae, the other extreme of variation.

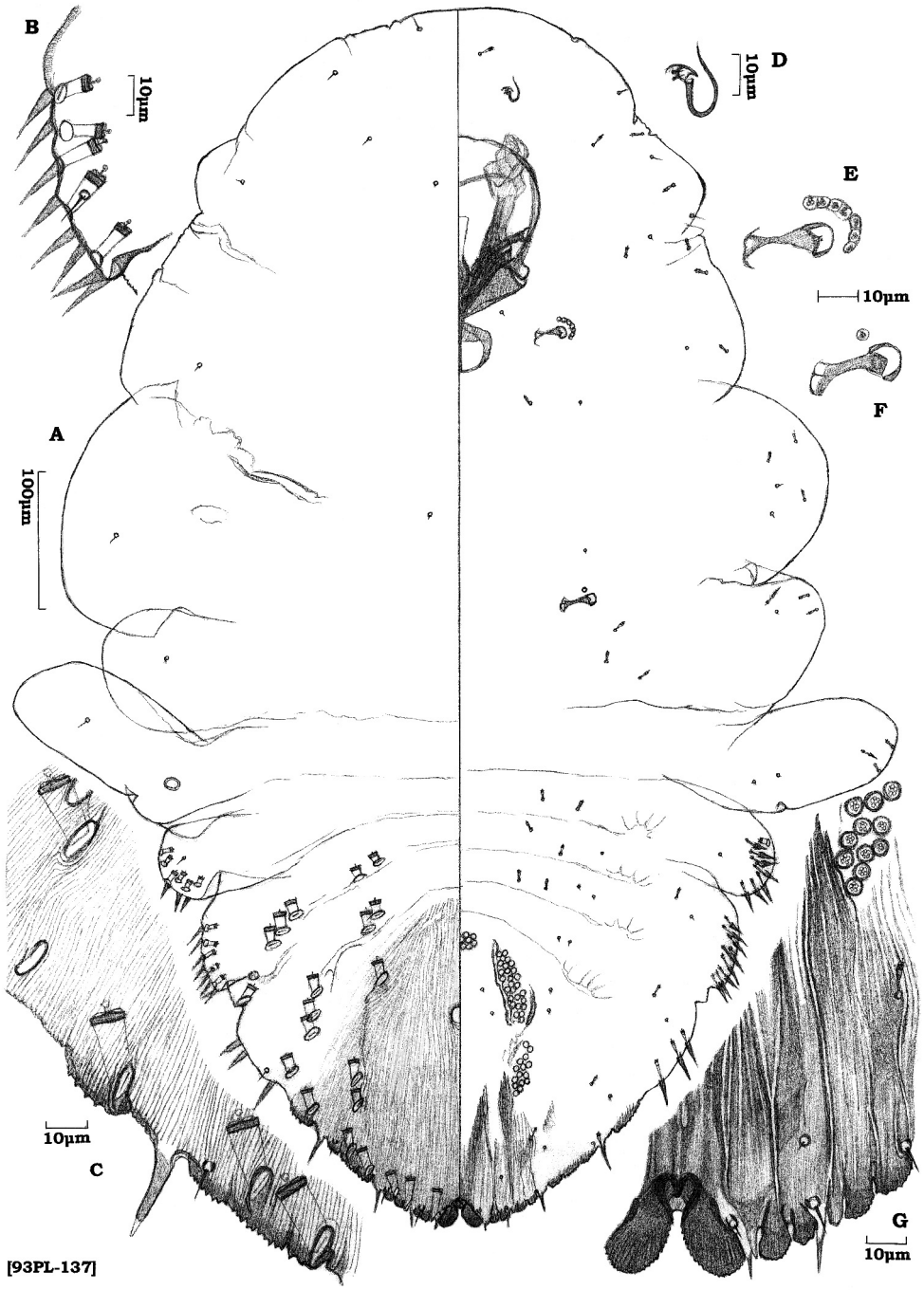

Fig. 18. *Aulacaspis digitifera* (2.8.), adult female, full-grown. Palawan, on *Litsea garciae*, leaf [93PL-137]. B, lateral lobe of abd III, dorsal; C, pygidial margin, dorsal, abd IV and V; D, antenna; E, anterior spiracle; F, posterior spiracle; G, trullae.

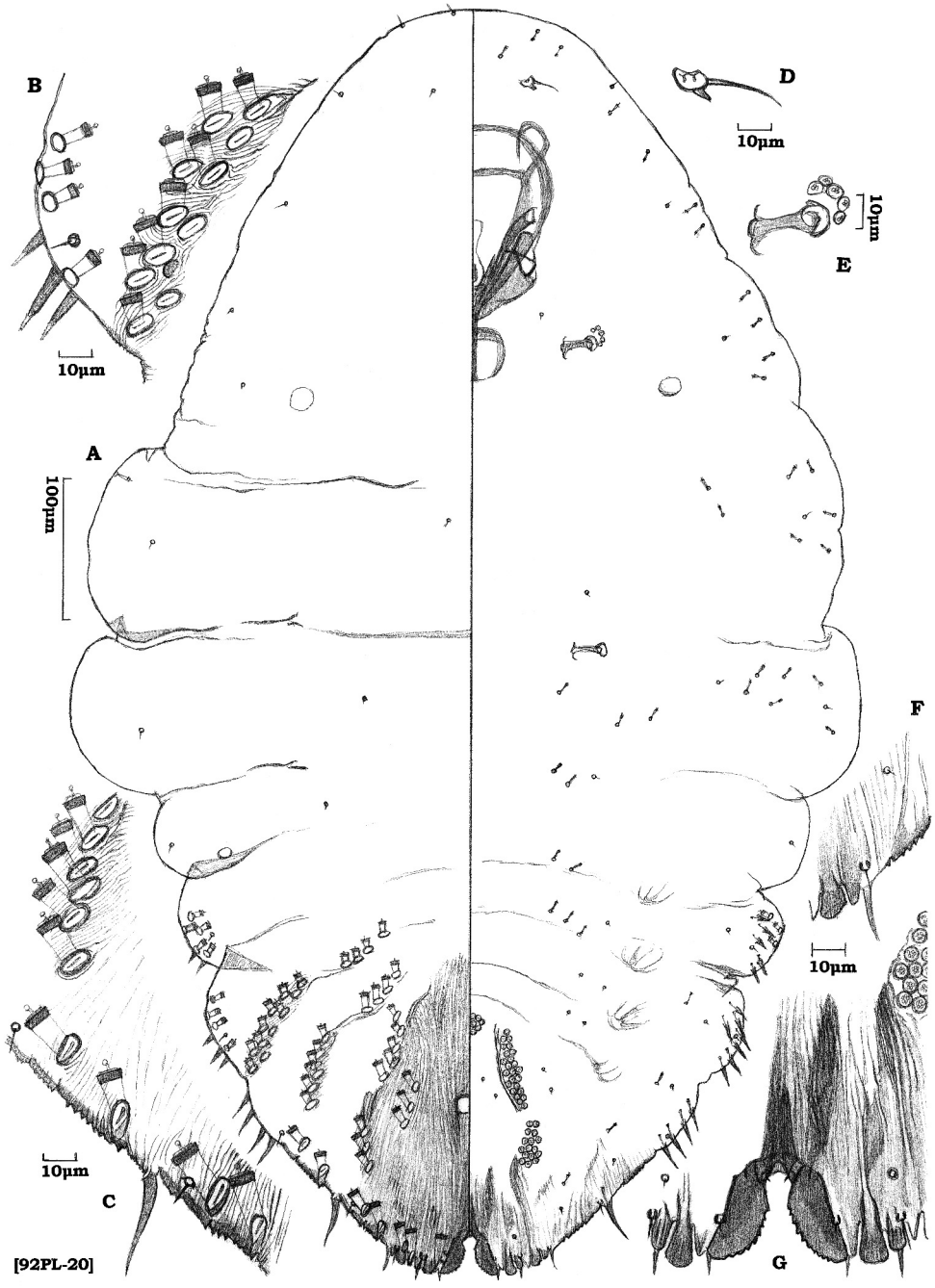

Fig. 19. *Aulacaspis pellucida* (2.9.), adult female, meso- and metathorax expanded on one side alone. Luzón, on *Macaranga tanarius*, leaf blade [92PL-20]. B, lateral lobe of abd III, dorsal; C, pygidial margin, dorsal, abd IV and V; D, antenna; E, anterior spiracle; F, third trulla; G, median and second trullae.

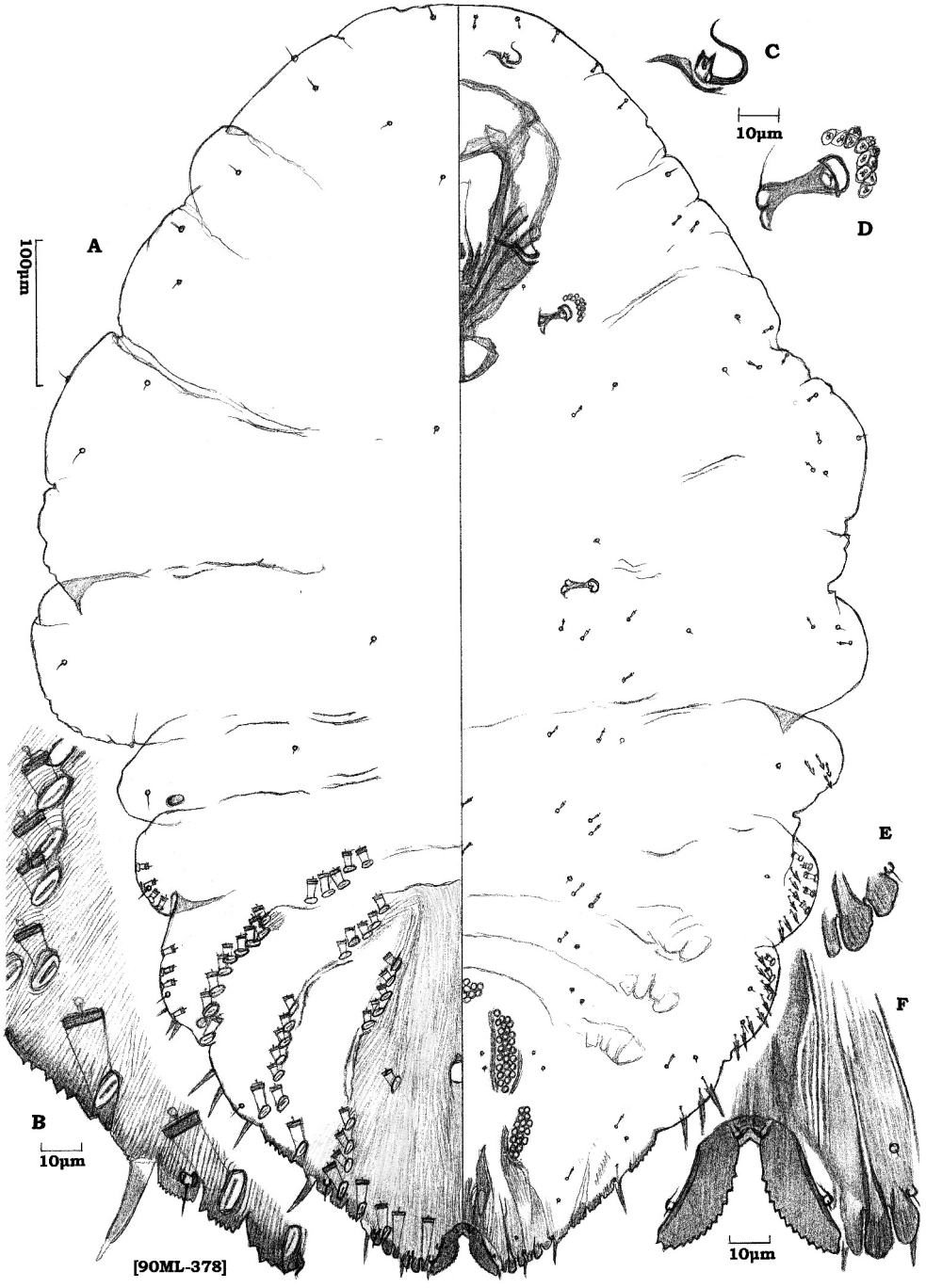

Fig. 20. *Aulacaspis pellucida* (2.9.), adult female, full-grown. Kuala Lumpur, on *Macaranga tanarius*, calyx [90ML-378]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, third trulla; F, median and second trullae.

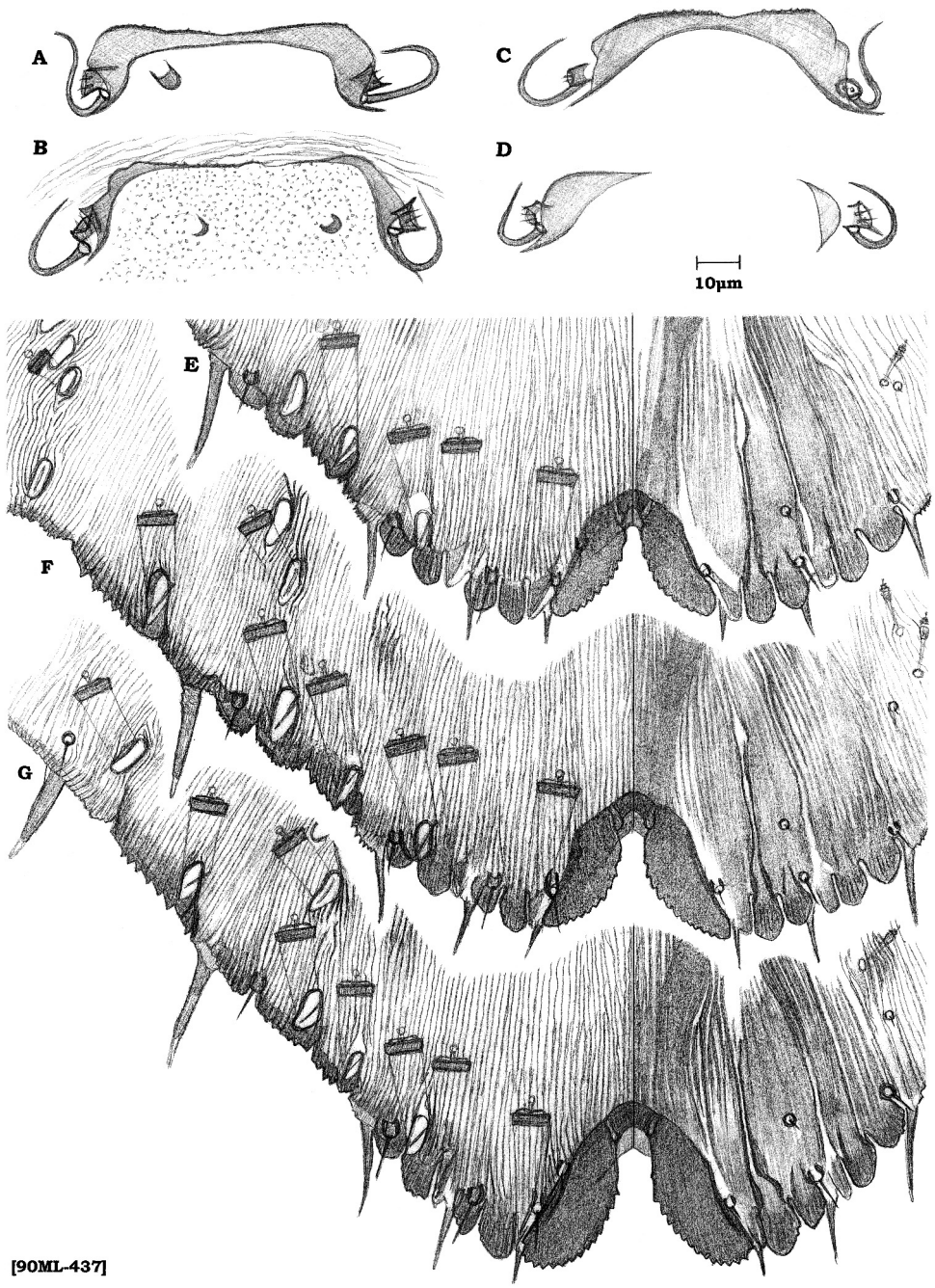

Fig. 21. *Aulacaspis pellucida* (2.9.), adult female. Kuala Lumpur, on *Macaranga gigantea*, leaf blade (G, twig) [90ML-437]. A–D, interantennal tubercle (A–C) or swellings (D), with interantennal derm pockets (A, B); E–G, pygidial margin, on leaf blade (E and F) and twig (G).

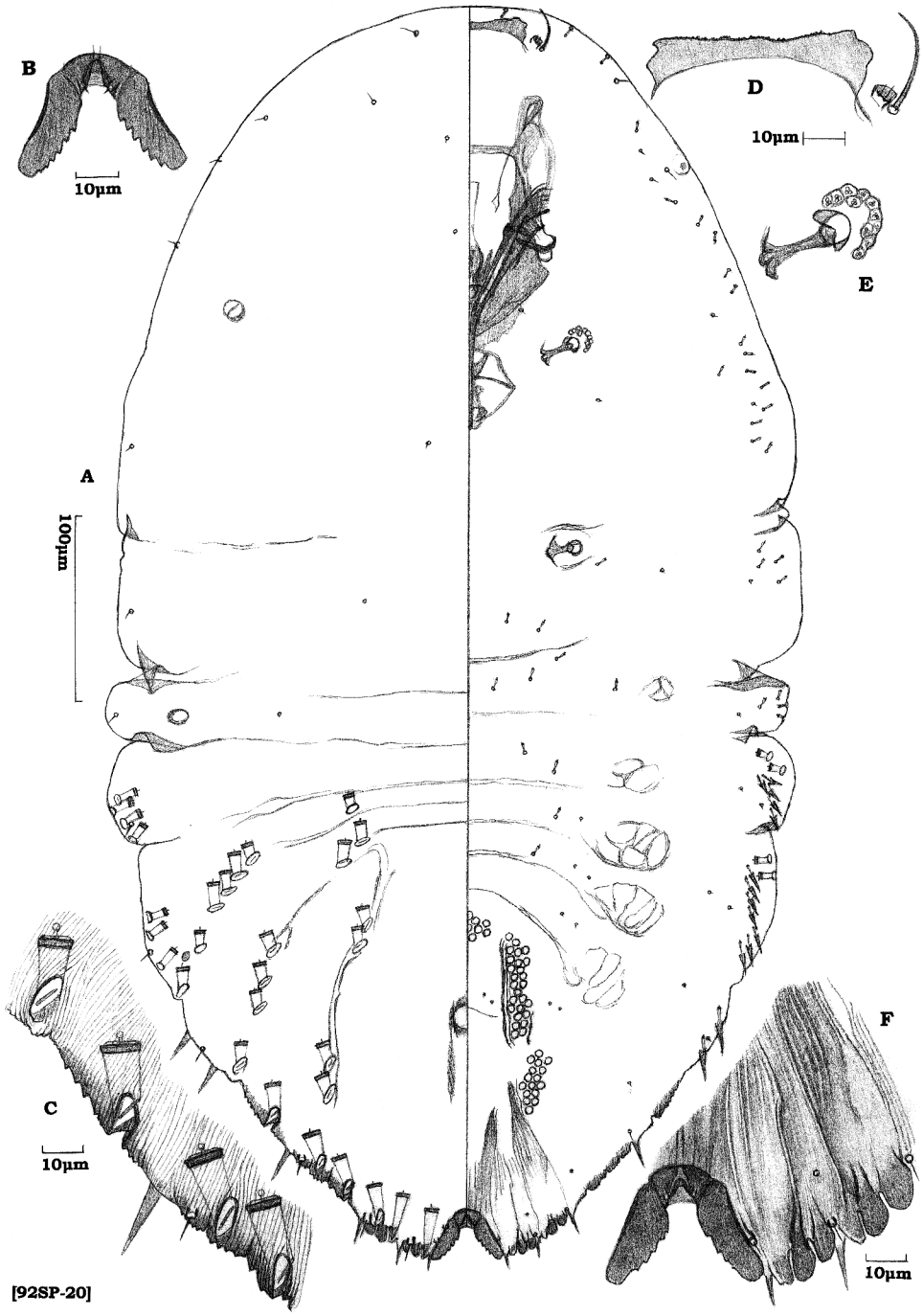

Fig. 22. *Aulacaspis pellucida* (2.9.), adult female, juvenile. Singapore, on *Campnosperma auriculatum*, branch [92SP-20]. B, median trullae; C, pygidial margin, dorsal, abd IV and V; D, antenna and interantennal tubercle; E, anterior spiracle; F, trullae.

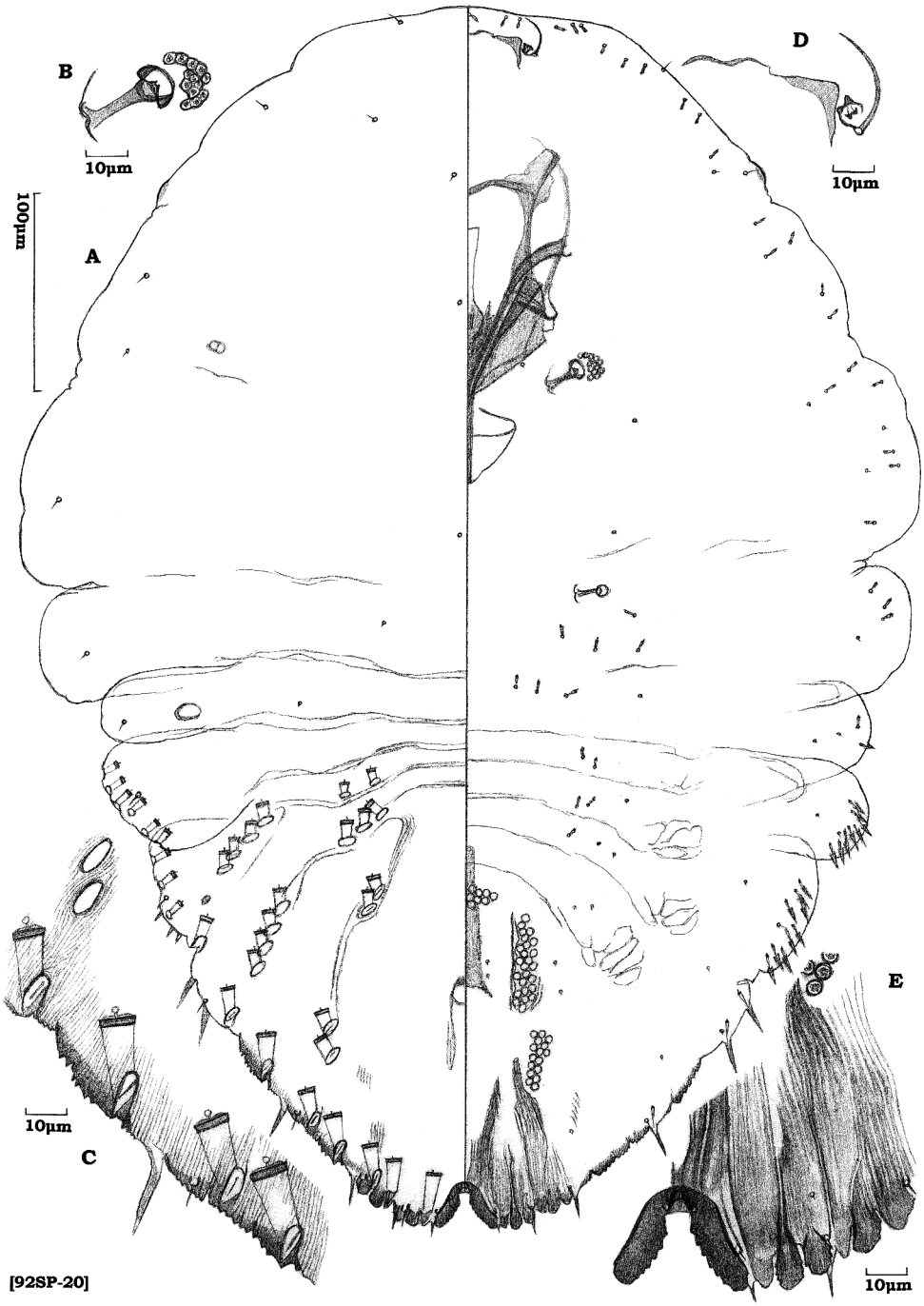

Fig. 23. *Aulacaspis pellucida* (2.9.), adult female, nearly fully grown. Singapore, on *Campnosperma auriculatum*, leaf blade [92SP-20]. B, anterior spiracle; C, pygidial margin, dorsal, abd IV and V; D, antenna and interantennal tubercle (part); E, trullae.

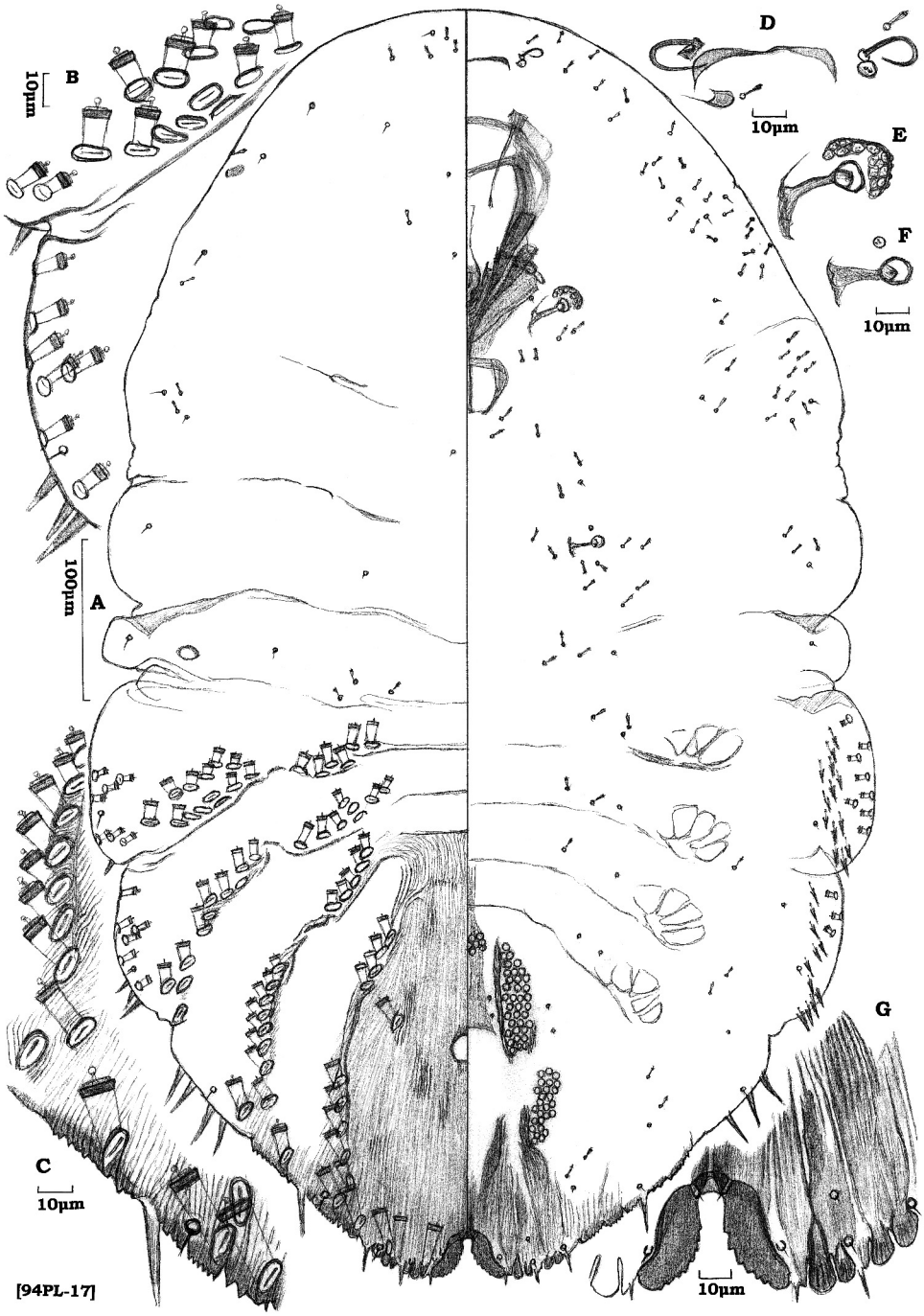

Fig. 24. *Aulacaspis binunga* (2.10.), adult female, teneral. Mindoro, on *Macaranga tanarius*, leaf blade [94PL-17]. B, submarginal macroducts on abd II and lateral lobe of abd III; C, pygidial margin, dorsal, abd IV and V; D, antennae, interantennal tubercle, derm pocket, and microducts; E, anterior spiracle; F, posterior spiracle; G, trullae.

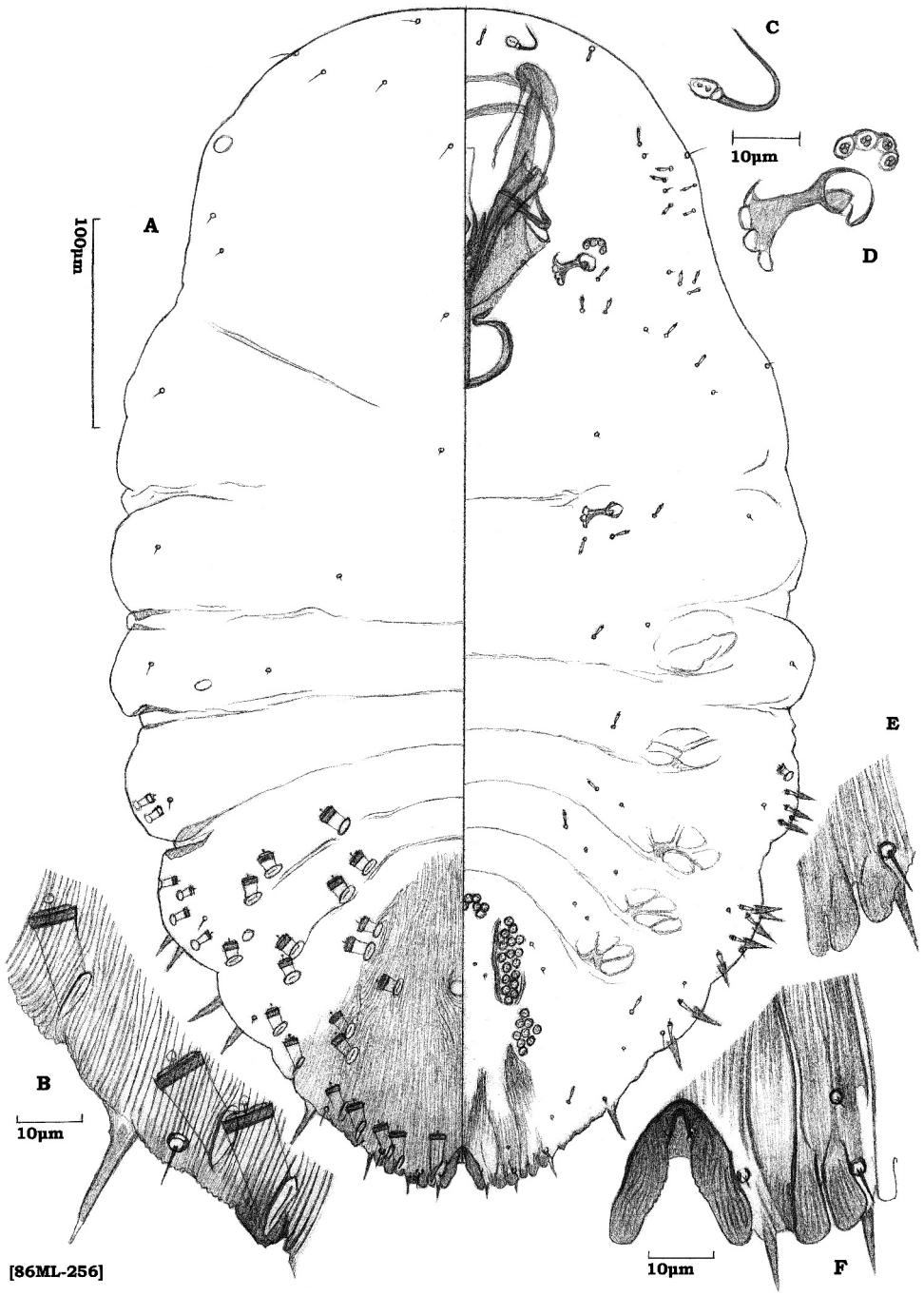

Fig. 25. *Aulacaspis macarangae* (2.11.), adult female, juvenile. Cameron Highlands, 1400m, Malaya, on *Macaranga* sp., leaf [86ML-256]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, third trullae; F, median and second trullae.

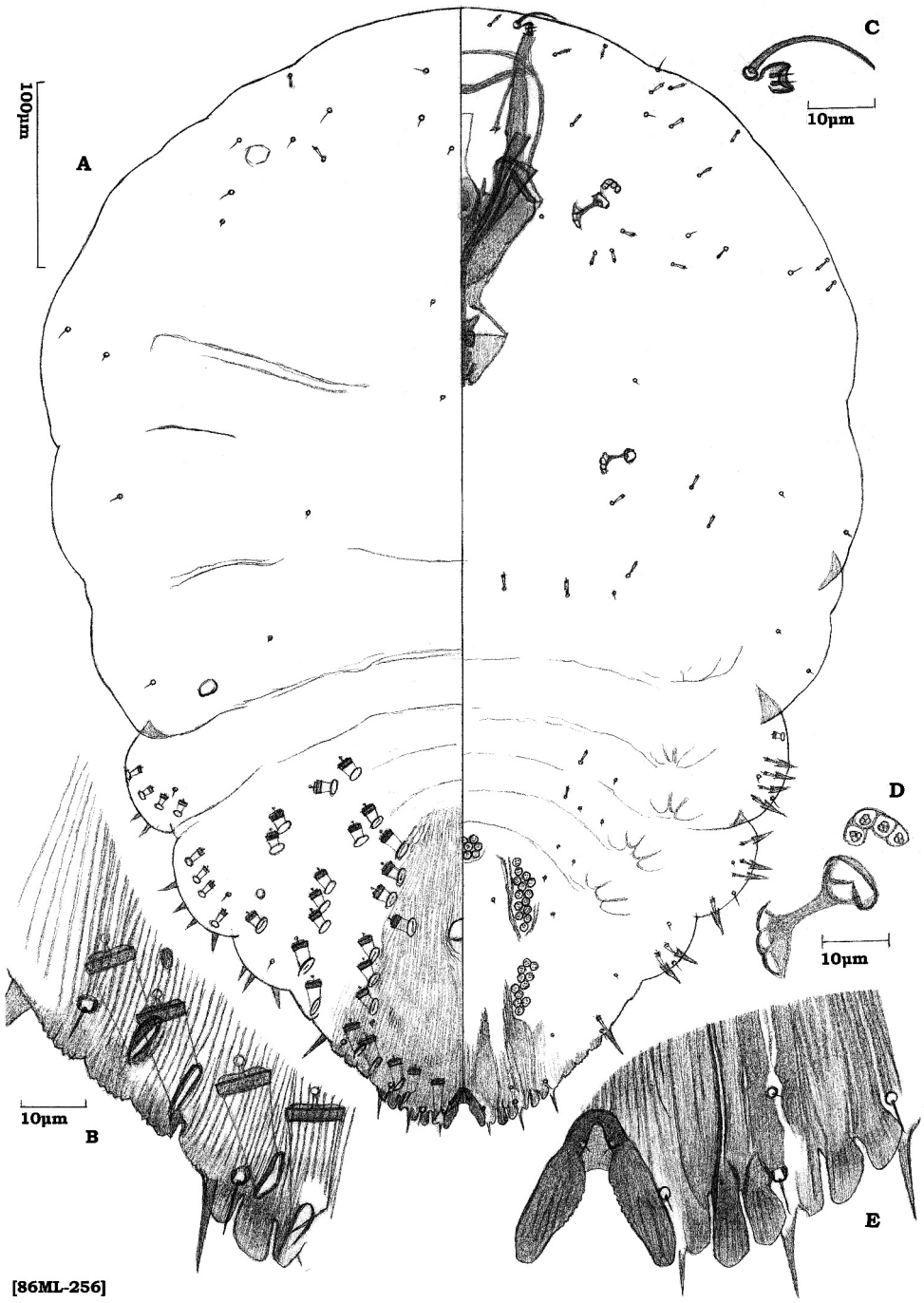

Fig. 26. *Aulacaspis macarangae* (2.11.), adult female, full-grown. Cameron Highlands, 1400m, Malaya, on *Macaranga* sp., leaf [86ML-256]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, trullae.

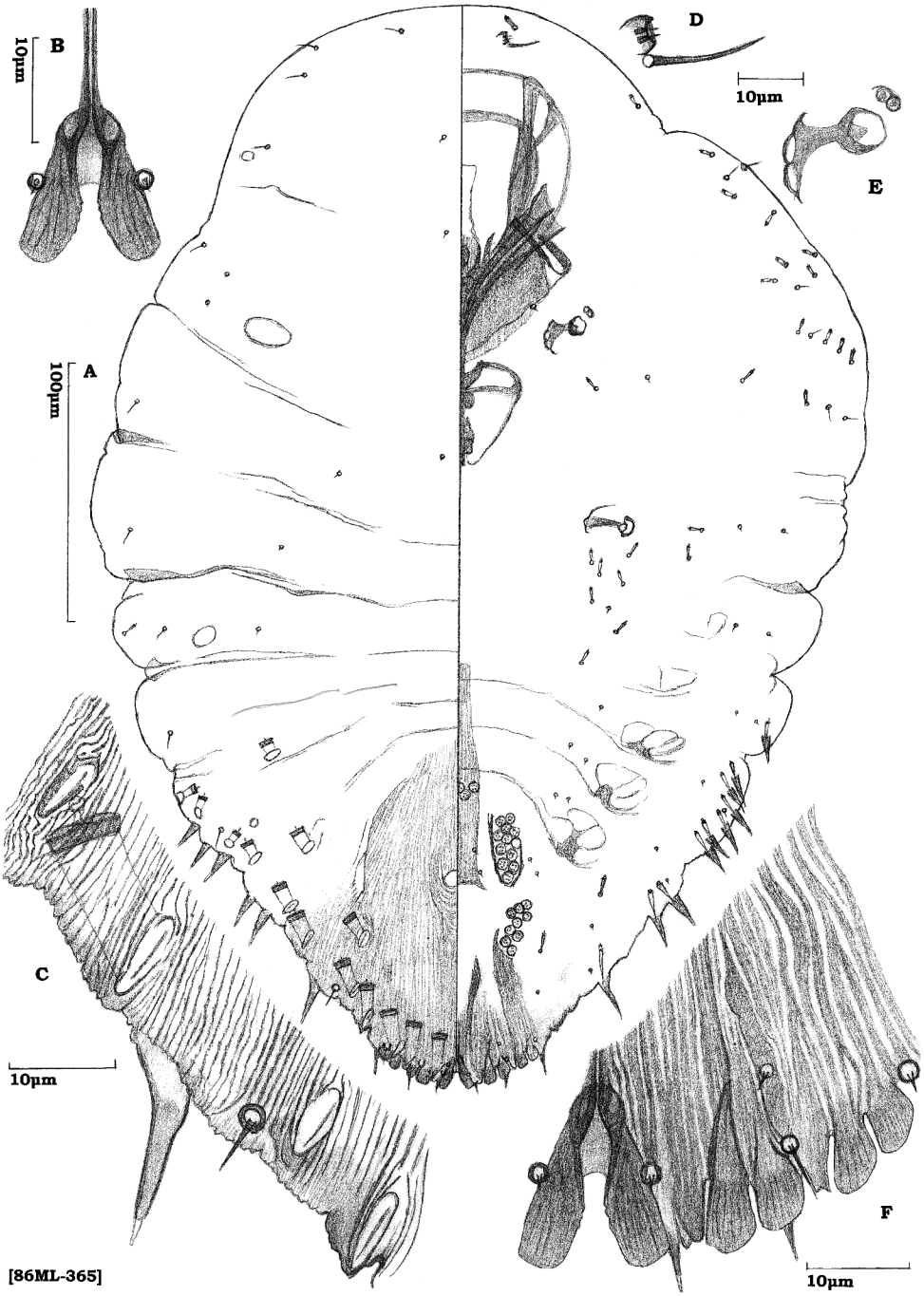

Fig. 27. *Aulacaspis mahangena* (2.12.), adult female, with mesothorax expanded on one side alone. Bukit Fraser, 1250m, Malaya, on *Macaranga curtisii*, leaf [86ML-365]. B, median trullae; C, pygidial margin, dorsal, abd IV and V; D, antenna; E, anterior spiracle; F, trullae.

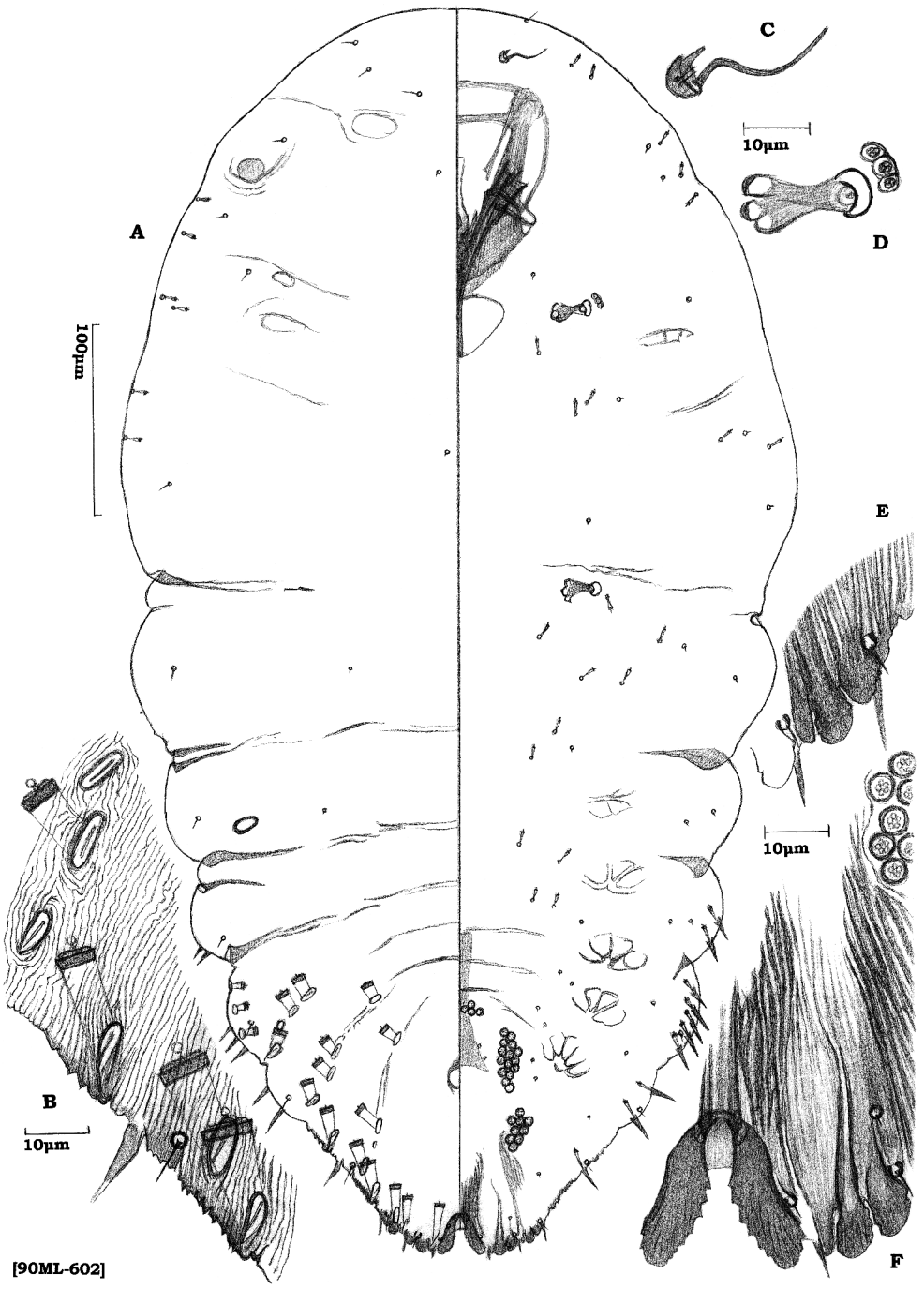

Fig. 28. *Aulacaspis canarii* (2.13.), adult female, probably fully grown. Kuala Lumpur, on *Canarium pilosum*, leaf [90ML-602]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, third trulla; F, median and second trullae.

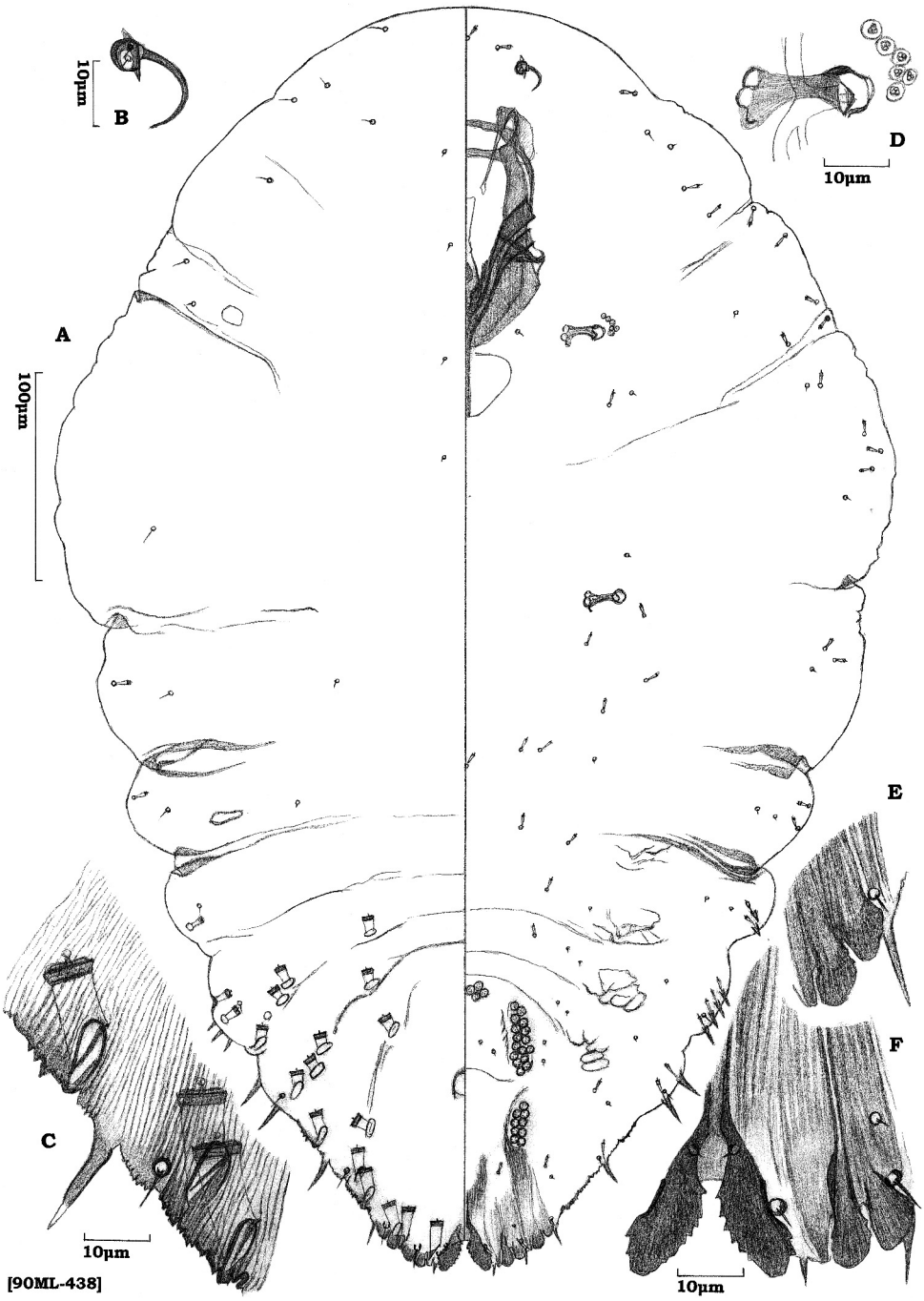

Fig. 29. *Aulacaspis canarii* (2.13.), adult female, probably fully grown. Kuala Lumpur, on *Canarium pilosum*, leaf [90ML-438]. B, antenna; C, pygidial margin, dorsal, abd IV and V; D, anterior spiracle; E, third trulla; F, median and second trullae.

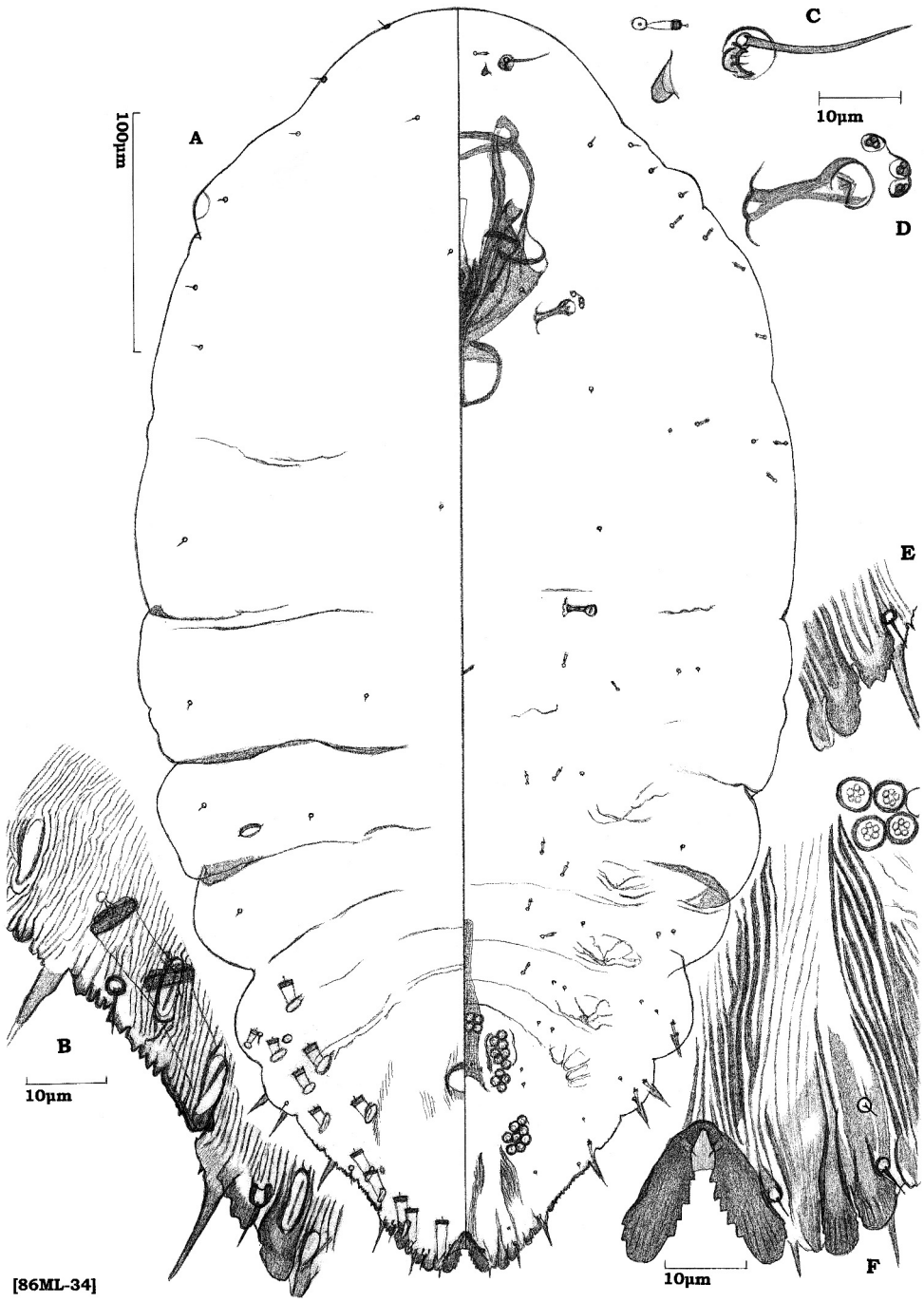

Fig. 30. *Aulacaspis canariicola* (2.14.), adult female, moderately grown. Pasoh Forest Reserve, Malaya, on *Canarium littorale*, leaf [86ML-34]. B, pygidial margin, dorsal, abd IV and V; C, antenna, interantennal derm pocket, and microduct; D, anterior spiracle; E, third trulla; F, median and second trullae.

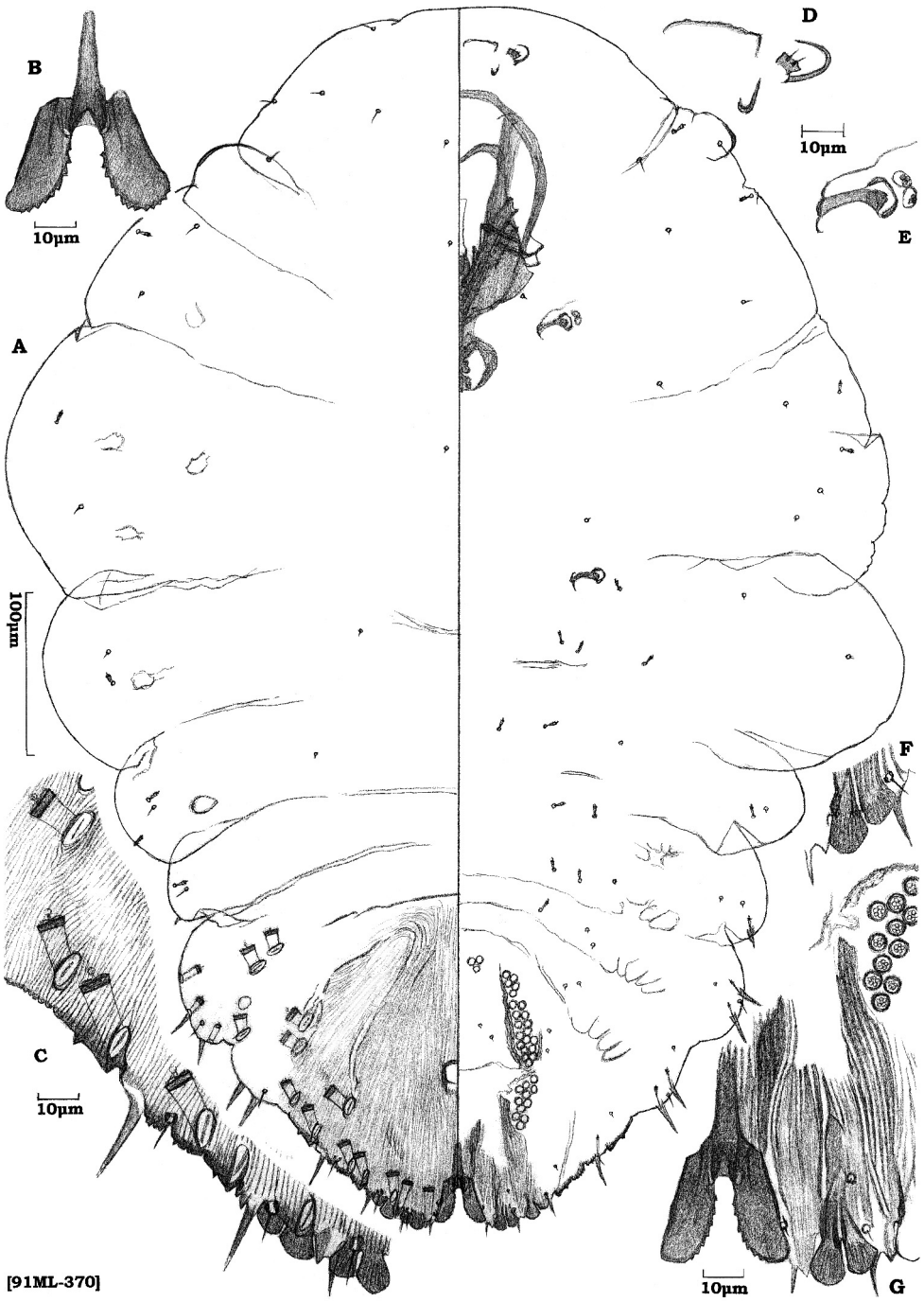

Fig. 31. *Aulacaspis canariiphila* (2.15.), adult female, full-grown. Gunong Jerai, Malaya, on *Canarium littorale*, leaf [91ML-370]. B, median trullae; C, pygidial margin, dorsal, abd IV and V; D, antenna, interantennal tubercle (part), and interantennal derm pocket; E, anterior spiracle; F, third trulla; G, median and second trullae.

Fig. 32. *Aulacaspis elongata* (2.16.), adult female, full-grown. Kuala Lumpur, on *Scaphocalyx spathacea*, leaf [90ML-72]. B, antennae and interantennal tubercle (interrupted medially); C, anterior spiracle; D, posterior spiracle; E, lateral lobe of abd III and marginal area of abd IV; F, pygidial margin, dorsal; G, part of pygidium, ventral.

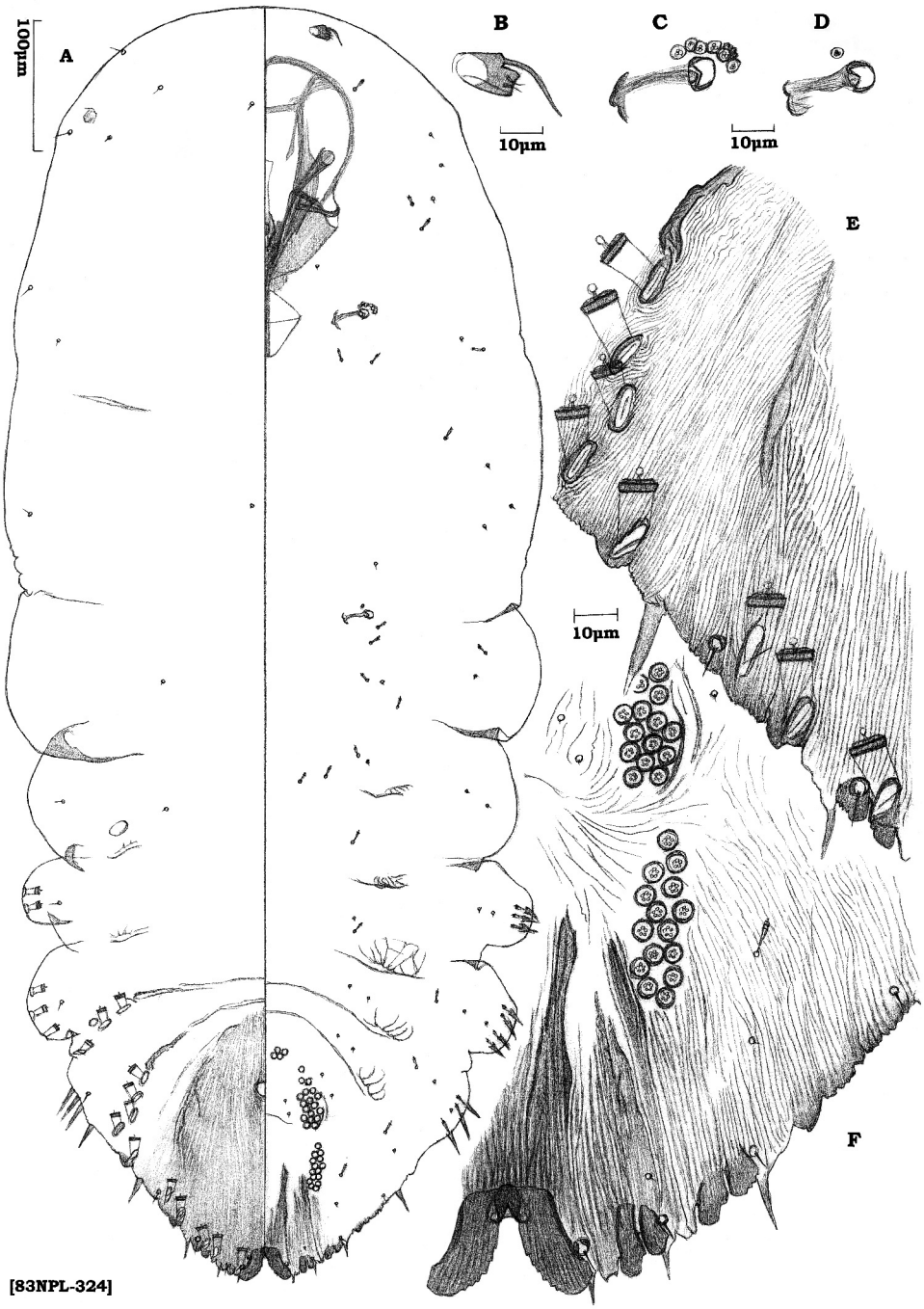

Fig. 33. *Aulacaspis katus* (2.17.), adult female, moderately grown. Pokhara District, 900m, Nepal, on *Castanopsis tribuloides*, leaf [83NPL-324]. B, antenna; C, anterior spiracle; D, posterior spiracle; E, pygidial margin, dorsal, abd IV–VI; F, part of pygidium, ventral.

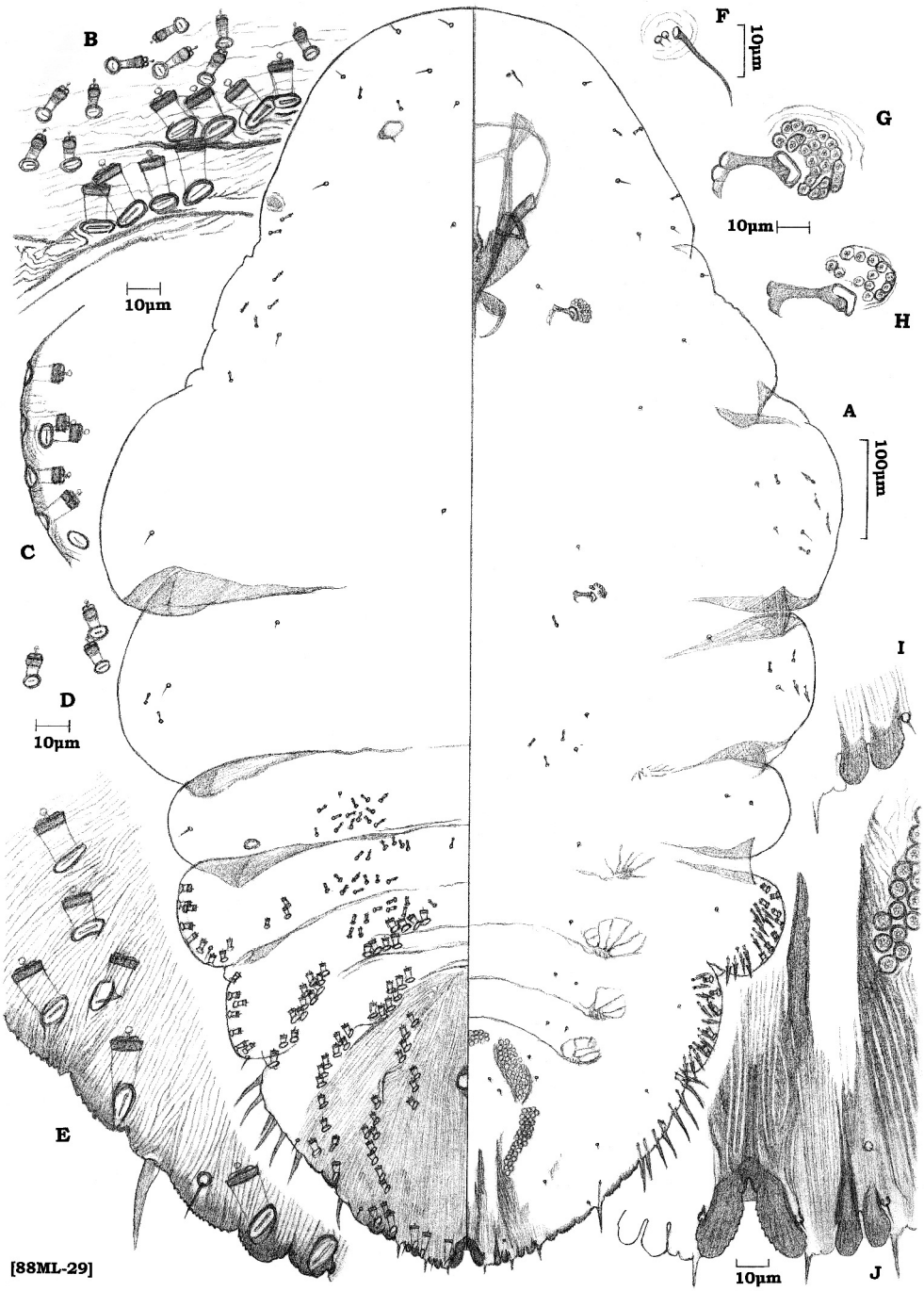

Fig. 34. *Aulacaspis dilleniae* (2.18.), adult female, moderately grown. Mt. Kinabalu, 2750m, Sabah, on *Dillenia* sp., leaf [88ML-29]. B, submedian dorsal macro- and microducts on abd III; C, lateral margin of abd III, dorsal; D, submarginal dorsal ducts on abd II; E, pygidial margin, dorsal, abd IV and V; F, antenna; G, anterior spiracle; H, posterior spiracle; I, third trulla; J, median and second trullae.

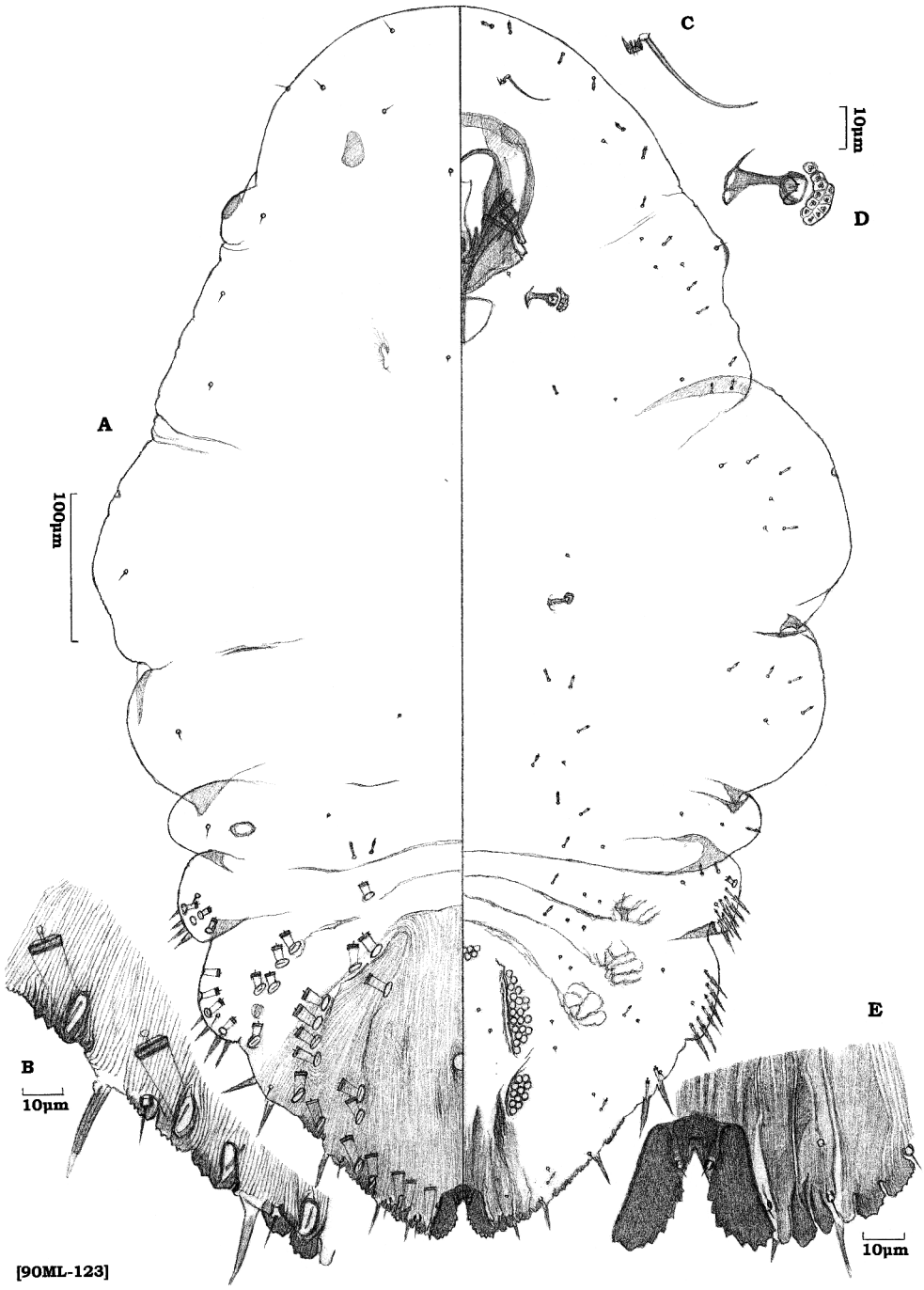

Fig. 35. *Aulacaspis guioae* (2.19.), adult female, nearly fully grown. Kuantan, Malaya, on *Guioa pleuropteris*, leaf [90ML-123]. B, pygidial margin, dorsal, abd IV–VI; C, antenna; D, anterior spiracle; E, trullae.

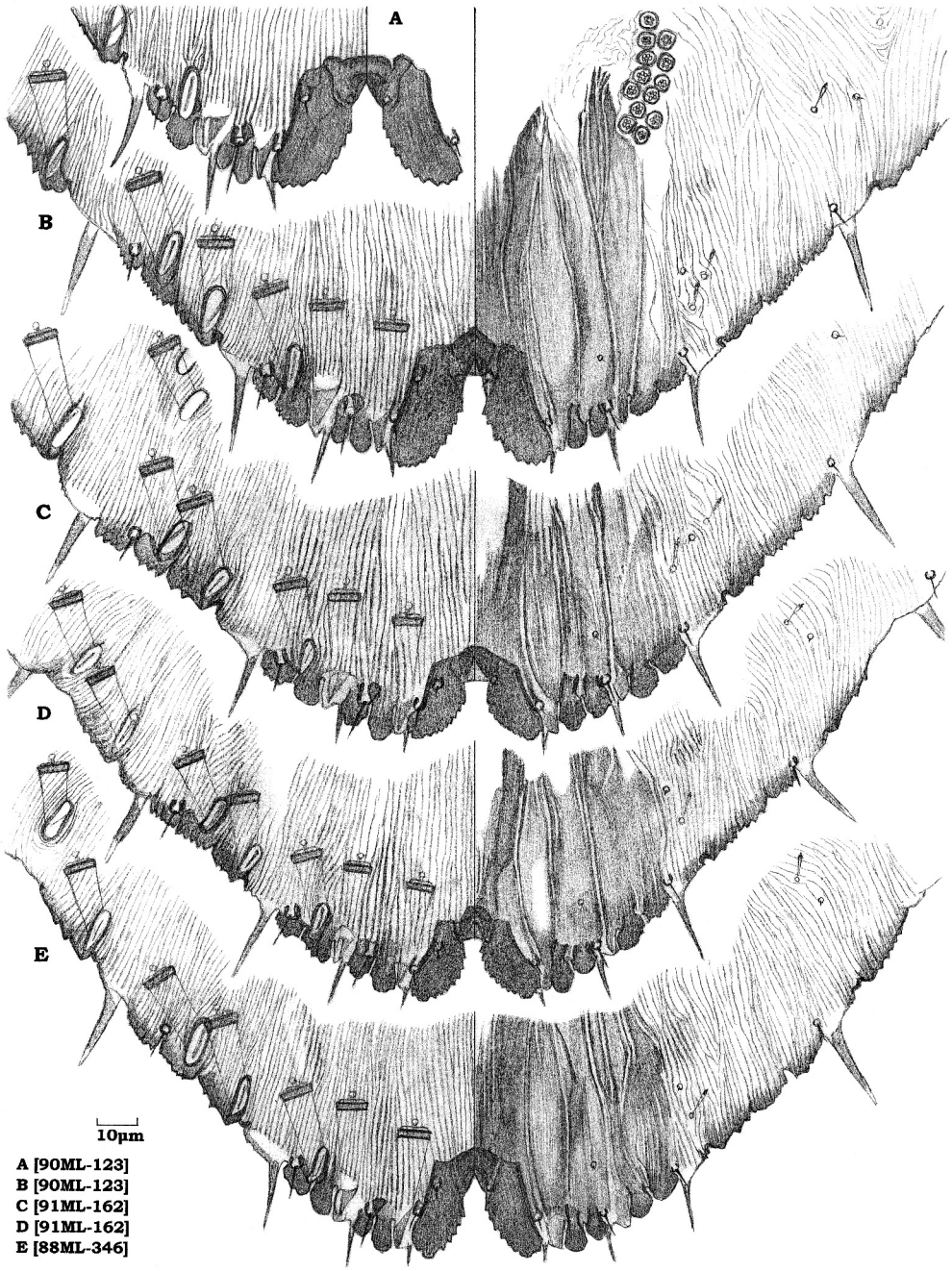

Fig. 36. *Aulacaspis guioae* (2.19.), adult female, pygidial margin. A and B, Kuantan, Malaya, on *Guioa pleuropteris*, leaf [90ML-123]; C and D, Bako National Park, Sarawak, on *Guioa* sp., leaf [91ML-162]; E, Sepilok, Sabah, on a sapindaceous plant, leaf [88ML-346].

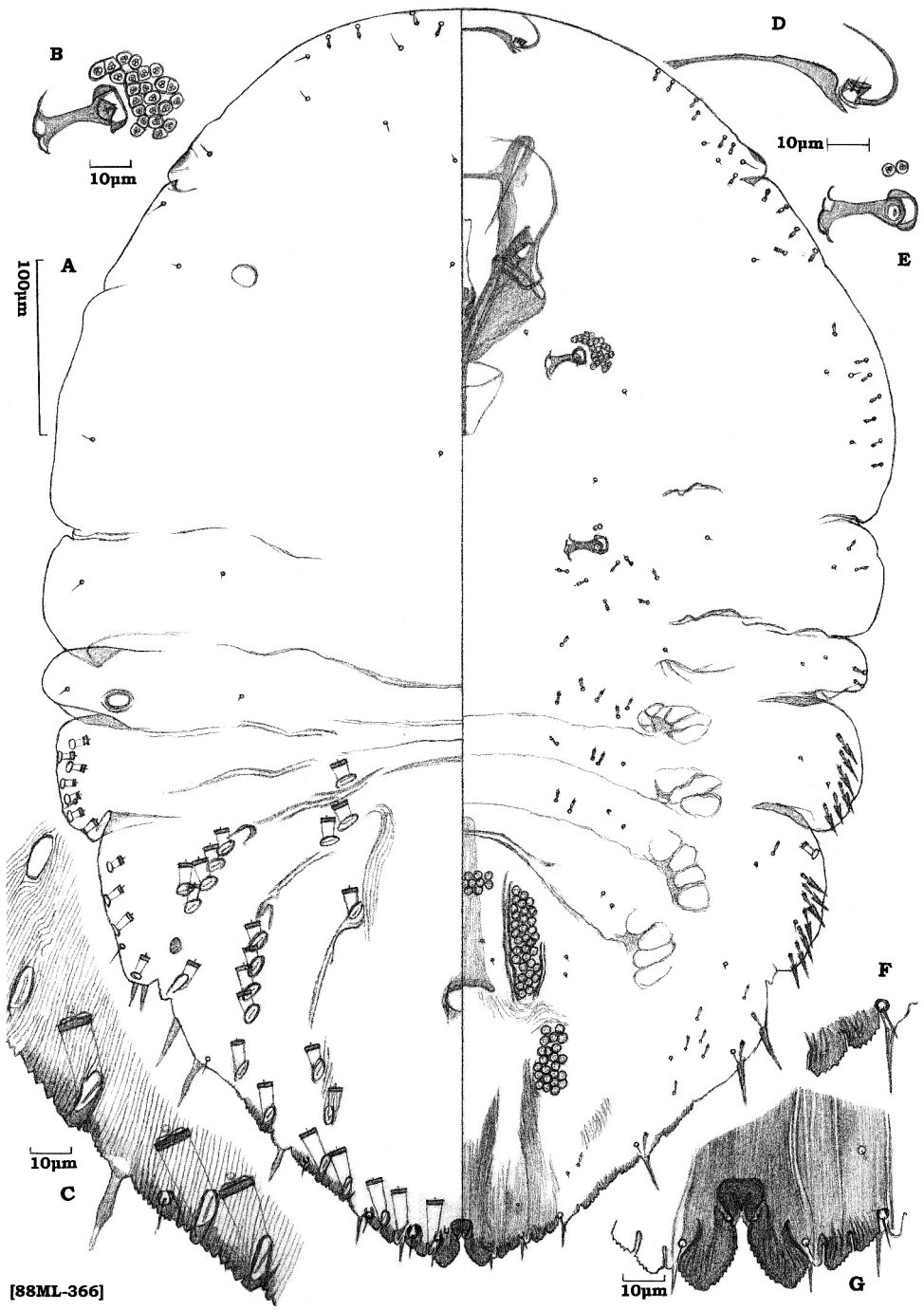

Fig. 37. *Aulacaspis enkleiae* (2.20.), adult female, juvenile. Kabili-Sepilok Forest Reserve, Sabah, on *Enkleia malaccensis*, leaf [88ML-366]. B, anterior spiracle; C, pygidial margin, dorsal, abd IV and V; D, antenna and interantennal tubercle (part); E, posterior spiracle; F, third trulla; G, median and second trullae.

Fig. 38. *Aulacaspis enkleiae* (2.20.), adult female, nearly fully grown. Kabili-Sepilok Forest Reserve, Sabah, on *Enkleia malaccensis*, twig [88ML-366]. B, lateral lobe of abd III; C, pygidial margin, dorsal, abd IV and V; D, antenna and interantennal swelling; E, anterior spiracle; F, posterior spiracle; G, trullae.

Fig. 39. *Aulacaspis artocarpi* (2.21.), adult female, probably fully grown. Kuala Lumpur, on *Artocarpus elasticus*, leaf [86ML-382]. B, lateral lobe of abd III; C, pygidial margin, dorsal; D, antennae, interantennal tubercle (interrupted medially), and interantennal derm pocket; E, anterior spiracle; F, third trulla; G, median and second trullae.

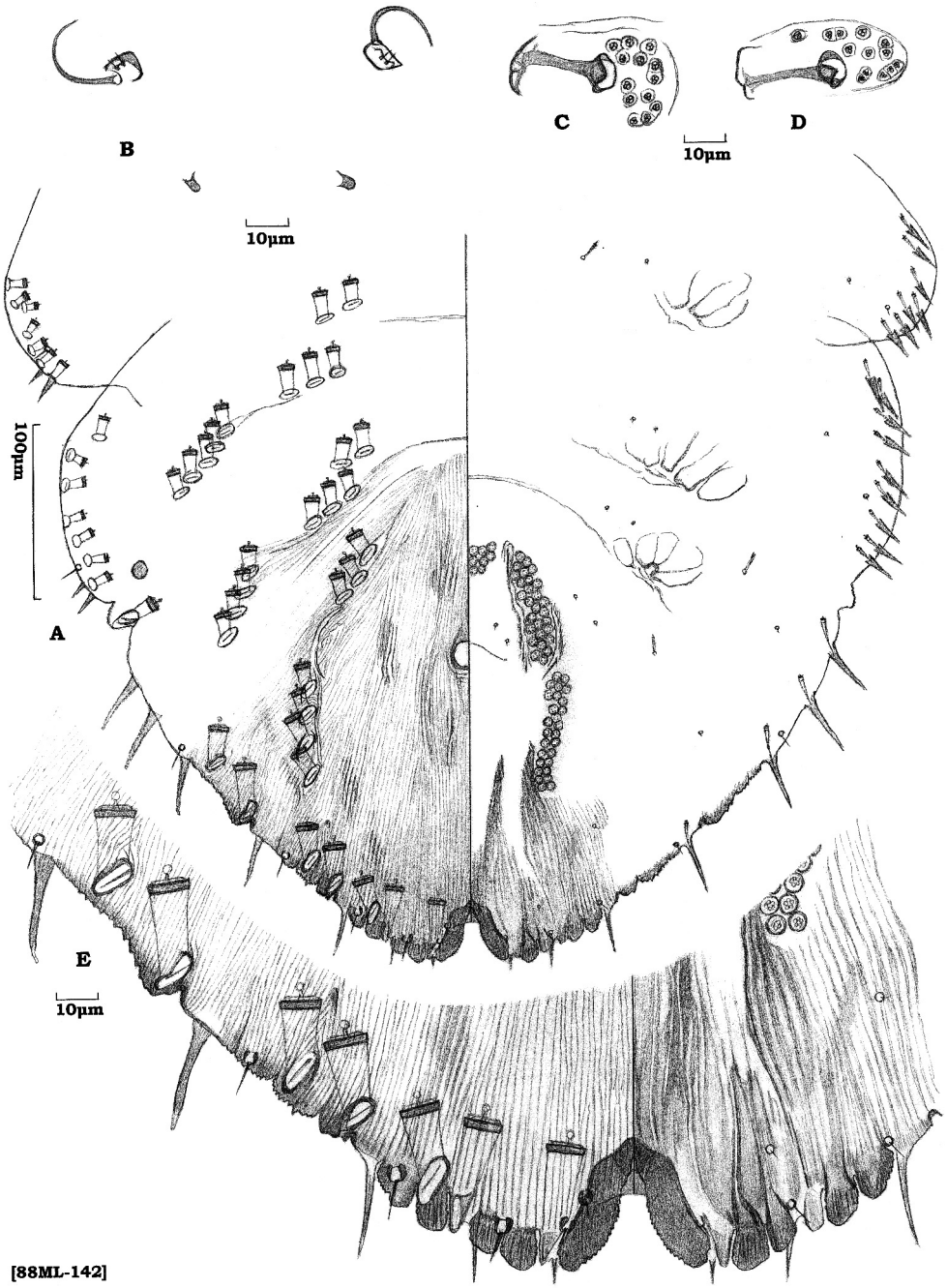

Fig. 40. *Aulacaspis* 88Kn-*Ap* (3.1.), adult female, probably fully grown. Mt. Kinabalu, 1780m, Sabah, on *Actinodaphne pruinosa*, leaf [88ML-142]. B, antennae and interantennal derm pockets; C, anterior spiracle; D, posterior spiracle; E, pygidial margin.

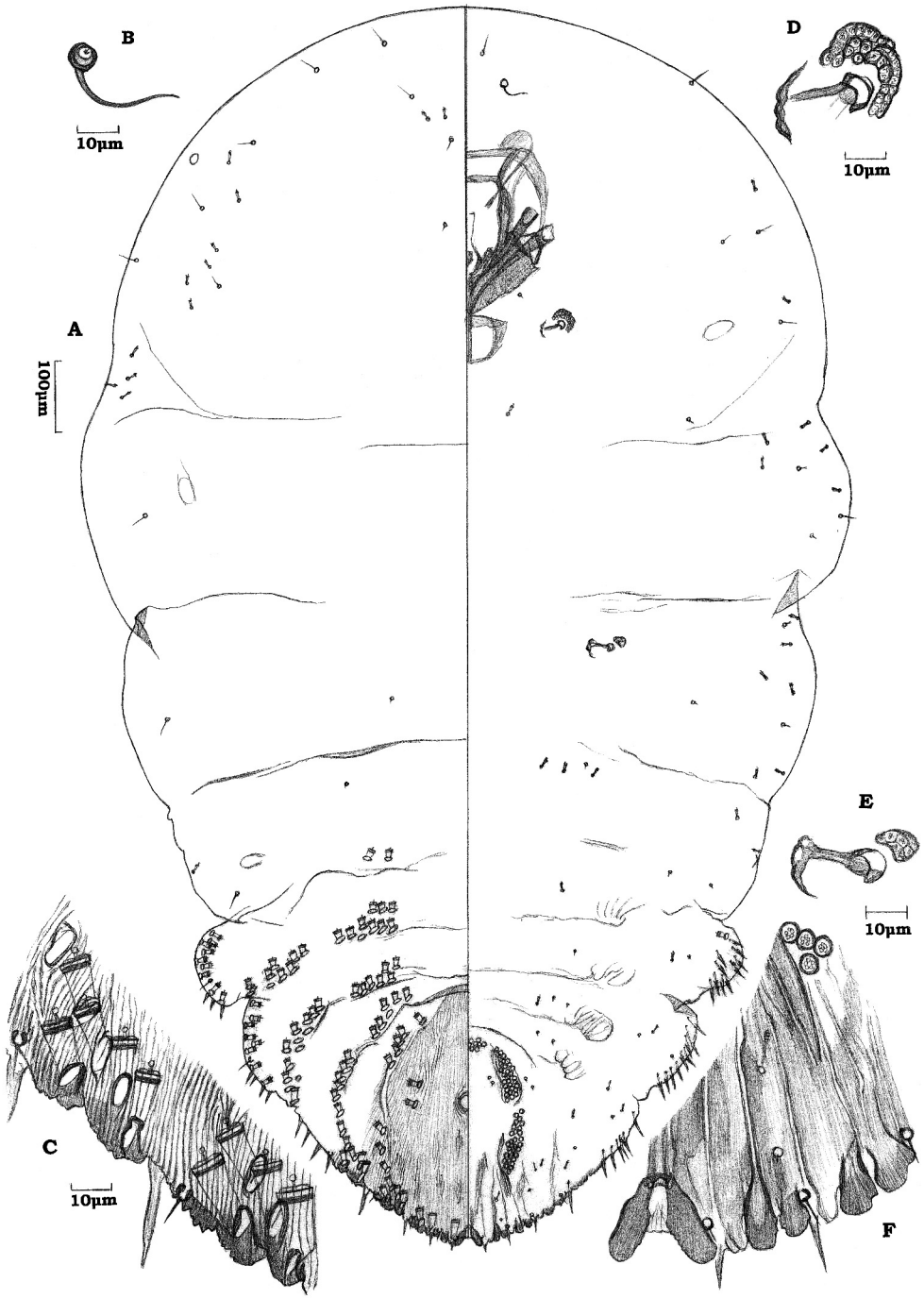

Fig. 41. *Aulacaspis* 65FCH-*Be* (3.2.), adult female, nearly fully grown (?). Fenchihu, Taiwan, on *Beilschmiedia erythrophloia*, leaf. B, antenna; C, pygidial margin, dorsal, abd IV and V; D, anterior spiracle; E, posterior spiracle; F, trullae.

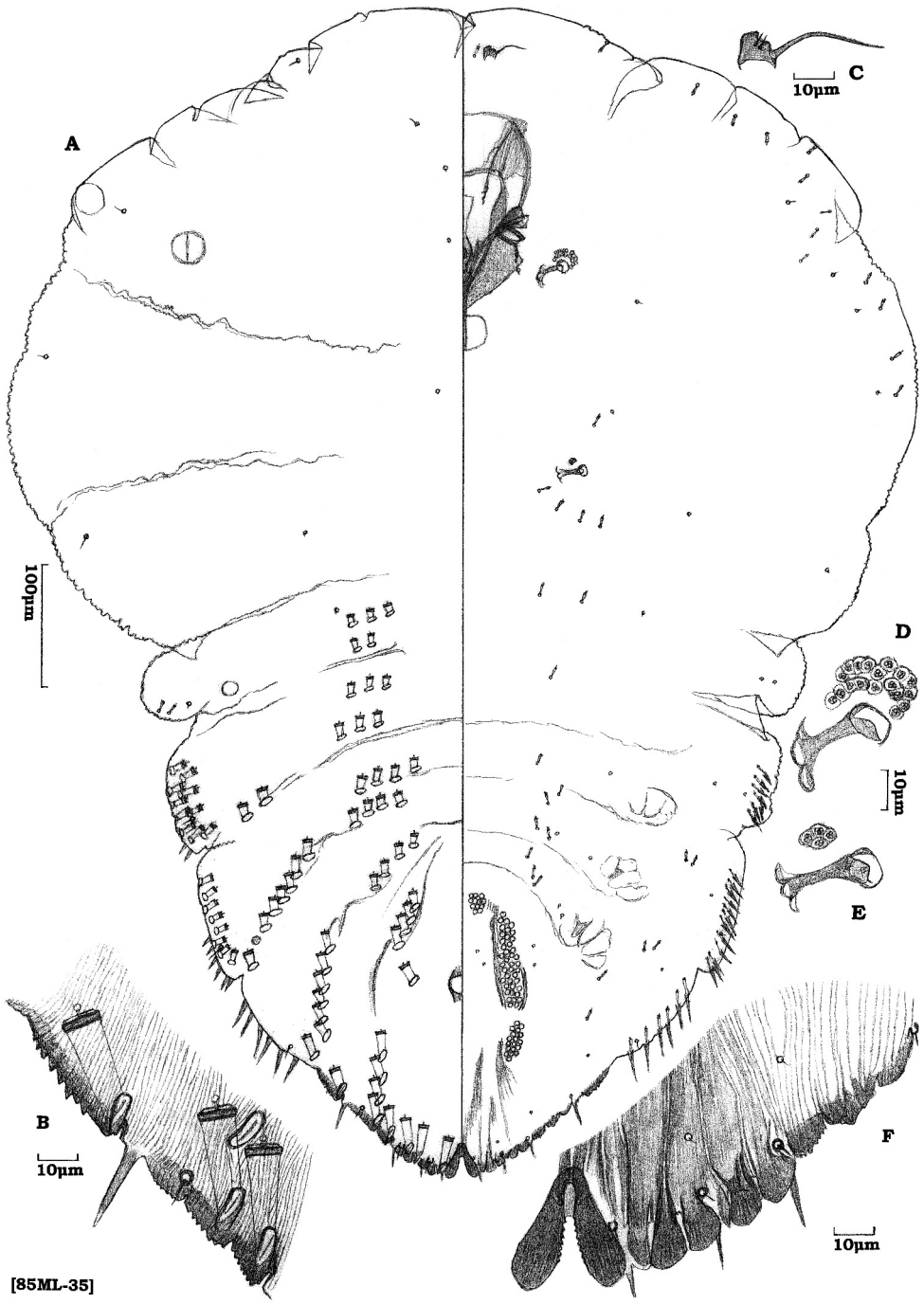

Fig. 42. *Aulacaspis* 85Ps-*N* (3.3.), adult female, full-grown. Pasoh Forest Reserve, Malaya, on *Neoscortechinia* sp., leaf [85ML-35]. B, pygidial margin, dorsal, abd IV and V; C, antenna; D, anterior spiracle; E, posterior spiracle; F, trullae.

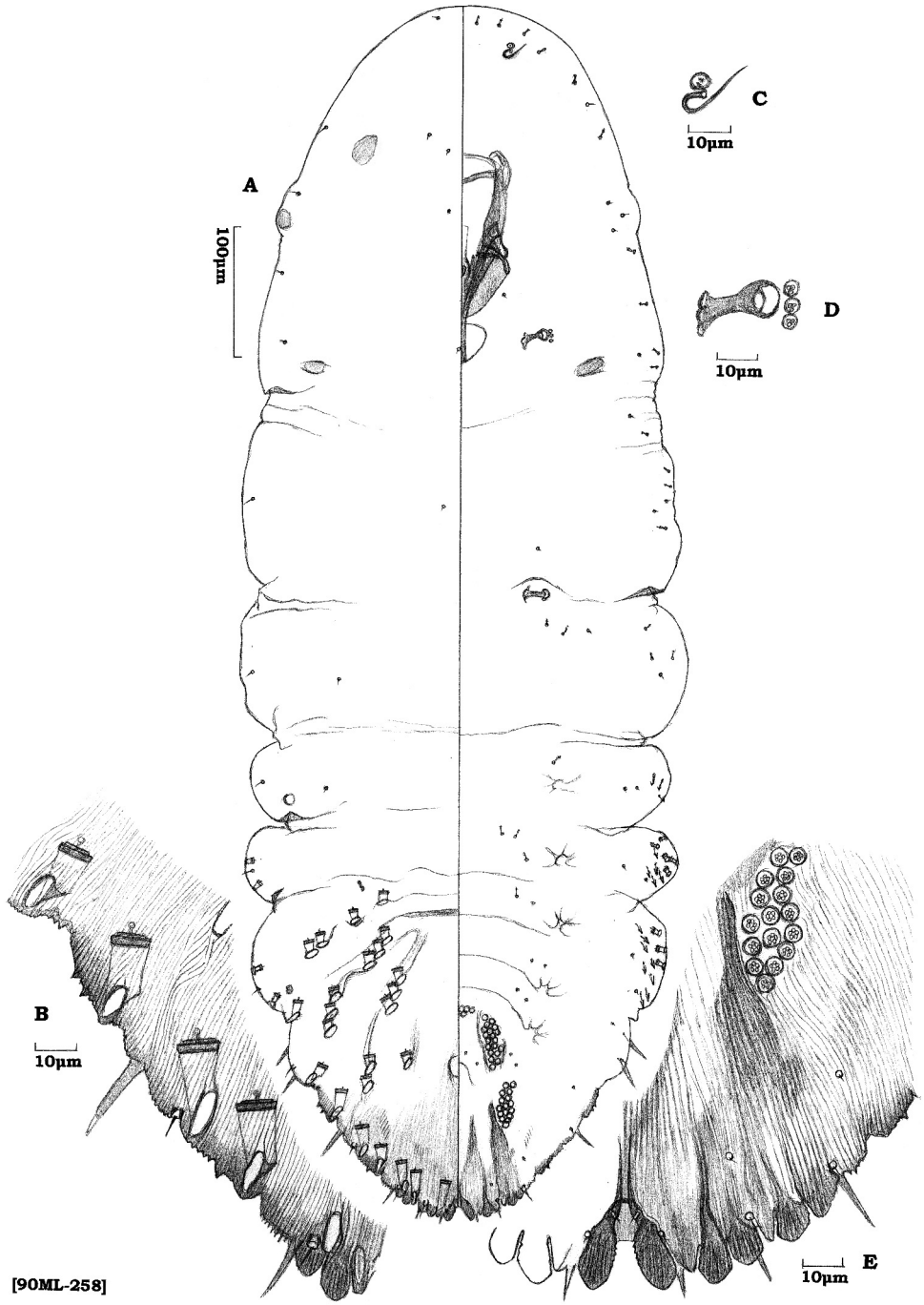

Fig. 43. *Aulacaspis* 90KD-*Lp* (4.1.1.; united with *Aulacaspis calcarata*), adult female, full-grown. Kuala Dungun, Malaya, on *Linostoma pauciflorum*, leaf [90ML-258]. B, pygidial margin, dorsal, abd IV–VI; C, antenna; D, anterior spiracle; E, trullae.

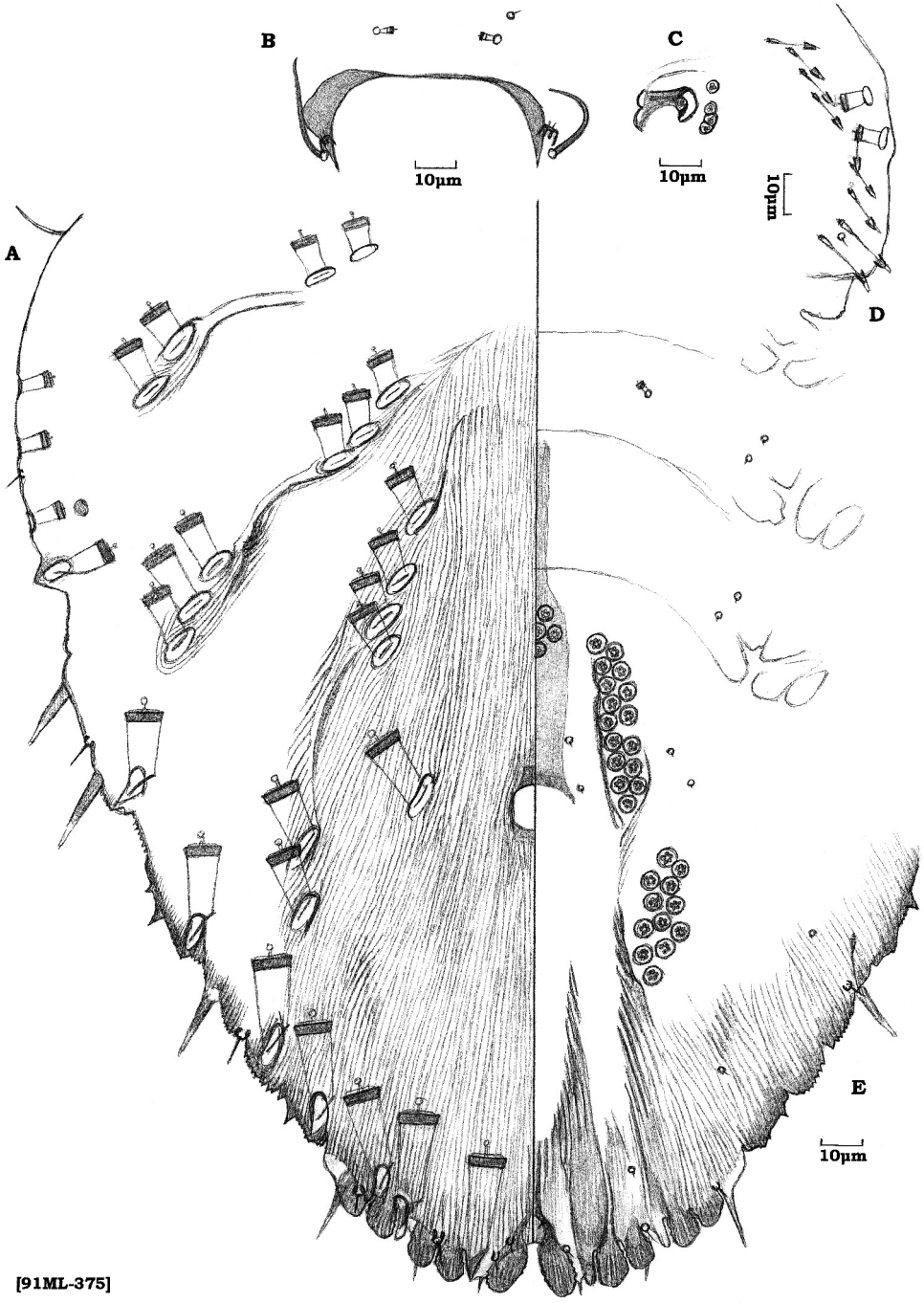

Fig. 44. *Aulacaspis* 91BP-*Dg* (4.1.2.; united with *Aulacaspis calcarata*), adult female, full-grown. Kedah, Malaya, on *Durio griffithii*, leaf [91ML-375]. B, antennae, interantennal tubercle, and microducts; C, anterior spiracle; D, lateral lobe of abd III, ventral; E, pygidium.