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FOUR EXTRAORDINARY DIASPIDIDS (HOMOPTERA: COCCOIDEA)

By SADAO TAKAGI

Systematic and Ecological Surveys on Some Plant-parasitic
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Abstract

TAKAGI, S. 2000. Four extraordinary diaspidids (Homoptera: Coccoidea). *Ins. matsum. n. s.* 57: 39–87, 34 figs.

Part I. *Sinistraspis unilateralis*, an extraordinarily asymmetrical diaspidid, is revised on the basis of specimens collected in Malaysia and the Philippines. It is especially peculiar in having huge multiglandular spines on the left lobes of the second and third abdominal segments. It is also asymmetrical in the occurrence of lateral and submarginal macroducts. But the asymmetrical state is not always stable, and the huge spine on the second abdominal segment is at times replaced by gland spines of usual size. As a result, the species appears less extraordinary and rather similar to *Pseudaulacaspis*. On the other hand, it is similar to the African *Heimaspis centrafricana* in the possession of the huge gland spines and in other characters. The two species may be closely related to each other, representing a connection between the diaspidid faunas of tropical Asia and tropical Africa. In any case, the asymmetrical state is of minor taxonomic importance, and *S. unilateralis* is referable to the subtribe Fioriniina, Diaspidini, together with *Pseudaulacaspis* and *Heimaspis*.

Part II. *Crockeraspis fungosa*, gen. et sp. nov., is described from Sabah (Borneo Is.), Malaysia. The female produces tubular wax filaments the same as *Sclopetaspis danumensis*, another Bornean species, does. *C. fungosa* is similar to *S. danumensis* in some characters of the adult female, but it is remarkably different from the latter in having robust zygotic median trullae. It is referable to the advanced subtribe Fioriniina, Diaspidini, whereas *S. danumensis* is a relatively primitive form of the tribe. Although the production of tubular wax filaments is quite extraordinary for diaspidids, the common occurrence of them in *Crockeraspis* and *Sclopetaspis* is attributable to parallel evolution. The adult females of these forms are similar probably owing to parallelism or convergence associated with the production of tubular wax filaments and the manner of test formation. According to this interpretation, the production of tubular wax filaments is not restricted to any particular lineage of the Diaspididae.

Part III. *Mempelaspis serpentina*, gen. et sp. nov., is described from Sarawak (Borneo Is.), Malaysia. It is referred to the tribe Lepidosaphedini, yet it is extraordinary for a member of the tribe in having well-developed pectinae. It is supposed to represent the most primitive form among the known Lepidosaphedini in the organization of the pygidial fringe, and a new subtribe, Mempelaspidina, is proposed for it. On this supposition the evolutionary stage it represents in the Lepidosaphedini approximately corresponds to that represented by the Kuwanaspidina in the Diaspidini. Even at this stage the tribe Lepidosaphedini is distinct from the Diaspidini, and the phylogenetic relationship between them remains uncertain.

Part IV. *Icaraspidiotus chaetopterus*, gen. et sp. nov., is described from Palawan Is., the Philippines. It is referable to the subtribe Pseudaonidiina, Aspidiotini, on the basis of the adult female, but there is little evidence to support this taxonomic position in the morphological characters of the first instar larva, which is extraordinary in having enormous laminate marginal setae. The significance of these setae is discussed in connection with aerial dispersal in the closed forest, and the first instar larva is supposed to have undergone a great morphological change with the emergence of a new manner of dispersal.

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INTRODUCTION

The armoured scale insect family Diaspididae is a fairly homogeneous group in spite of the fact that it is the largest among the families of the Coccoidea. Occasionally we come across extraordinary forms, but the possession of unusual characters does not always mean that such forms represent any isolated taxa. For example, the adult female of *Amphisoma erectum* is unique in having a set of well-differentiated submedian, submarginal and marginal macroducts on the ventral as well as dorsal surface of the pygidium. This character is associated with the habit. This species occurs on the hairy twigs of the host plant, 'standing' among the dense erect hairs, and constructs a bivalve test, of which the ventral valve is as elaborate as the dorsal. Other characters show that the species belongs to the Diaspidini, and suggest that it is related to *Pinnaspis*, a familiar genus (Takagi, 1995).

Four diaspidid species are described and discussed in this paper. They exhibit extraordinary characters in the adult female or the first instar larva. Explanations have been sought for these characters, and plausible ones are proposed. So far as the proposed explanations are accepted, these species do not violate the current taxonomic system, representing, however, their own genera and, in the case of one of them, even a new subtribe. In other words, traditional higher taxa, based principally on relative discontinuity in the correlation of characters, are robust enough to accept these extraordinary forms. Thus the four species are referred to the Diaspidini, the Lepidosaphedini, or the Aspidiotini, and, as regards three of them, to certain subtribes which have already been proposed.

ON A FEW TERMS AND ABBREVIATIONS ADOPTED

The term 'trullae' is used in place of 'lobes', and 'pectinae' in place of 'plates', of authors. 'Megaducts' corresponds to the French term 'mégapores' and 'glanduliferous craters' (adopted by Takagi, 1999) to 'cratèrs glandulifères'. One of the new species described below, *Mempelaspis serpentina*, is provided on the pygidial margin with glanduliferous pectinae, which are peculiar in having an elongate glanduliferous process. They are termed 'spiniferous pectinae', and non-glanduliferous pectinae are called 'simple pectinae'.

The abbreviations 'Abd I–IX' stand for the first to ninth abdominal segments.

PART I. SINISTRASPIS UNILATERALIS, AN ASYMMETRICAL DIASPIDINE

INTRODUCTION

Arthropods are among bilaterally symmetrical animals. Insects of the superfamily Coccoidea are usually illustrated in a composite figure divided by a line into the right and left halves, with the dorsal surface on one of the lateral halves and the ventral surface on the other. In reality, however, they are only approximately symmetrical, the correspondence between the lateral halves lacking mirror-image exactitude, and sometimes noticeably deviate from symmetry. *Asymmetraspis distorta* (=*Chionaspis distorta* Newstead, 1917) was described on the basis of specimens rather remarkably distorted in body outline. Generally such a distortion is due to different growth rates induced incidentally between the right and left side. Distortions are especially observable in full-grown adult females occurring on the margin of a leaf, on the side of a leaf vein, and so on. In such cases growth is depressed on the body side which is in contact with the leaf edge, the vein, or other plant structures, resulting in asymmetry in the shape of body, in the positions of appendages, in the development of features, and so on. All these variations are apparently non-genetic. Examples are known especially in the family Coccidae. In the family Diaspididae the adult females of *Coronaspis malesiana* and *C. malabarica* are obviously asymmetrical at full growth. They always occur on the leaf margin, and the body side lying just on the leaf edge becomes considerably undergrown (Takagi, 1999).

The diaspidid *Sinistraspis unilateralis* has been known to be extraordinarily asymmetrical in the body structure of the adult female. It is especially characterized by having huge multiglandular spines on the second and third abdominal segments, but these spines are confined to the left side. The occurrence of submarginal macroducts is limited to the right side, and the gland spines and lateral macroducts are more numerous on the right side. The pattern of unilateral preponderance is constant, and indicates that the asymmetrical state is genetic. Because genetic asymmetry is quite unusual in scale insects, the species may be supposed to be very peculiar taxonomically. But the asymmetrical state is not fully stable as shown below, and the occasional breakdown of asymmetry leads us to another view.

DESCRIPTIONS

Sinistraspis unilateralis

Newstead, 1913 [original description under the name *Chionaspis unilateralis*; Barbados Is., on leaves of a palm (*Thrinax*?)]. — MacGillivray, 1921 [erection of *Sinistraspis* for *C. unilateralis*]. — Ferris, 1936 [figures]. — Rao and Kumar, 1952 [Trivandrum, Kerala, India, on a palm].

Material. Collected in Malaysia (Malaya; Sarawak and Sabah [Borneo Is.]) and the Philippines (Luzon Is.; Palawan Is.). The material includes two distinct types of the second instar male: crater type and craterless type.

Material with the second instar male of the crater type. Malaya — Cape Rachado, Negeri Sembilan, on *Artocarpus integer* (Moraceae) [material 86ML-448]; Beserah Forest Reserve, Kuantan, Pahang, on *Streblus elongatus* (Moraceae) [90ML-104]; Bukit Bauk, Terengganu, on *Scaphium macropodum* (Sterculiaceae) [90ML-233]; Air Terjun Kota Tinggi, Johor, on *Parastemon urophyllus* (Rosaceae) [90ML-562]; Gunung Jerai, alt. ca. 930m, Kedah, on *Leptospermum flavescens* (Myrtaceae) [91ML-328]. Sarawak — Santubong, Kuching District, on *Drypetes* sp. (Euphorbiaceae) [91ML-255]. Sabah—Sandakan, on *Strychnos* sp. (Loganiaceae) [88ML-354]. Palawan Is.—Puerto Princesa, on *Parinari bicolor* (Rosaceae) [93PL-36].

Material with the second instar male of the craterless type. Sarawak — Santubong, Kuching District, on *Dracontomelon dao* (Anacardiaceae) [91ML-250].

Material with no specimens of the second instar male. Malaya — Beserah Forest Reserve, Kuantan, Pahang, on *Dacryodes rostrata* (Burseraceae) [90ML-118] and *Strychnos ignati* (Loganiaceae) [90ML-308]; Bukit Bauk, Terengganu, on *Swintonia schwenkii* (Anacardiaceae) [90ML-253]. Sarawak — Bako National Park, Kuching District, on *Eugenia* sp. (Myrtaceae) [91ML-158]; Gunung Lundu, Kuching District, on *Spatholobus* sp. (Fabaceae) [91ML-210]. Sabah — Sandakan, on *Artocarpus integer* (Moraceae) [88ML-258]. Luzon Is. — Grounds of the University of the Philippines at Los Baños, Laguna, on *Arenga pinnata* (Arecaceae) [92PL-29].

Habit. Occurring on the leaves. Female test slender, white, thin; exuvial casts pale yellow to light brown; male test felted, with a median carina.

Adult female (typically asymmetrical form) (Fig. I-1). On the left side of the body:

lateral lobes of Abd II and III tuberculate, each apically produced into a single huge spine bearing microducts, which are much larger than microducts associated with gland spines occurring on the right side (huge spine of Abd II with 5–15 microducts, that of Abd III with 3–10); 1 marginal gland spine on Abd IV with 2 microducts; 1–5 lateral macroducts on Abd I, no macroducts on other prepygidial segments; no submarginal macroducts on pygidial segments. On the right side of the body: lateral lobes of Abd II and III little produced, with 2–8 and 1–5 gland spines of usual type; Abd IV with 1 or 2 marginal gland spines; lateral macroducts present on metathorax and Abd I–III (4–10 on metathorax, 4–12 on Abd I, 2–9 on II, 1–3 on III); submarginal macroducts present on Abd IV and V (1–8 on Abd IV, 1–5 on V). No remarkable asymmetry is recognized in other features. Body slender, when fully grown about 4 times as long as wide owing to especially elongated thoracic region; frontal margin flatly roundish, head and thorax with lateral margins nearly straight and parallel; pygidium rather narrow, roundish along margin. Antennae situated just within frontal margin, separated from each other by a space narrower than mouthparts, each with a single curved seta. Anterior spiracles each with 1 trilocular disc pore, at times with 2–4; posterior spiracles with no disc pore. Perivulvar disc pores in 5 groups; 1–4 (usually 2) medians, 3–9 (usually 5 or 6) anterolaterals, and 6–11 (usually 7–9) posterolaterals. Anus a little anterior to centre of pygidium. Median trullae united basally, forming a notch at apex of pygidium, mesal margins divergent, roughly serrate, with a pair of well-developed setae basally; variable in size (Figs. I-2, -3). Second trullae well represented, bilobulate, inner lobule round apically, with a pair of long slender basal scleroses extending onto ventral surface of pygidium, outer lobule smaller than the inner. Marginal macroducts: 1 between median and second trullae (on Abd VII), associated with a pointed pore prominence, 2 on each of Abd VI, V, and IV, and 1 at base of pygidium (belonging to Abd III), each associated with a robust pore prominence. No submedian macroducts. Marginal gland spines single on Abd V–VIII, slender.

Second instar male (Figs. I-4, -5). Heteromorphic (that is, remarkably differing from the adult and second instar females in character pattern), agreeing in principal pattern with the heteromorphic second instar males of many other Diaspidini. Two pairs of trulla-like unilobed marginal appendages on pygidium; the appendages of the mesal pair are serrate and may correspond to the median trullae of the adult and second instar females, but are separated from each other by a space much wider than one of them; outer pair fimbriate rather than serrate, thus less trulla-like, accompanied just laterally by 1 or a few spiniform processes. Specimens from some localities possess a glanduliferous crater and some short ducts between the dorsal marginal setae of Abd VI and VII (crater type; Fig. I-4); specimens mounted from the material collected at Santubong, Sarawak, on *Dracontomelon dao* [91ML-250] have no crater (craterless type; Fig. I-5).

Breakdown of asymmetry

The asymmetrical state of the adult female described above breaks down to various degrees. The huge multiglandular spine occurring on the left side of Abd II is sometimes replaced by 2–4 smaller spines, and each of these spines bears 1–5 microducts. At times gland spines occurring on the right lobes of Abd II and III are enlarged to bear 2–7 microducts, and on Abd III they are even replaced by 1 huge spine, which is nearly as large as the multiglandular spine on the left side. A few to several submarginal macroducts normally occur on the right side of Abd III and IV, but occasionally none is seen on either or both of these segments. On the left side, where no submarginal macroduct normally occurs, 1 submarginal macroduct is rarely seen on Abd III and 1–5 ducts are sometimes found on IV. On the left side, lateral macroducts normally occur only on Abd I, but are sometimes found on other segments, too. These variations have been observed not in all the examined samples but in some of them. The mounted specimens of many samples, however, are represented by too few specimens to see if the variations are associated with any particular samples and with any particular localities or host plants.

DISCUSSIONS

More than one species?

The examined specimens of the adult female as a whole are very variable in the size of the median trullae (Figs. I-2, -3). In Fig. I-3 Dice-grams are prepared for only six samples, which are represented by relatively numerous (14–27) specimens. The ranges largely overlap, and it is expected that a completely continuous series will be formed when more samples are added. The second trullae are also somewhat variable in size, but no other features vary in correlation with the median trullae. All the examined specimens are similar in the numbers of the spiracular disc pores and perivulvar disc pores. Indeed the difference between the smallest and the largest trullae appears great, but the examined adult females cannot be divided into discrete forms.

On the other hand, the presence of two distinct types of the second instar male, the crater type (Fig. I-4) and the craterless type (Fig. I-5) as defined in the description above, favours the suspicion that more than one species is present in the examined material. Second instar males of the craterless type have been found only in the material collected at Santubong, Sarawak, on *Dracontomelon dao* [91ML-250]. The specimens of the adult female mounted from the same material are characterized by having especially large median trullae (Fig. I-2, G, H; Fig. I-3, F). Adult females collected at the same locality on *Drypetes* sp. [91ML-255] have much smaller median trullae (Fig. I-2, A, B; Fig. I-3, A), and are associated with second instar males of the crater type. The sympatric occurrence of the two distinct forms suggests that they are different species.

Adult females collected in Palawan [93PL-36] have very large median trullae (Fig. I-2, E, F; Fig. I-3, E) and are very similar to those of the form associated with *Dracontomelon* at Santubong, whereas the second instar males mounted from the same material belong not to the craterless type but to the crater type. Thus the distinction drawn between the two Santubong forms is now blurred. The adult female samples other than shown in Fig. I-3 are represented by very few specimens. Not all of the examined samples are accompanied by specimens of the second instar male. Under these conditions the problem should be kept pending, and all the examined samples are tentatively referred to *Sinistraspis unilateralis*.

Newstead (1913) described *Chionaspis unilateralis* on the basis of specimens collected in Barbados, the easternmost of the Caribbean islands, on an undetermined palm at 'Merton Lodge' (name of a hotel?), and Rao and Kumar (1952) recorded *Sinistraspis unilateralis* from southern India as occurring on 'a garden palm'. The adult females examined in the present study were collected from a wide variety of dicotyledons except those collected at Los Baños, Luzon, on the palm *Arenga pinnata* [92PL-29]. I have found no appreciable difference between the sample from the palm and some of the samples associated with the dicotyledons (Figs. I-2, -3). Balatibat (1991) described and figured a scale insect collected on Mt. Makiling, Los Baños, from *Arenga pinnata*; he gave it another name, but I have no doubt that it is the same as that I collected from the palm. Neither he nor I got the scale insect from any dicotyledon at Los Baños, whereas in Malaysia I got no material of *Sinistraspis* from any palm. It is, therefore, another pending problem whether the dicotyledon-associated forms are really conspecific with the palm-feeding form.

The genus *Sinistraspis* is undoubtedly native to Southeast Asia, being represented there by various forms as shown in the present study. The occurrence of *Chionaspis unilateralis* in Barbados should be attributed to introduction.

Unstable asymmetry and its consequence

The asymmetrical occurrence of gland spines and macroducts and especially of the huge multiglandular spines may be supposed to give a good reason to believe that *Sinistraspis unilateralis* represents a peculiar taxon. As described above, however, the asymmetrical state is not stable. The huge spine on the second abdominal segment can be replaced by gland spines of usual size, and on the right side of the third segment the usual gland spines can be changed into a huge spine. These features are homologous and easily interchangeable. When this is taken into consideration, the taxonomic value of the huge multiglandular spine is much diluted. In fact, *S. unilateralis* does not essentially differ from *Pseudaulacaspis* in the characters of the pygidial margin. *Pseudaulacaspis* is a very large genus with many undescribed species occurring in Asia, and its limits are still uncertain. There are in tropical Asia some satellite forms around it, requiring critical study of their generic positions, and *S. unilateralis* may be among them. However, the elongate, slender body and the absence of submedian macroducts are unusual for a *Pseudaulacaspis* species. *Sinistraspis* may tentatively be accepted as a valid genus related to *Pseudaulacaspis* [for an alternative view, see 'African connection?' below].

African connection?

Balachowsky and Ferrero (1967) described *Heimaspis centrafricana* [originally *Heimaspis centrafricanus*] from the forest of La Maboké, the Republic of Central Africa. This species is similar to *Sinistraspis unilateralis* in the lateral lobe of the second abdominal segment and also of the third produced into an eminent multiglandular spine (which, however, occurs on either side of the body and bears only three microducts). It agrees with *S. unilateralis* also in the elongate body, in the absence of submedian macroducts, in the zygotic median trullae having a pair of well-developed setae between them, etc. These two species, therefore, may be closely related to each other, contributing to the connection between the diaspidid faunas of tropical Africa and tropical Asia.

A huge multiglandular spine is, however, interchangeable with a group of gland spines of usual size as shown in the preceding section. Usual gland spines may develop into huge multiglandular spines in remotely related forms in parallel. In this regard, the possibility is not excluded that *Heimaspis centrafricana* and *Sinistraspis unilateralis* are not particularly closely related, representing analogues occurring in the different tropical regions.

Conclusion

The tropical Asian *Sinistraspis unilateralis* is characteristic in the asymmetrical occurrence of some features, and especially in having huge multiglandular spines on the left lobes of the second and third abdominal segments. Occasionally the huge spine of the second segment is replaced by gland spines of usual size, and the gland spines occurring on the right side of the third segment are changed into a huge spine. These variations decrease the taxonomic value of the huge multiglandular spine. In fact, in the characters of the pygidial margin the species does not essentially differ from *Pseudaulacaspis*. On the other hand, in the occurrence of the huge spines *S. unilateralis* is similar to the tropical African *Heimaspis centrafricana*, and may be closely related to the latter. In any case, the asymmetrical state of *S. unilateralis* is of minor importance taxonomically, and the species is undoubtedly referable to the subtribe Fioriniina, Diaspidini, together with *Pseudaulacaspis* and *Heimaspis*.

PART II. ANOTHER DIASPIDINE COVERED WITH TUBULAR WAX FILAMENTS

Introduction

SEM [scanning electron microscope] studies have shown that wax secretions of Coccoidea are not uniform. Many armoured scale insects and especially the females including those of the primitive subtribe Protodiaspidina secrete depressed, ribbon-like wax filaments to form a test. In advanced diaspidids the female makes rotative movements, thus forming a test of thin and tight texture. On the other hand, the very primitive diaspidid genus *Ulucoccus* produces cylindrical (and solid) wax filaments in both the male and the female (Takagi, 1992, fig. 68). In the female *U. gombakensis* the insect body is covered with a loose mass of entangled curved filaments (Takagi, 1998). Cylindrical filaments have also been observed in the males of Diaspidini (for example: Takagi, 1993, fig. 53).

In 1992 I described *Sclopetaspis danumensis* from the Danum Valley, Sabah (Borneo Is.), Malaysia, in connection with a revision of two species of the lepidosaphedine genus *Mitulaspis* occurring in Uganda and Malaya. The genus *Sclopetaspis* had been known only by two species described from tropical Africa, and the Bornean species was referred to the genus on the basis of adult female characters. SEM observations revealed that *S. danumensis* is extraordinary for a diaspidid in producing tubular wax filaments in both sexes, and that the test is composed of filaments secreted by the immobile insect body not only in the male but also in the female. It was assumed from the descriptions of the tests that the African species, too, produce tubular wax filaments. Comparisons of the larval instars as well as SEM observations on the tests of the African species are necessary to confirm the supposed relationship of the Bornean species to the African species. If all these species are really congeneric, they will afford good evidence for the presence of some connection between the armoured scale insect faunas of tropical Asia and tropical Africa [for another possible example, see Part I].

Tubular wax filaments occur in another Bornean diaspidid, which, however, does not seem to be closely related to *S. danumensis*.

Descriptions

Crockeraspis, gen. nov.

Type species. *Crockeraspis fungosa*, sp. nov.

This genus seems to be related to *Pseudaulacaspis* in having strongly zygotic median trullae and a pair of well-developed setae between them, but definitely differs from the latter in the second trullae reduced into small pointed processes, in lacking well-differentiated marginal macroducts on the pygidium, and in having a number of small, short ducts on the dorsal surface of the prosoma. It is also quite different in the female test, which is composed mainly of tubular wax filaments. In this respect and in some characters of body features it is very similar to *Sclopetaspis* (as represented by *S. danumensis*), but may not be closely related to the latter as will be discussed.

Crockeraspis fungosa, sp. nov.

Material. Collected on the Crocker Range, at an altitude of 1,300–1,400m, on the roadside between Keningau and Ulu Kimanis, near Gunung Rinangsan, Sabah (Borneo Is.), Malaysia, on *Adinandra* sp. (Theaceae), 8 Nov. 1988 [material 88ML-284].

Holotype: adult female, deposited in the collection of the Entomology Division, Forest Research Institute of Malaysia.

Habit. Occurring on the lower surface of leaves. Completed female test (Fig. II-7) globular, dirty grayish brown, appearing like a mass of hyphae (Fig. II-8); beneath the mass of wax filaments the central body of the test is hard and shell-like in texture, forming a space to accommodate the insect body. Male test (Fig. II-12) appearing to be of a usual diaspidine type, oblong, white, smooth, with no median carina. In SEM observations the female test is composed mainly of tubular wax filaments (Fig. II-10), and the male test is a rather loose mass of coiled ribbon-like filaments (Figs. II-13).

Adult female (based on 30 specimens) (Figs. II-1, -2). Body robust, pyriform, broadest across metathorax and base of abdomen, narrowing towards head. Pygidium composed of Abd V and succeeding segments, broad, roundish on margin. Median trullae large and robust, zygotic basally, divergent, forming a deep notch at apex of pygidium and almost wholly sunken in the notch, the mesal margins rather roughly serrate, with a pair of well-developed setae basally. Second trullae bilobulate, both lobules small and pointed; similar conical processes occurring along pygidial margin (tending to be set back within the margin on the ventral surface). Short marginal gland spines occurring singly on Abd V–VIII; Abd II–IV each with 1 or 2 similar gland spines laterally; thoracic region with a few very minute gland spines. About 120–200 small, short ducts on dorsal surface of prosoma, each with a round orifice (Fig. II-6) and with inner end presenting a distorted 8- or S-shape; these ducts are irregularly strewn, but as a whole form a broad band approximately of an inverted U-shape. Submedian and submarginal macroducts small and few. Marginal macroducts not well differentiated on pygidium: 1 duct associated with a conical process between median and second trullae (on Abd VII), 2 situated near margin on Abd VI and also on V. Antennae just in front of mouthparts, set close, each with a seta; sometimes their tubercles are united together. Anterior spiracles each with 3–8 trilocular disc pores; posterior spiracles with none. Perivulvar disc pores in 5 groups, 6–11 medians, 6–16 anterolaterals, and 8–15 posterolaterals. Anus rather small, a little anterior to centre of pygidium.

Second instar female (Fig. II-3). Similar to adult female especially in pygidial characters and in having short ducts on dorsal surface of prosoma.

Second instar male (Fig. II-4). Heteromorphic (that is, greatly differing in principal characters from the adult and second instar females), similar to the heteromorphic second instar males of many other Diaspidini in the arrangements of ducts and gland spines. A pair of robust, sclerotized, roughly serrate processes at apex of pygidium; these processes apparently correspond to the median trullae of the adult and second instar females, but are not zygotic. There are no other marginal processes. Some ducts occurring along the margin of the abdomen appear to be of a modified type, being noticeably shorter than neighbouring macroducts. No glanduliferous craters.

First instar larva (Fig. II-5). Similar to the larvae of many other Diaspidini. A pair of enlarged ducts present on head. Antennae 5-segmented, terminal segment annulate, with a rather short apical seta. Tibiotarsal articulation distinct; tibiae with apical margin slanting; tarsi with no distinct seta ventrally. Three pairs of submedian dorsal ducts on thorax. Gland spines around thorax and abdomen. Sclerotized marginal appendages on pygidium. Anus very small.

SEM OBSERVATIONS ON THE FEMALE TEST

The female of *Crockeraspis fungosa* is covered with tubular wax filaments like the female and male of *Sclopetaspis danumensis*. Its test, however, is fairly compact (Fig. II-7), thus appearing quite different from the tests of *S. danumensis*. In the latter species the female test is, externally, a loose mass of filaments somewhat like a pile of hay, and the male test also has a loose appearance (Takagi, 1992, figs. 54 and 64). When I was studying *S. danumensis* it did not come to my knowledge that another species, *C. fungosa*, produces tubular filaments, which fact is recognizable only with the aid of a SEM. In both species these filaments are produced by the adult and second instar females, and in *S. danumensis* also by the second instar male.

A cross section of the test shows not only holed cut ends of filaments various in the diameter of the hole but also solid cut ends (Fig. II-10). The frequency of solid cut ends is variable among the observed cross sections. A filament may be variable along its length in the diameter of the hollow space and may partly be solid, but it is also possible that the insect produces two kinds of cylindrical filaments, tubular (with the top closed) and solid. Further, very slender wax filaments are found, but only occasionally among cylindrical filaments. No ribbon-like filaments have been observed.

Both the adult female and the second instar female have numerous short ducts on the dorsal surface of the prosoma in addition to macroducts, which are small but appear to be of the usual diaspidine type. I am inclined to believe that the macroducts secrete tubular filaments and the prosomatic dorsal ducts secrete solid cylindrical filaments; the very slender filaments observed must have been secreted by microducts. I have failed, however, to confirm all these suppositions. The material used had been preserved dry, and was relaxed in moist atmosphere for SEM observations. Needless to say, insects collected in the midst of wax secretion and fixed in alcohol are adequate for the confirmation.

If the suppositions mentioned above are correct, *S. danumensis*, too, should produce solid cylindrical filaments in addition to tubular filaments, because it has short dorsal ducts on the prosoma not only in the adult female but also in the second instar female and male. These ducts are, however, few as compared with those occurring in the adult and second instar females of *C. fungosa*.

Eventually the adult female is covered with a thick mass of wax filaments (Fig. II-9). The portion of the test beneath the insect body is incomplete at the beginning of its formation, but the opening becomes gradually narrower until it is closed. Impressions of stomata of the host plant leaf are found on the ventral surface of the test (Fig. II-11). Apparently they were shaped by stomatal movements (opening and shutting), and the shaping process is well understood on the supposition that the insect makes no movements in secreting wax filaments (compare the impressions shown in Fig. II-11, which represent various stages of shaping). In the completed test the insect body is enclosed within a dome-like space, of which the wall is hardened probably by excreted substance.

DISCUSSION: RELATIONSHIP BETWEEN CROCKERASPIS AND SCLOPETASPIS

Crockeraspis fungosa and *Sclopetaspis danumensis* agree in producing tubular wax filaments for constructing the female test — a character quite extraordinary in the family Diaspididae. They are similar in the general shape of the body, in the narrowing head, in the rugged pygidial margin, in the occurrence of a number of small, short ducts on the prosoma, in the small, scattered macroducts, and in the poorly differentiated marginal macroducts of the pygidium. On the other hand, the two species are remarkably different in the median trullae. In *C. fungosa* these trullae are very large, confluent through a well-developed basal zygosis, and provided with a pair of strong setae between them. In *S. danumensis* the median trullae are weak and non-zygotic (the non-zygotic state is evident in the second instar female, in which the median trullae are widely separated from each other), with a pair of small setae between. *C. fungosa* with the strong and zygotic median trullae is fairly advanced as compared with *S. danumensis*. The problem here is how to evaluate all these similarities and differences, which appear to be contradictory.

The agreement in the production of tubular wax filaments and the similarities in the characters of some body features may be evaluated as significant phylogenetically. *Sclopetaspis* and *Crockeraspis* may be interpreted to belong to the same evolutionary lineage, which is characteristic in producing tubular wax filaments, and to represent a primitive and an advanced form of that lineage. This interpretation, however, faces a serious difficulty. In my view, strong trullae are useful in cutting, slicing, or peeling off the upper epidermal layer, or removing epidermal excrescences, of the host plant when the insect makes oscillatory or rotative movements in forming the test. The adult female of *Crockeraspis* apparently makes no movements at test formation and is eventually enclosed within a hard shell-like core of the test [see the preceding section]. The question here is why and how the robust and strongly zygotic median trullae of *C. fungosa* could have evolved in association with this type of test.

The alternative interpretation, therefore, seems more plausible: the two genera are not particularly related to each other. *Sclopetaspis* is a relatively primitive form of the Diaspidini (Takagi, 1992), whereas *Crockeraspis* belongs to the Fioriniina (s. lat., including *Pseudaulacaspis* and other non-pupillarial forms), an advanced subtribe of the tribe. According to this interpretation, the production of tubular wax filaments common to the two genera is due to parallel evolution, and the similarities in body features between them are also due to parallelism or convergence associated with the production of tubular filaments and the manner of test formation. This interpretation also has a difficulty: we have to explain why *C. fungosa* still retains the strong median trullae, making movements no longer in forming the test. But it may be easier to accept the retention than to require the evolution of such trullae.

Furthermore, the second instar male of *S. danumensis* is nearly homomorphic with the second instar female and is covered with tubular wax filaments as well, whereas the second instar male of *C. fungosa* is heteromorphic and its test is composed of coiled ribbon-like filaments. The first instar larva of *S. danumensis* has only two pairs of submedian dorsal ducts on the thorax (no ducts being discernible on the prothorax); it is provided with fimbriate pygidial appendages. The first instar larva of *C. fungosa* shows a typical diaspidine pattern except for the tibiae slanting on the apical margin. These larval characters must have some significance, but I am not sure how they are helpful in clarifying the phylogenetic relationship between the two genera. The second instar males of the Diaspidini are too variable phenotypically, and homomorphism and heteromorphism in the second instar occasionally occur in a group of species which are closely related so far as based on female characters. Morphology of the first instar larva may be supposed to be relatively stable phylogenetically [for an exception, see Part IV], but detailed studies of this stage are still limited.

CONCLUSION

Sclopetaspis, covered with tubular wax filaments, was once assumed to be an escape out of many experiments attempted in the relatively early course of diaspidid evolution, representing a side branch off the main stock of the family (Takagi, 1992). Indeed, the production of tubular wax filaments is quite extraordinary in the extant Diaspididae so far. But tubular filaments occur also in *Crockeraspis*, a fairly advanced form, and the possibility cannot be excluded that their occurrence in the two genera is due to parallel evolution. In the present circumstances the occurrence of tubular filaments alone does not definitely indicate the presence of an isolated lineage. The essential problem, then, is to clarify the significance it has in the life of these scale insects. Is the thick test composed of tubular wax filaments effective against any natural enemy, or is it superior in creating a stable microenvironment under it? Why is it so rare, if it is really favourable for the insect in any sense? I have no answer to these questions. I have no idea what change in the duct structure is responsible for the production of tubular filaments, either. However, if the supposed parallel evolution is true, we may expect further forms producing tubular wax filaments and belonging to other groups of the Diaspididae.

PART III. A LEPIDOSAPHEDINE WITH PECTINAE

INTRODUCTION

Armoured scale insects of the tribe Lepidosaphedini are characterized, above all, by having megaducts, which are enlarged marginal macroducts with the longitudinal axis of the orifice perpendicular to the margin. They have gland spines and bilobulate lateral trullae in common with the Diaspidini, and are referable to the subfamily Diaspidinae together with the latter. The phylogenetic relationship between these tribes, however, is still unknown (Takagi, 1992). Moreover, there are other forms which lack megaducts but are referable to the Lepidosaphedini on the basis of other characters. They were treated under the 'Groupe II' of lepidosaphedines by Balachowsky (1954) and tentatively lumped together under the subtribe Coccomytilina (including *Howardia*, the type genus of Howardiina) by Takagi (1992).

Recently I (1993; 1999) have revised the subtribes Protodiaspidina and Kuwanaspidina, which I have referred to the tribe Diaspidini in spite of the fact that they do not agree with other Diaspidini in having pectinae and, in the case of the Protodiaspidina, also in lacking distinct trullae. In this treatment they are interpreted to be primitive Diaspidini, representing successive early stages in the evolution of the tribe. In fact, there are no other characters peculiar to these subtribes. The first instar larvae examined of the subtribes show characters common to many other Diaspidini, and afford no definite evidence against the view that the subtribes should belong to the Diaspidini.

The new diaspidid described below is provided with megaducts, and referable to the Lepidosaphedini also on the basis of characters of the first instar larva. It is, however, extraordinary for a lepidosaphedine in having simple (that is, non-glanduliferous) pectinae and, moreover, glanduliferous pectinae of a peculiar type, for which the term 'spiniferous pectinae' is proposed. The view is adopted that it represents a primitive form of the Lepidosaphedini. Thus pectinae occur in both the Diaspidini and the Lepidosaphedini as well as in the tribes of the Aspidiotinae.

DESCRIPTIONS

Mempelaspis, gen. nov.

Type species: *Mempelaspis serpentina*, sp. nov.

This genus is referable to the tribe Lepidosaphedini, but it remarkably differs from the other known genera of the tribe in having pectinae provided with a glanduliferous spine-like process ('spiniferous pectinae') and occurring on the seventh to ninth abdominal segments. It has simple (non-glanduliferous) pectinae, too, on the pygidium. In other features it is similar to the genera of the subtribe Lepidosaphedina except that the antennal setae are very thick and fleshy.

Mempelaspis serpentina, sp. nov.

Material. Collected at Semonggok [material 91ML-30] and Santubong [91ML-231, -276], Kuching District, Sarawak (Borneo Is.), Malaysia, on vines of the genus *Tetracera* (Dilleniaceae; 'akar mempelas' in Malay), Oct. 1991.

Holotype: adult female mounted from material 91ML-276, deposited in the collection of the Entomology Division, Forest Research Institute of Malaysia.

Habit. Occurring on the lower surface of the leaves. Female test (Figs. III-6, -7, -8) slender, very long when completed, often curved, highly convex dorsally, with conspicuous transverse ridges, thus looking as if it were segmented; brown and coriaceous. Male test (Figs. III-9, -10) much shorter, straight, not 'segmented'; light brown.

Adult female (based on 30 specimens mounted from 91ML-231, another 30 from 91ML-276, and some specimens from 91ML-30) (Figs. III-1, -2A). Body small, attaining about 0.5mm in length, slender, cylindrical, with lateral sides nearly parallel and with both ends rounded. Pygidium composed of Abd VI–IX; prepygidial segments little lobed laterally. Derm remaining membranous; head minutely granulate; pygidium with dorsal surface striate longitudinally and with a sclerotic patch on ventral surface in front of median trulla and also of the second. Trullae in 2 pairs, well sclerotized; median trullae small, separated from each other by about twice the width of one of them, squat, quadrate, basally with a pair of scleroses extending anteriorly; second trullae very small, usually unilobed and conical, rarely bilobulate, the outer lobule similar to the inner in shape and size. A pair of spiniferous pectinae between median trullae, 2 between median and second trullae, and 1 laterally to second trulla; 1 simple pectina laterally to the lateralmost spiniferous pectina (on Abd VI), much less developed than spiniferous pectinae. Gland spines occurring on Abd I–VI, short on Abd I, gradually longer on the posterior segments; variable in number, up to 8, on I, 2–4 on II, 2 (at times 1 or 3) on III, 1 (at times 2) on IV, and 2 (at times 1) on V and VI each. Marginal macroducts much larger than other macroducts, with axis of orifice perpendicular to margin, 1 on Abd VII (between median and second trullae), 2 on VI and V each, and 1 on IV, those on V and IV each opening in an obvious marginal prominence; similar lateral prominences 1 on each of I–III, basally accompanied by 1 macroduct. Macroducts occurring as anteriorly as mesothorax, mainly ventrally on meso- and metathorax and Abd I and dorsally on the succeeding segments, their numbers are as follows on one side of the body (including macroducts associated with lateral prominences): 2–5 on mesothorax laterally, usually with another duct isolated anteromesally and smaller; 6–10 on metathorax laterally to posterior spiracle; 6–13 on Abd I, mostly in a transverse row laterally in front of gland spines; 4–8 on II laterally; 4–8 on III on lateral to submarginal area; 4–7 almost scattered on IV; 3–5 on Abd V along posterior margin of the segment; 5–7 on pygidium in a longitudinal band. Antennae situated between head margin and mouthparts, separated from each other by a space narrower than mouthparts, each with a very thick, fleshy seta and 2 minute invaginated setae, the fleshy seta often incompletely split to form 2 or 3 prongs (Fig. III-4). Anterior spiracles each with 1 trilocular disc pore. Perivulvar disc pores present, of the capitate type (Fig. III-5), arranged in 5 groups, the median and anterolateral groups often continuous, 1 or 2 (usually 2) medians, 2 or 3 (usually 3) anterolaterals, 3–5 (usually 4) posterolaterals. Anus large, near base of pygidium.

Second instar female and male (Fig. III-2B, C). Both the female and the male are 'homomorphic' (agreeing in the principal morphological characters) with the adult female as usual in the Lepidosaphedini. They differ from the adult female mainly in having much fewer macroducts and in the marginal macroducts (occurring on Abd IV–VII) all single. Female with a submedian macroduct on each of Abd IV and V (2 in total on one side) and with lateral macroducts on meso- and metathorax and Abd I–III; male with a submedian macroduct on each of Abd IV–VI (3 in total on one side), lateral macroducts on meso- and metathorax and Abd I and II, a lateral prominence accompanied by a macroduct on each of II and III, and a submarginal macroduct on each of II–V. In the marginal appendages the second instar female and male differ from the adult female as follows: 1) the median trullae are small and conical, and thus are similar to the second trullae; 2) there are two pectinae between the median and second trullae as in the adult female, but the outer one is not glanduliferous, thus being a simple pectina. Antennae each with a single seta, which is much less thick than in the adult female though still fleshy. Gland spines: 1 laterally to posterior spiracle, 3 submarginal on Abd I, and 1 lateral or marginal on each of II–VI. Anterior spiracles each with a trilocular disc pore.

First instar larva (Fig. III-3). Antennae 6-segmented, the terminal segment a little shorter than the preceding segments combined, not annulate, with an apical and a subapical seta, both these setae being short and stiff. A pair of enlarged dorsal ducts opening on frontal margin, which is somewhat produced. Tibiotarsal articulation distinct. Tarsi short, with a strong ventral seta. Dorsal submedian setae on thoracic and abdominal segments, and ventral submedian setae on abdominal segments. Three microducts followed by 8 gland spines on each side of body. Marginal appendages of pygidium well represented, but trullae not especially enlarged. Anterior spiracles each with a trilocular disc pore.

Mempelaspidina, subtrib. nov.

Type genus. *Mempelaspis*, gen. nov.

This subtribe is erected on the supposition that *Mempelaspis* represents a primitive form of the Lepidosaphedini [see Discussions: Taxonomic position]. It is distinct from the Lepidosaphedina (including Andaspidina) in having simple pectinae and spiniferous pectinae, and from the Coccomytilina also in having megaducts.

DISCUSSIONS

Taxonomic position

In the first instar larva, *Mempelaspis serpentina* agrees with other Lepidosaphedini in principal morphological characters: antennae 6-segmented, the terminal segment with an apical and a subapical seta; tarsi with a strong seta ventrally; submedian setae occurring through thoracic and abdominal segments dorsally and on abdominal segments ventrally; gland spines along abdominal margin; a set of appendages on pygidial margin. The trullae are, however, not enlarged into enormous processes as in many other Lepidosaphedini. In this respect it is especially similar to *Aonidomytilus albus* (Takagi, 1992, fig. 8). It differs from *A. albus* and other species of the Lepidosaphedini in the terminal antennal segment not annulate, in lacking submarginal dorsal setae on the meso- and metathorax, and in the position of the enlarged cephalic ducts, which open on the produced frontal margin. These differences as against the agreements in the principal characters mentioned above appear to be too subtle to exclude *M. serpentina* from the Lepidosaphedini.

In the adult female, however, *Mempelaspis serpentina* is not particularly related to *Aonidomytilus albus* or any other Lepidosaphedini. The mentioned resemblance to *A. albus* in the first instar may be superficial, the small trullae in this instar in both these species appearing to be incidental to the small trullae in the adult females.

The spiniferous pectinae, the most noteworthy feature of *Mempelaspis serpentina* in the adult female and the second instar female and male, differ from the glanduliferous pectinae of the Aspidiotinae in having a produced glanduliferous spine. The segments bearing them, the seventh to ninth abdominal segments, lack gland spines in spite of the fact that in many other Lepidosaphedini these segments (as well as the preceding abdominal segments and metathorax) are provided with gland spines. On the other hand, there occur in *M. serpentina* on each side of the sixth abdominal segment a simple pectina and one or two gland spines. The assumption, therefore, is adopted that each spiniferous pectina originated from the union of a simple pectina and a gland spine.

According to the assumption above, simple pectinae and gland spines once occurred together on each of the seventh to ninth abdominal segments in the lineage leading to *Mempelaspis serpentina*. The hypothetical ancestor, thus, had a set of trullae, simple pectinae and gland spines on the pygidium in common with the Kuwanaspidina, and probably behaved the same as the latter in forming the test [see Test formation]. It is not knowable whether it had megaducts, but it differed from the Kuwanaspidina in the presence of gland spines between the median trullae (the space corresponding to the ninth abdominal segment).

It is concluded from all these considerations that *Mempelaspis serpentina* is the most primitive form among the known Lepidosaphedini so far as the organization of the pygidial fringe is concerned. The evolutionary stage it represents in the Lepidosaphedini approximately corresponds to that represented by the Kuwanaspidina in the Diaspidini. Even at this stage the tribe Lepidosaphedini is distinct from the Diaspidini not only in the adult female but also in the first instar larva, and the phylogenetic relationship between the two tribes remains uncertain.

Primitive or simplified features?

The conclusion adopted above does not necessarily mean that *Mempelaspis serpentina* is primitive in all its characters. This species is very small in body size for a lepidosaphedine and simple or reductive in some features. Is it small and simple because it is primitive?

The second trullae are usually unilobed not only in the adult female but also in the second instar female and male, whereas about four percent of the examined trullae in the adult female are bilobulate. This observation, combined with the fact that the lateral lobes are bilobulate universally in the Diaspidinae (bi- or multilobulate in the Kuwanaspidina), suggests that the unilobed second trullae of *M. serpentina* represent a modification and a simplification.

The antennal setae of the adult female are unusually thick, and about 42 percent of the examined antennae are incompletely split to form two or three prongs (Fig. III-4). According to Mr. F. Porcelli (Istituto di Entomologia Agraria, Bari, Italy), such 'abnormalities' are evidence for the numerical reduction of antennal setae by joining unless the splitting is only accidental. The frequent occurrence of split setae in *M. serpentina* indicates that the antennal setae with prongs are not mere abnormalities, and that, on Porcelli's hypothesis, the antennae of *M. serpentina* are equivalent to the bi- or trisetose antennae of many other Lepidosaphedini.

The anterior spiracles in the adult female are always accompanied by a single trilocular disc pore (as in the larval stages); the macroducts are rather poorly represented in number and distribution; the perivulvar disc pores are few. All these characters may be associated with the small body, whereas it is possible but not self-evident that primitive diaspidids are small in body size. The Protodiaspidina are generally small-sized, but the Kuwanaspidina are various and some of them are fairly large.

Test formation

In many Lepidosaphedini the female test is shaped like an oyster-shell, gradually broadening posteriorly, and is formed by oscillatory movements of the insect body. *Mempelaspis serpentina* apparently makes no oscillatory movements in forming the test, which, when completed, is very long and slender, with both sides parallel. Fig. III-6 shows a completed female test, which is composed of 11 segment-like sections preceded by the first instar exuvial cast and the portion formed by the second instar larva. These sections except the posteriormost are considerably smooth on the surface, which shows an obscure transverse running of the secreted substance (Fig. III-7). It seems, therefore, that the substance was supplied by the rolling insect body. The test ends with a section shaped like a fishtail (Fig.III-8). Apparently this section was formed by a mass of substance secreted by the immobile insect body, because its outline nearly coincides with the arrangements of the dorsal macroducts and the marginal megaducts on the pygidium (compare Fig. III-8 with -1).

The insect constructs the sections, one after another, by moving backwards. Recently I (1999) have proposed the assumption that the trullae are used when the insect moves backwards (and also forwards), substituting for claws. Apparently the small trullae of *Mempelaspis serpentina* are used only for that purpose. I have also mentioned that simple pectinae are well developed in primitive forms in both the Diaspidini (Protodiaspidina; Kuwanaspidina) and the Aspidiotinae (*Thysanaspis*; Leucaspidini). They must have some function for these insects, which do not make either oscillatory or rotative movements at test formation. *M. serpentina* is similar to the Kuwanaspidina, especially *Kuwanaspis* species, in the assumed test-forming behaviour, and it nearly agrees with the latter in the composition of the pygidial fringe. The female tests of *Kuwanaspis* species occurring on bamboo leaves are straight in accordance with the parallel veins of the leaves, whereas *M. serpentina* often forms a strongly curved test possibly owing to the rugged lower surface of the host plant leaves (the structure of leaf surface is shown in Figs. III-6, -9).

The male test is formed by the second instar larva. While the larva grows to about

450μm in length, the test (Fig. III-9) becomes about 700μm long. Apparently the second instar male, which is homomorphic with the adult female, moves backwards when forming the test. The dorsal surface of the test (Fig. III-10) shows an obscure transverse running of the secreted substance as in the female test, and is ridged transversely but much less conspicuously than in the female.

CONCLUSION

Mempelaspis serpentina is extraordinary for a lepidosaphedine, having simple pectinae and modified pectinae, but it can be a primitive form of the tribe. It forms the test without making oscillatory or rotative movements of the body, representing an early evolutionary stage of test formation. Its pattern of pygidial appendages is derivable from a hypothetical lepidosaphedine possessing simple pectinae and gland spines on the pygidium-composing segments. Thus simple pectinae are universal to primitive forms of the Lepidosaphedini and the Diaspidini as well as of the Aspidiotinae. Even with such forms, these higher taxa are distinct from each other and their phylogenetic relationships remain uncertain.

PART IV. AN ASPIDIOTINE WITH ENORMOUS MARGINAL SETAE IN THE FIRST INSTAR LARVA

INTRODUCTION

In the postembryonic development of the Diaspididae the number of instars is extremely reduced. The female has only two larval instars, and the male has in addition the prepupal and pupal stages. In association with this reduction the roles of the instars in ontogeny are well differentiated: dispersal is the main role for the first instar larva, growth is the only role for the second instar larva, and reproduction is the dominant role for the adult. The adult female, however, continues to grow and constructs a great part of the test (except for the pupillarial forms), whereas the adult male is ephemeral and devotes itself to reproduction. The persistent adult female, thus, is supposed to occupy a central position in ontogeny in terms of adaptive evolution.

The first instar larva is provided with well-developed legs and antennae apparently for use in dispersal. In many species it has well-developed marginal appendages on the pygidium. I have been maintaining the view that the marginal appendages have primarily evolved in the adult female in connection with test formation and that they are incidentally manifested in the first instar larva, in which they are of no use. If we reject this view, we must explain not only how these features are useful for the first instar larva but also why they are rudimentary or absent in the larvae of other species. In a few known cases, the larvae are decorated fancifully. For example, the larva of *Pentacicola echinatus* is equipped with eminent dorsal processes and fimbriate strong marginal setae (Takagi, 1993). I discussed the significance of these features, and adopted the view that the decoration is another manifestation of the 'overgrowth' which makes the body of the adult female swollen dorsally. The test formed around the immobile swollen body of the adult female is dome-like when completed and, as the body shrinks after releasing eggs, leaves an ample space, which probably creates a microenvironment favourable for the deposited eggs and newly hatched crawlers. According to this view, the decoration itself has no adaptive significance. Excepting such supposedly incidental features, morphology of the first instar larva is assumed to be relatively free from adaptive evolution and, therefore, to be conservative. This earliest stage in the postembryonic development may be expected to be very useful in pursuing phylogenetic researches.

The species described below is referable to the tribe Aspidiotini so far as based on the adult female and some features of the first instar larva. The first instar larva, however, is quite extraordinary for an aspidiotine or even for a diaspidid in having enormous laminate marginal setae. I do not think that these setae, too, are incidental in occurrence, because there is in the adult female no feature which can be responsible for their manifestation in the first instar larva. The nature of these setae strongly implies that they have evolved in connection with dispersal, the main role of the first instar larva.

Descriptions

Icaraspidiotus, gen. nov.

Type species. *Icaraspidiotus chaetopterus*, sp. nov.

This genus is referable to the tribe Aspidiotini in having unilobed lateral trullae and one-barred ducts, and to the subtribe Pseudaonidiina in having a deep constriction between the cephaloprothorax and the mesothorax and in possessing disc pores associated with the anterior spiracles. It agrees with *Duplaspidiotus* (Pseudaonidiina) in the presence of conspicuous scleroses arising from the pygidial margin, but there is no other noteworthy character commonly possessed by these genera. Because mushroom-shaped or clavate scleroses are found in various aspidiotines, their occurrence alone affords no good evidence for a close relationship. *Icaraspidiotus* differs from *Duplaspidiotus* mainly in the lateral trullae reduced into membranous processes, the pectinae modified into acuminate processes (except those occurring between the median trullae), and the anus situated near the apex of pygidium. It differs from most *Duplaspidiotus* species (including the type species) also in lacking areolations on the dorsal surface of the pygidium. *Gomphaspidiotus cuculus* (=*Aspidiotus cuculus* Green, 1905) has 'spiniform' (Green, 1905) or 'very slender, almost seta-like' (Borchsenius and Williams, 1963) pectinae, but it is not particularly similar to *I. chaetopterus* in other characters.

In the present state of our knowledge the subtribe Pseudaonidiina apparently has its centre of distribution in Australia, with an extension into tropical Asia, except for *Pseudaonidia* and *Duplaspidiotus*, of which the species are scattered in the tropics of the world. It should be emphasized, however, that the Australian genera and species were brought to our knowledge mostly through the activities of only one author, A. R. Brimblecombe, and also that tropical Asia, especially eastern Malesia, has been investigated very insufficiently. There must exist unknown genera of the subtribe in these regions. Under these circumstances the taxonomic position of *I. chaetopterus* in the subtribe should remain pending.

Icaraspidiotus chaetopterus is especially characterized by the enormous marginal setae occurring in the first instar. Some other diaspidids have spiniform marginal setae in this instar, but none of them is comparable to *I. chaetopterus* in the size of the setae.

Icaraspidiotus chaetopterus, sp. nov.

Material. Collected in the Maasin Forest, Brooke's Point, Palawan Is., the Philippines, on *Sideroxylon velutinum* (Sapotaceae), 20 Aug. 1993 [material 93PL-92].

Holotype: adult female, deposited in the collection of the Natural History Museum, University of the Philippines at Los Baños.

Habit. Tests of both sexes occurring on the upper surface of the leaves along lateral veins. Female test scallop-shaped rather than circular, flat, smooth, coriaceous, black, with posterior margin brownish; larval exuvial casts laid on test margin osculating the vein (it seems, however, that the first exuvial cast is usually lost at an early stage of test formation). Male test much smaller, slightly elongate, blackish brown, with posterior margin whitish.

Adult female (based on 12 specimens, not all of them in good condition). (Figs. IV-1, -2, -3). Body robust, oblong, about 1.2–1.4 times as long as wide. Head and prothorax completely fused, forming a division depressed ovate in outline and demarcated from mesothorax by a deep constriction marginally; meso- and metathorax and Abd I lobed laterally; pygidium broad triangular, demarcated from Abd V by a distinct intersegmental furrow in median to submedian area, but not clearly definable in marginal to submarginal area, Abd II and succeeding segments forming a smooth margin on each side without intersegmental notches. Derm moderately sclerotized at maturity. Trullae in 3 pairs; median pair alone well developed, the lateral pairs represented by membranous oblong processes, overlapping with pectinae, which are longer than these trullae; median trullae set close, with a pair of very small pectinae between them, broad, with apical margin slightly roundish and a little sloping. Lateral pectinae modified into longish acuminate processes, all appearing non-glanduliferous: 2 laterally to median trulla, the outer overlapping with second trulla; 2 laterally to marginal setae of Abd VII, the outer overlapping with third trulla; 2 laterally to marginal setae of Abd VI; 2 or 3 laterally to marginal setae of Abd V; and, beyond a space, another pectina, which is broadened basally and often divided apically. A sclerotized process just laterally to the outermost pectina, conical and as large as the pectina or reduced to a flat prominence; another conical process near marginal setae of Abd III. Two pairs of very conspicuous slender scleroses arising from mesal bases of second and third trullae, each terminating with a heavily sclerotic swollen part, which is usually shaped like a pileus; another pair of scleroses laterally to marginal setae of Abd V, arising from between the pectinae, much shorter and irregular in shape, sometimes nearly obsolete. Ducts one-barred, with orifice very small and round. Dorsal ducts: short ducts occurring submarginally on pro- and metathorax and Abd I, numerous on prothorax; longer ducts scattered across meso- and metathorax and Abd I and II; numerous ducts on Abd III–V, very long and filiform, with orifices arranged submarginally in oblique rows. Ventral ducts: many very long and filiform ducts on Abd III–V, the orifices tending to be a little larger than those of the dorsal filiform ducts and arranged submarginally in oblique rows; some much shorter ducts occurring submedially on Abd II and III. Anus small, subapical. Perivulvar disc pores in a continuous row shaped like an inverted U and 2 or 3 disc pores thick for most part, 58–78 in total. Antennae situated within frontal margin, separated from each other by a space wider than mouthparts, each composed of a robust tubercle, one fleshy seta, and 2 invaginated minute setae. Anterior spiracles each with 2–5 disc pores, which are usually trilocular and sometimes quadri- or quinquelocular; posterior spiracles without disc pores. A submarginal dorsal boss between Abd I and II, another one between Abd III and IV near the conical process, and an obscure one on supposed border between Abd VI and VII. Fimbriate scaly processes on ventral derm posterolaterally to mouthparts, medially on prepygidial abdominal segments, just anteriorly and laterally to curved row of perivulvar disc pores, and posteromesally to each end of that row.

First instar larva (Fig. IV-4). Body broadly elliptic, provided on each side with 5 enormous marginal setae arising from pro-, meso-, and metathorax, and Abd I and IV.

These setae are nearly twice as long as antenna, depressed dorsoventrally, broadened basally, gradually narrowing towards apex, gently curved (so that, when reposed on the body side, they nearly fit the body margin), and heavily sclerotized except for the extreme apex. Other marginal setae much smaller than the enormous setae, yet unusually strong, spiniform, and gently curved as well. Caudal setae rather short, nearly as long as one of the enormous marginal setae. Pygidium not striate on dorsal surface, with no trace of marginal appendages. Antennae 5-segmented, the terminal segment about 1.3 times as long as the first to fourth segments combined, annulate, with 2 apical setae. Tibiotarsal articulation indistinct; tarsi with a well-developed seta ventrally. A minute duct on each of meso- and metathorax near margin (depicted in Fig. IV-4 as occurring on the dorsal surface of the body, though the orifice is hard to observe); there seem to be no other ducts. A submedian dorsal seta on each of meso- and metathorax and Abd I and II; a submarginal dorsal seta on each of meso- and metathorax. Submedian ventral setae present on abdominal segments. Anterior spiracles each accompanied with a duct-like structure (which may be an invaginated disc pore: see under 'First instar larval characters in comparison with *Pseudaonidia paeoniae*'). Ventral derm spiculate medially across segments posterior to mouthparts. Anus nearly apical.

First instar larval characters in comparison with *Pseudaonidia paeoniae*

The first instar larvae of *Icaraspidiotus chaetopterus* (Fig. IV-4) and *Pseudaonidia paeoniae* (Fig. IV-5) agree in some characters of the antennae and legs, and also in the occurring pattern of submedian and submarginal dorsal setae and submedian ventral setae. These characters, mentioned in the description of *I. chaetopterus* and shown in the figures, are common to other Aspidiotini, and, therefore, agreement in them does not mean any particular relationship within the tribe. In other features the two species are very different. The first instar larva of *I. chaetopterus* is remarkably characterized not only by the unusually developed marginal setae but also by the absence of marginal appendages and the non-striate dorsal surface of the pygidium. In addition, it has much fewer ducts, comparatively very short caudal setae, and a nearly apical anus. The dorsal surface of the prepygidial region is wrinkled transversely and longitudinally in *P. paeoniae*, whereas it is lined differently in *I. chaetopterus* as shown in the figure. All this makes the two species appear quite remote from each other.

The only noteworthy character commonly possessed by the first instar larvae of the two species is the occurrence of a duct-like structure in front of each anterior spiracle. I have found in a specimen of *P. paeoniae*, somewhat distorted on slide, that the structure is an invaginated trilocular disc pore. In connection with the present study I have examined the first instar larvae of *Pseudaonidia duplex*, *P. trilobitiformis*, and *Duplaspidiotus* sp. They are very similar to the larva of *P. paeoniae*, and all of them agree in the possession of the duct-like structure.

DISCUSSION: SIGNIFICANCE OF THE EXTRAORDINARY FIRST INSTAR LARVA

Icaraspidiotus chaetopterus is referable to the subtribe Pseudaonidiina on the basis of the adult female, but there is in the first instar larva little evidence to support this taxonomic position. The presence of a duct-like structure in front of each anterior spiracle is the only positive larval character for assigning the species to the subtribe. The taxonomic value of this character, however, is to be assessed by examining further species.

If we adopt the view that all the similarities to other species of the subtribe in adult female characters are superficial and due to convergence, we have to find the proper position of *I. chaetopterus* on the basis of the first instar larva. But the first instar larva of this species is so peculiarly characterized that the alternative view will find no related forms, either. The question here, therefore, is why it is so peculiar, irrespective of the taxonomic position of the species.

The slide-mounted specimens examined of the first instar larva are neonatal. Embryonic larvae have also been observed within the bodies of several adult females. In all these specimens the enormous marginal setae are usually reposed on the body side, but occasionally stretched out at various angles to the body margin. The first instar exuvial cast easily drops off the test, and I have observed only one specimen of the cast on an incipient test. In this specimen the enormous marginal setae are erect in contrast to the other marginal setae, which remain horizontal (Fig. IV-6). These observations suggest that the larva can move the enormous setae.

Coccoids of the family Margarodidae are hairy insects, and crawlers with long hairy setae are easily carried along by air currents as shown experimentally by Yasumatsu and Nakao (1957) for *Icerya purchasi*. Stictococcidae are also hairy, and the first instar females of some species are remarkable in having very long setae (Richard, 1971). In many families of the Coccoidea the first instar larvae are generally provided with a pair of long hairy caudal setae, which are supposed to contribute to their aerial dispersal. In three species of the eriococcid genus *Cystococcus* the male offspring complete their development within the maternal gall, whereas the female crawlers are phoretic on the adult males at dispersal (Gullan and Cockburn, 1986). According to information from Dr. P. J. Gullan, these larvae have rather weak and short caudal setae (Raman and Takagi, 1992, p. 30, footnote). The beesoniid *Mangalorea hopeae* has, unlike other species of the same family, no trace of caudal setae in the first instar male and female. In this species, too, male larvae feed on their maternal gall, and female crawlers are supposed to be conveyed by adult males (Raman and Takagi, 1992). The examples given above show that the development of the caudal setae, and probably also of some other setae, in the first instar larva is dependent on manners of dispersal. Crawlers with long hairy setae, when starting to disperse in the air, may simply be blown off by the wind. The elongate and laminate marginal setae of *Icaraspidiotus chaetopterus* imply another manner. Considering all this, we may logically suppose that these enormous setae have significance in dispersal and, therefore, have evolved independently of other stages. Other features of the larva may also have been modified in association with the new manner of dispersal. The caudal setae may have been shortened in trade-off for, and the spiniform marginal setae may have been appeared incidentally to, the development of the enormous setae. The manifestation of marginal appendages may have been suppressed incidentally to the genetic change brought about in connection with the evolution of the new manner [for my view concerned, see the introduction].

To proceed further with the problem of the enormous marginal setae may utterly be a matter of speculation, but I hope that there is nothing essentially wrong with the following comments. Supposing these setae can be spread sideways, they may induce lifting force in air currents of appropriate strength and thus enable the crawlers to soar and glide. The question arises why such enormous setae are unusual, if they are really useful in dispersal. On the forest canopy the sunshine causes rising air currents, by which crawlers with long hairy setae may easily be carried along to disperse broadly over the canopy. When dropping off the canopy, they may also colonize the lower storeys composed of young trees, saplings and seedlings of the canopy plants. Inside closed forests air currents, if any, are calm, and in this condition the development of enlarged and laminate marginal setae may greatly improve the efficiency of dispersal in the air. As regards temperature and humidity, too, the canopy bears the full brunt of daily and seasonal fluctuations, which stress promotes leaf fall, whereas the lower storeys are in buffered and stabilized conditions (Yamada, 1997, p. 276). We, therefore, have reason to suppose that there are scale insects inhabiting the lower forest storeys exclusively. In view of all this, the key question is whether *I. chaetopterus* is among such species.

CONCLUSION

Scale insect crawlers with long caudal setae are analogous to spiderlings releasing a length of silk for dispersal by the wind, whereas the first instar larva of *Icaraspidiotus chaetopterus* with enormous laminate marginal setae is comparable to certain plant seeds winged for aerial floating inside the forest. *I. chaetopterus* is referable to the subtribe Pseudaonidiina on the basis of the adult female, but there is little evidence to support this taxonomic position in the morphological characters of the first instar larva. Although it is apparently too easy to generalize from the single case, it is not unreasonable to suppose that in scale insects even the first instar will undergo a great morphological change with the emergence of a new behaviour. In contradiction to the expectation mentioned in the introduction, morphological characters of the first instar larva may not always reflect phylogeny more faithfully than the later stages do.

If all these arguments are accepted, further cases of extraordinary modifications may be expected in the first instar in connection with dispersal. The gall-inhabiting *Apiomorpha pileata* (Eriococcidae) may represent such a case. Crawlers of this species are entirely margined with a row of enlarged spine-like setae, and each of these setae is winged on either side with a horizontal, hyaline membrane, which is lost a few days after their emergence from the gall (Gullan, 1984).

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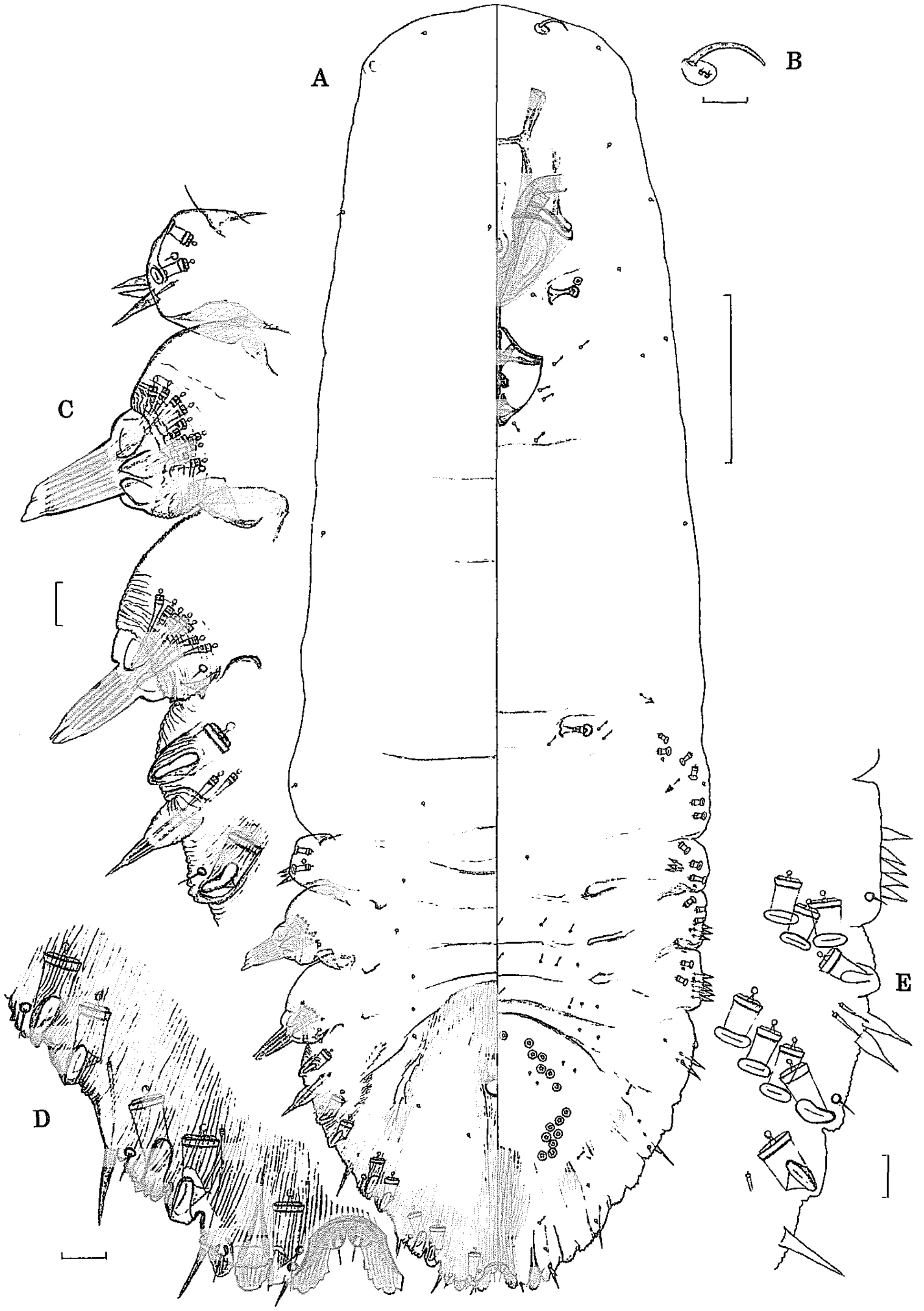

Fig. I-1. *Sinistraspis unilateralis*, adult female: B, antenna; C, Abd I–IV, lateral region of left side; D, pygidial margin, dorsal view; E, Abd III and IV, margin, dorsal surface of right side showing submarginal macroducts [90ML-104]. Scale: A, 100μm; B–E, 10μm.

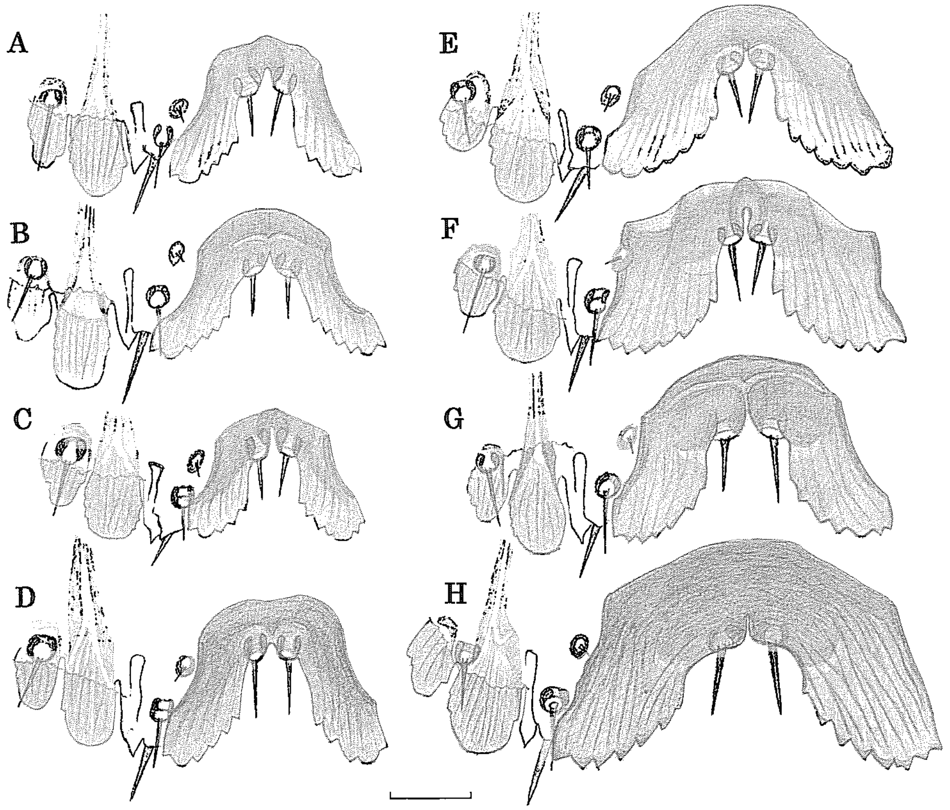

Fig. I-2. *Sinistraspis unilateralis*, adult female, median and second trullae, dorsal view: A and B, 91ML-255; C and D, 92PL-29; E and F, 93PL-36; G and H, 91ML-250. Scale:. 10μm.

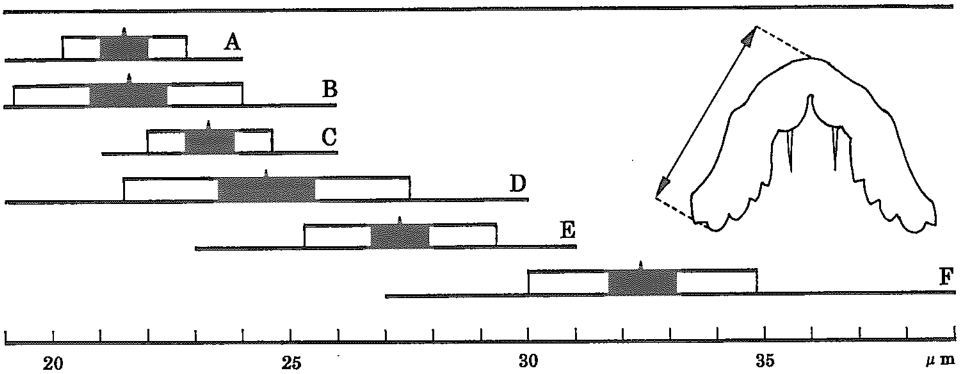

Fig. I-3. *Sinistraspis unilateralis*, adult female, size of median trullae as measured between middle base and apex: A, 91ML-255; B, 90ML-104; C, 86ML-448; D, 92PL-29; E, 93PL-36; F, 91ML-250. Each Dice-gram shows range, mean, and 2 standard errors (black box) and 1 standard deviation on either side of mean.

Fig. I-4. *Sinistraspis unilateralis*, second instar male, crater type [90ML-233]. Scale: 100μm.

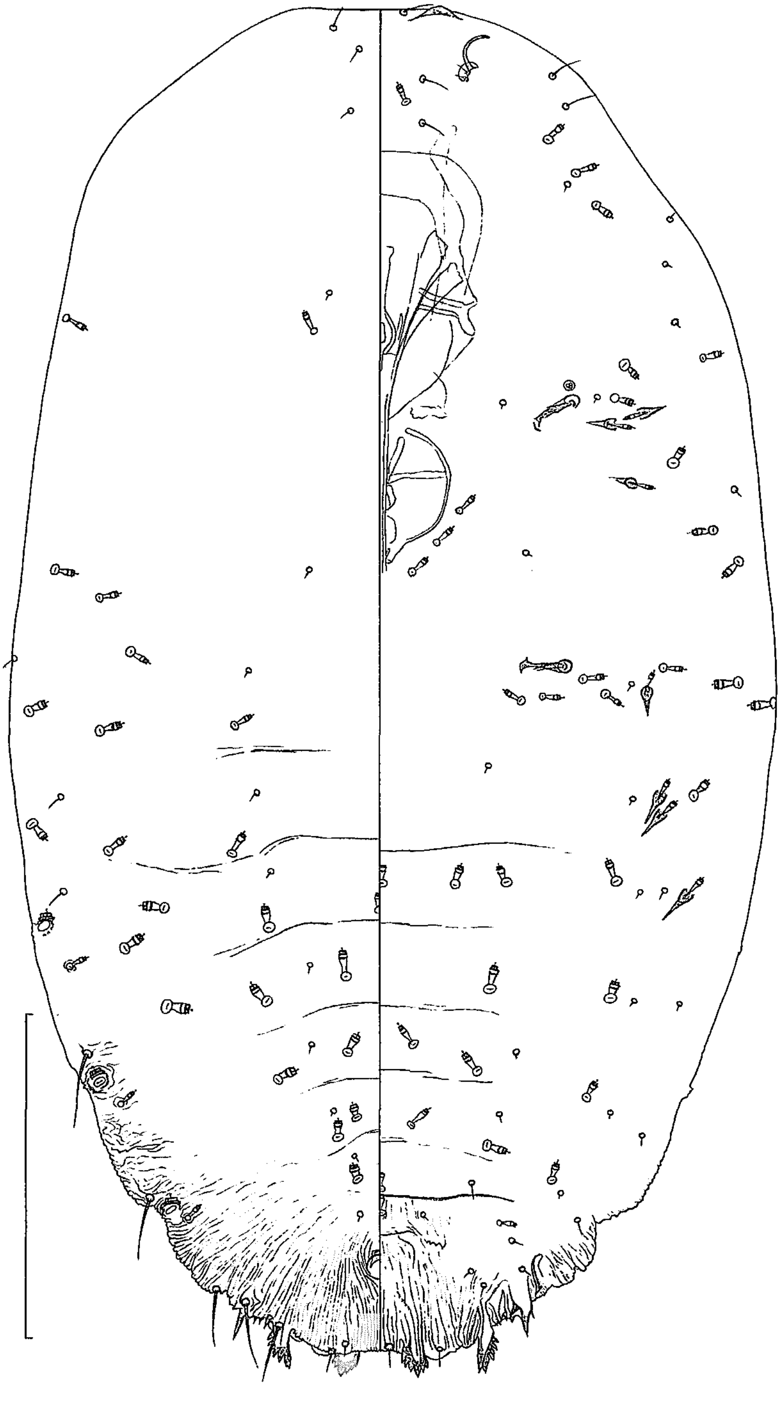

Fig. I-5. *Sinistraspis unilateralis*, second instar male, craterless type [91ML-250]. Scale: 100μm.

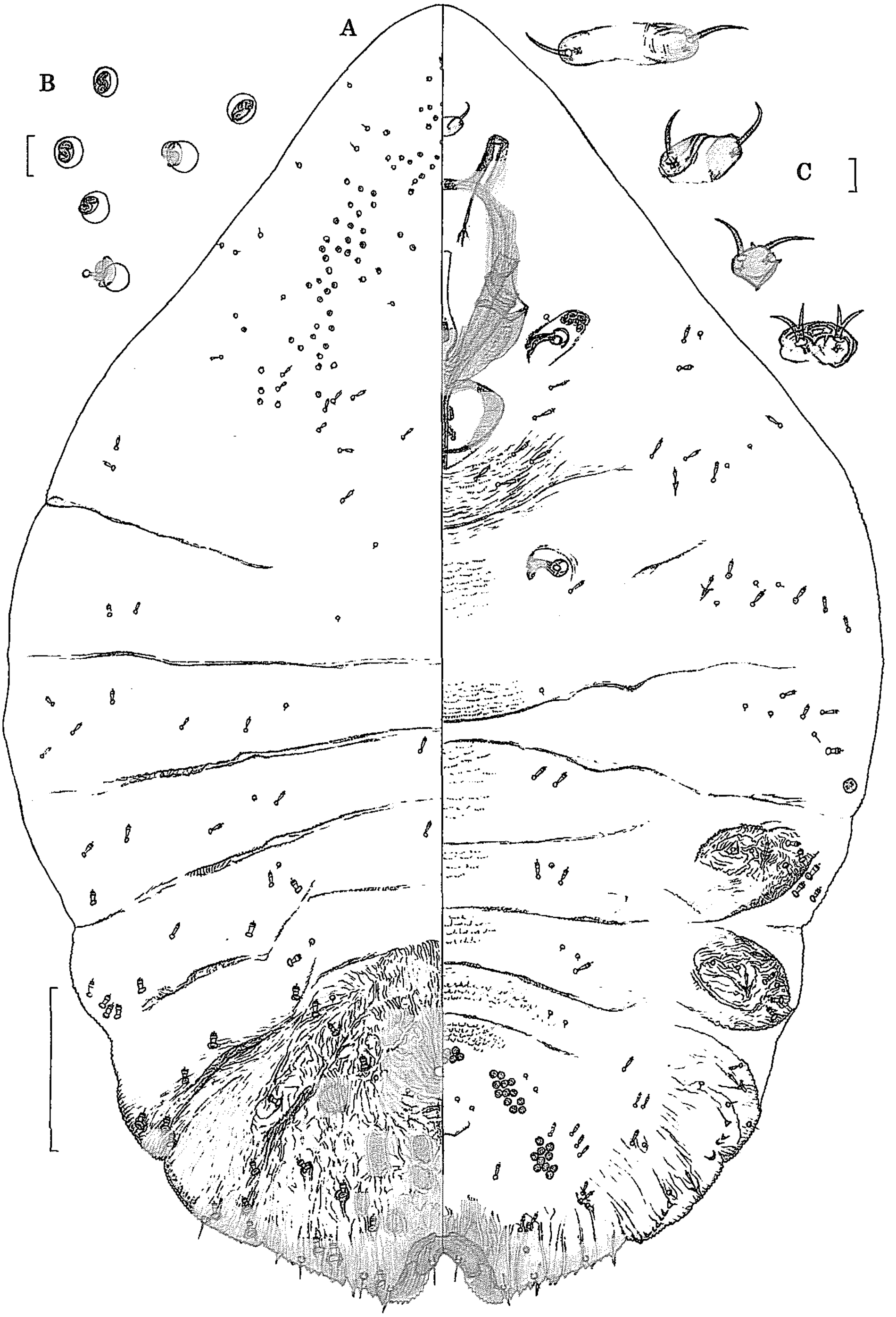

Fig. II-1. *Crockeraspis fungosa*, adult female. B, short dorsal ducts on prosoma; C, antennae, variation. Scales: A, 100μm; B and C, 10μm.

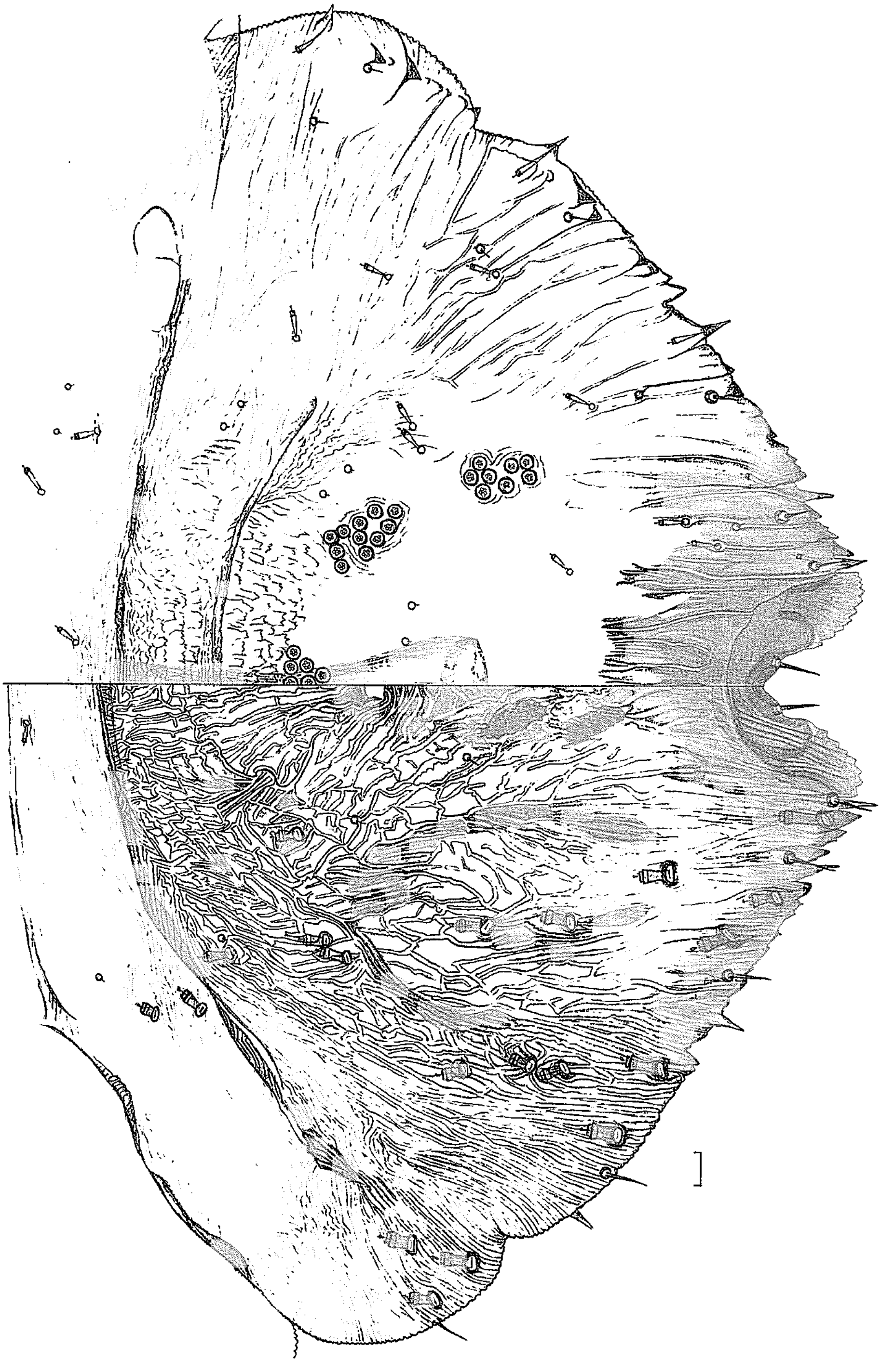

Fig. II-2. *Crockeraspis fungosa*, adult female, pygidium. Scale: 10μm.

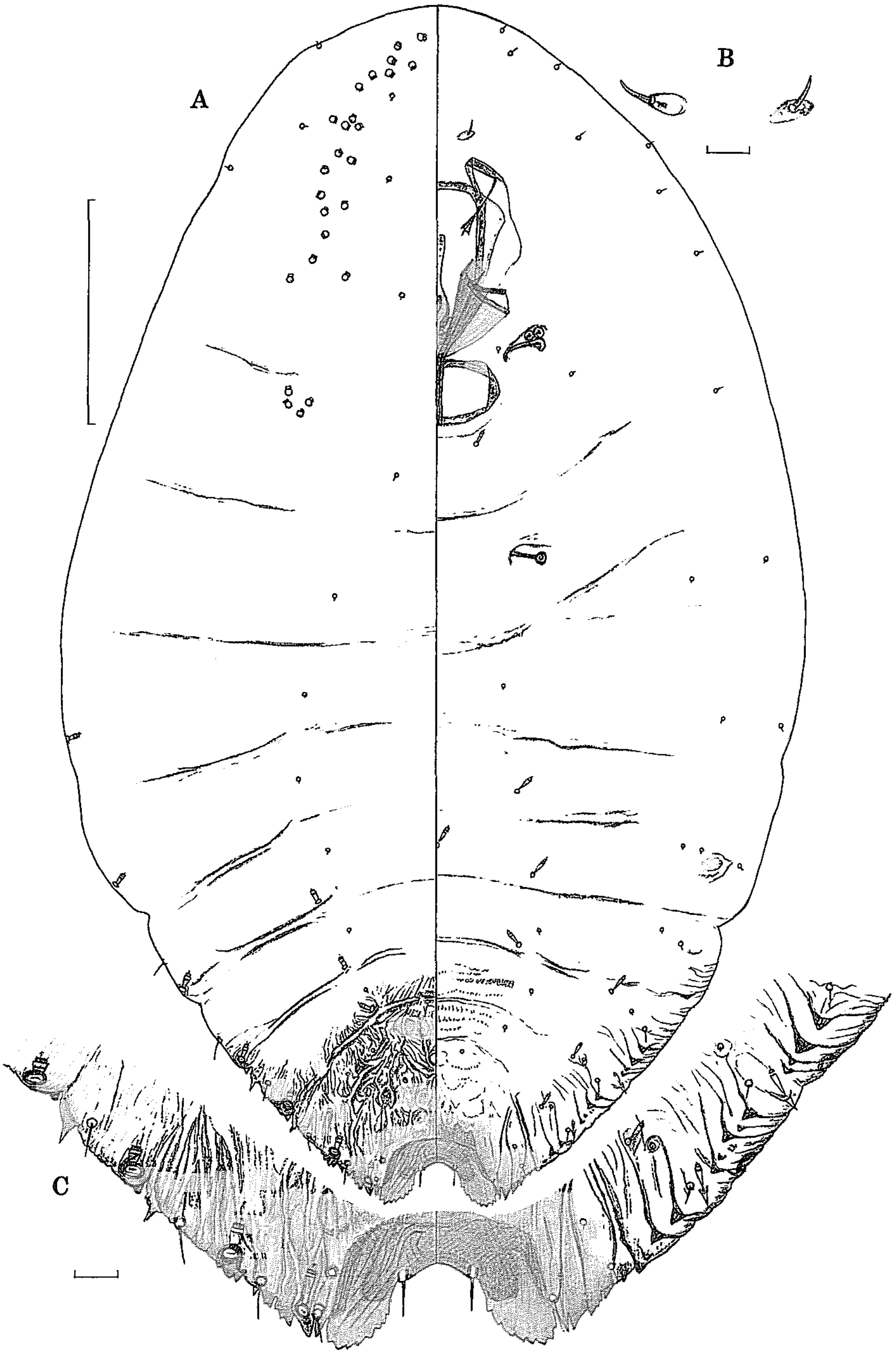

Fig. II-3. *Crockeraspis fungosa*, second instar female. B, antennae; C, pygidial margin. Scales: A, 100μm; B and C, 10μm.

Fig. II-4. *Crockeraspis fungosa*, second instar male. B, apex of pygidium. Scales: A, 50μm; B, 10μm.

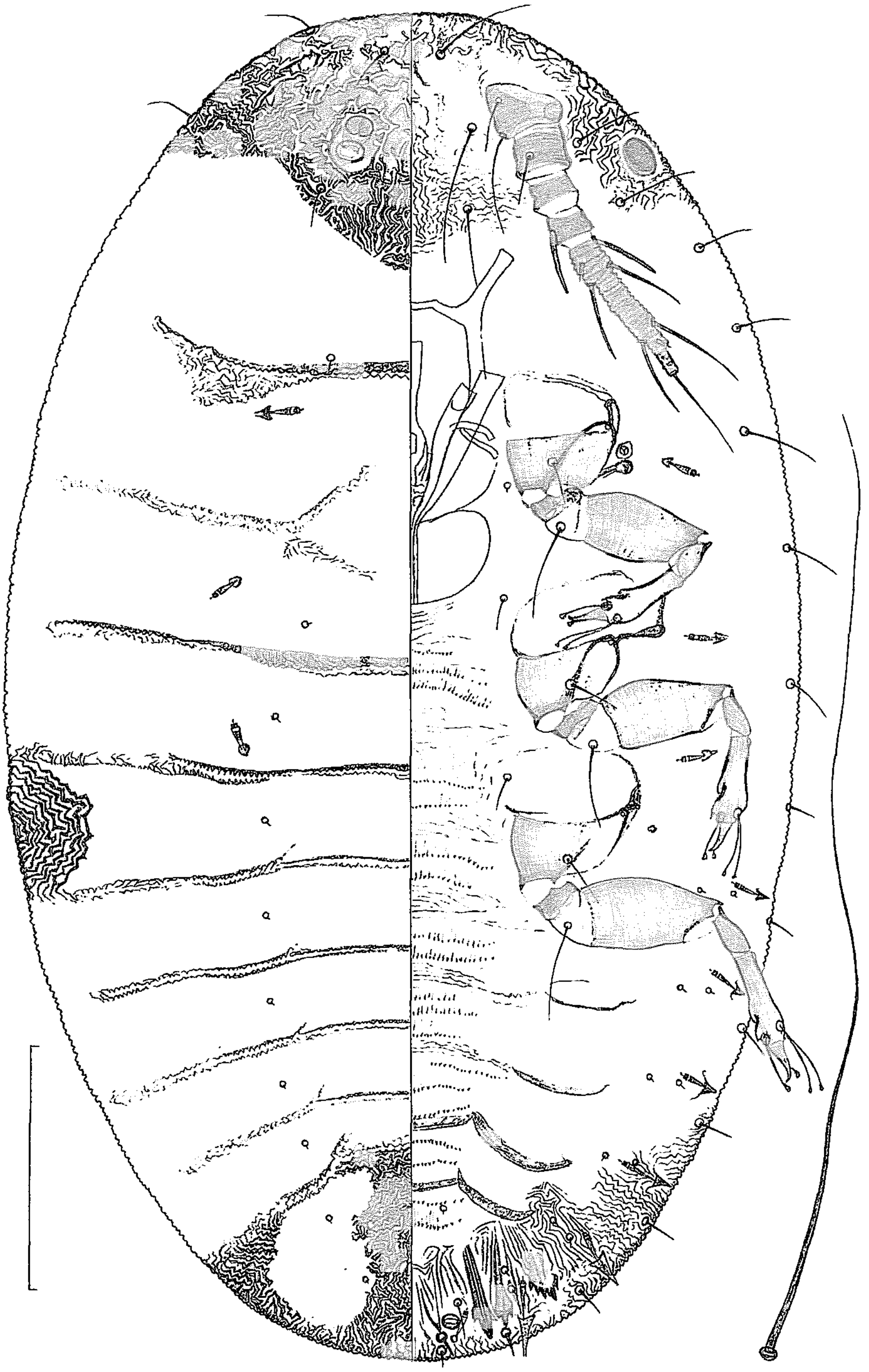

Fig. II-5. *Crockeraspis fungosa*, first instar larva. Scale: 50μm.

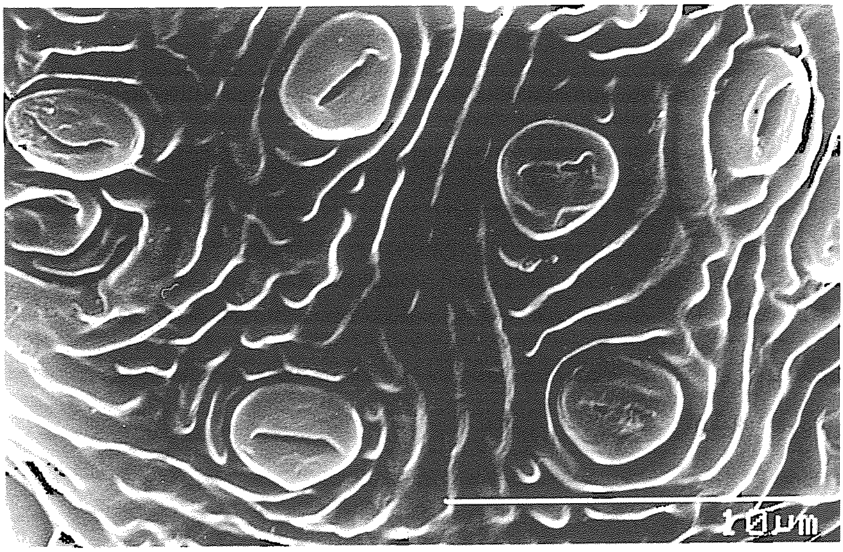

Fig. II-6. *Crockeraspis fungosa*, adult female, orifices of prosomatic dorsal ducts.

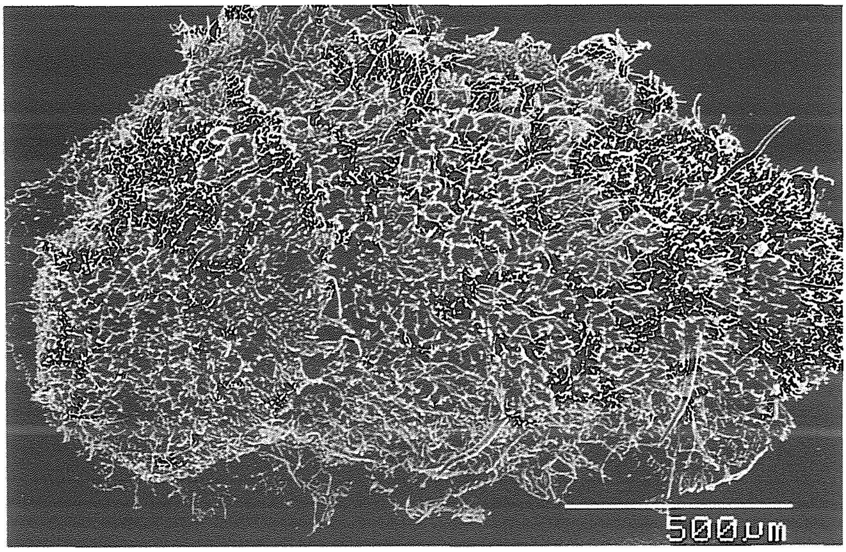

Fig. II-7. *Crockeraspis fungosa*, female test, dorsal view.

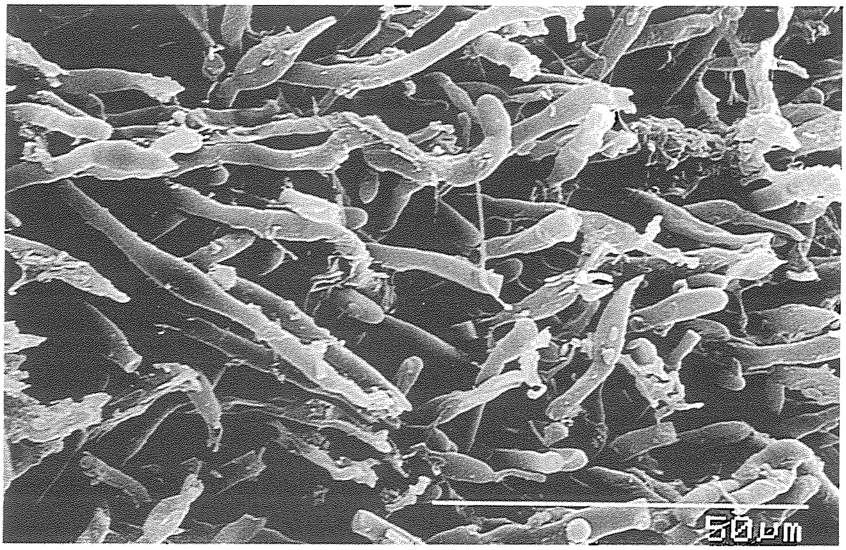

Fig. II-8. *Crockeraspis fungosa*, female test, showing wax filaments.

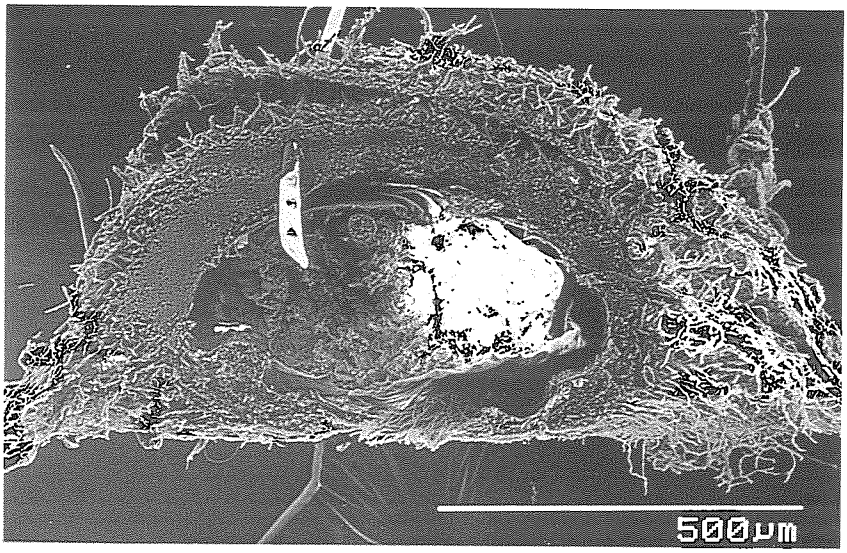

Fig. II-9. *Crockeraspis fungosa*, female test, cross section.

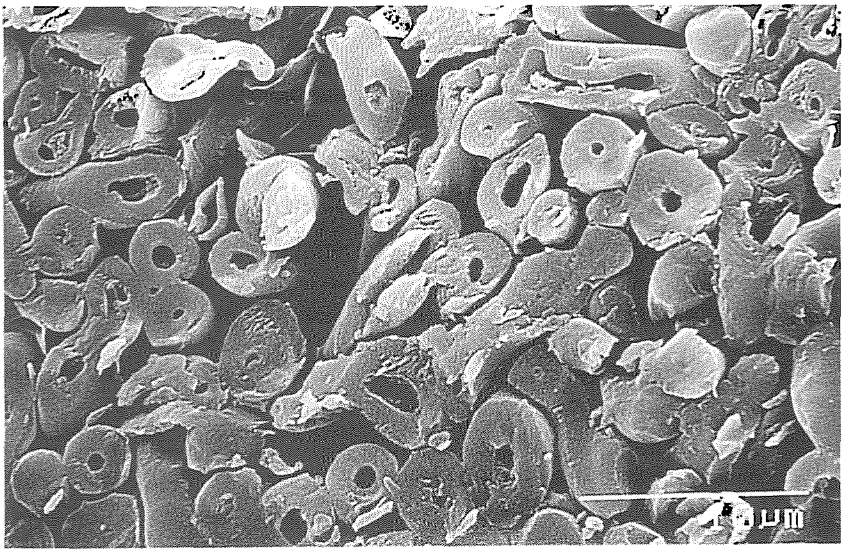

Fig. II-10. *Crockeraspis fungosa*, female test, cross section, showing cut ends of filaments.

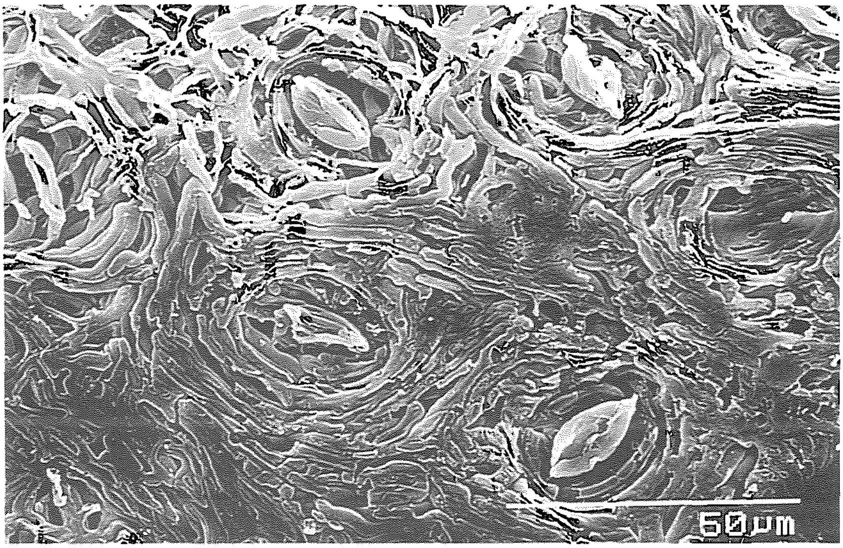

Fig. II-11. *Crockeraspis fungosa*, female test, ventral surface with impressions of stomata representing various shaping stages (an incipient impression near the left margin; a completed one just above the scale).

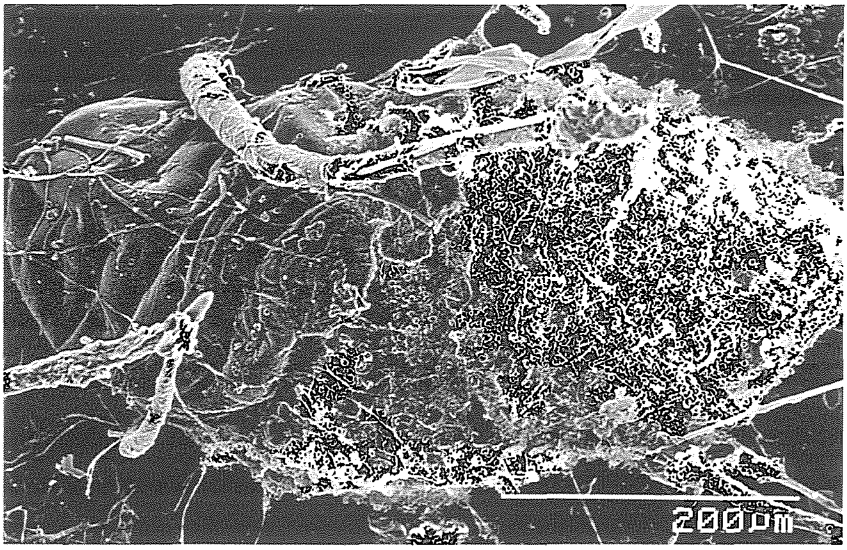

Fig. II-12. *Crockeraspis fungosa*, male test (not yet fully formed), dorsal view.

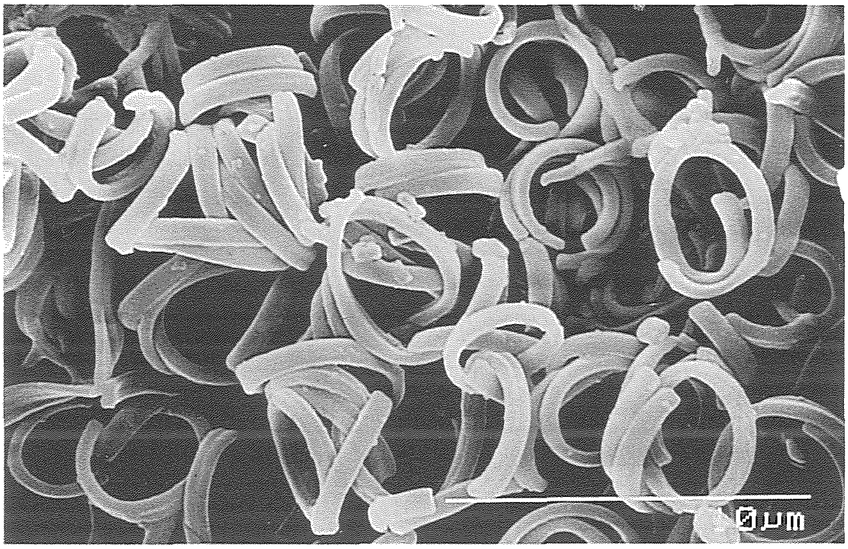

Fig. II-13. *Crockeraspis fungosa*, male test, showing coiled wax filaments.

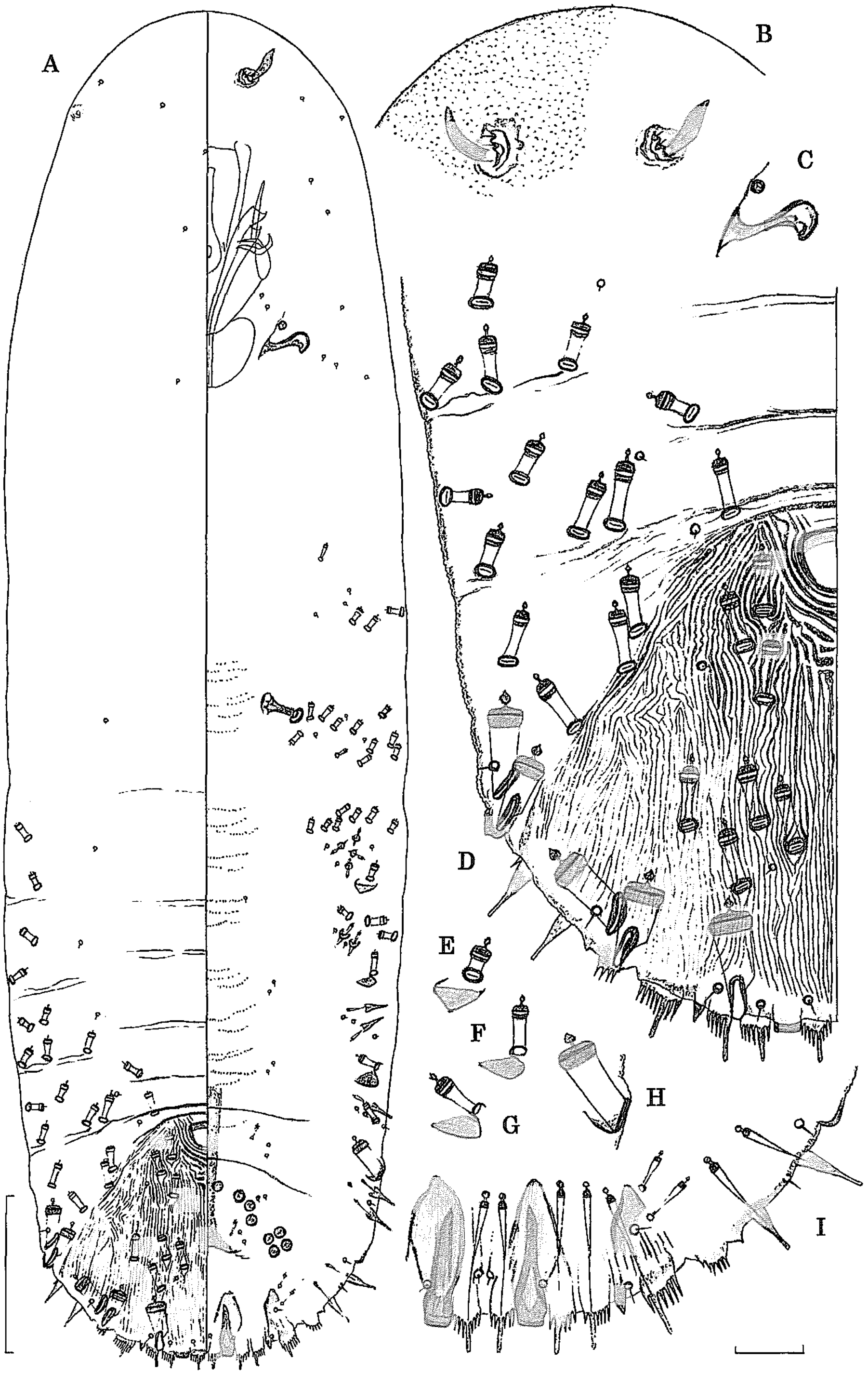

Fig. III-1. *Mempelaspis serpentina*, adult female: B, antennae; C, anterior spiracle; D, pygidium, dorsal surface; E–H, lateral or marginal prominences on Abd I–IV; I, pygidial margin, ventral view [91ML-276]. Scale below left (for A): 50μm; scale below right (for B–I): 10μm.

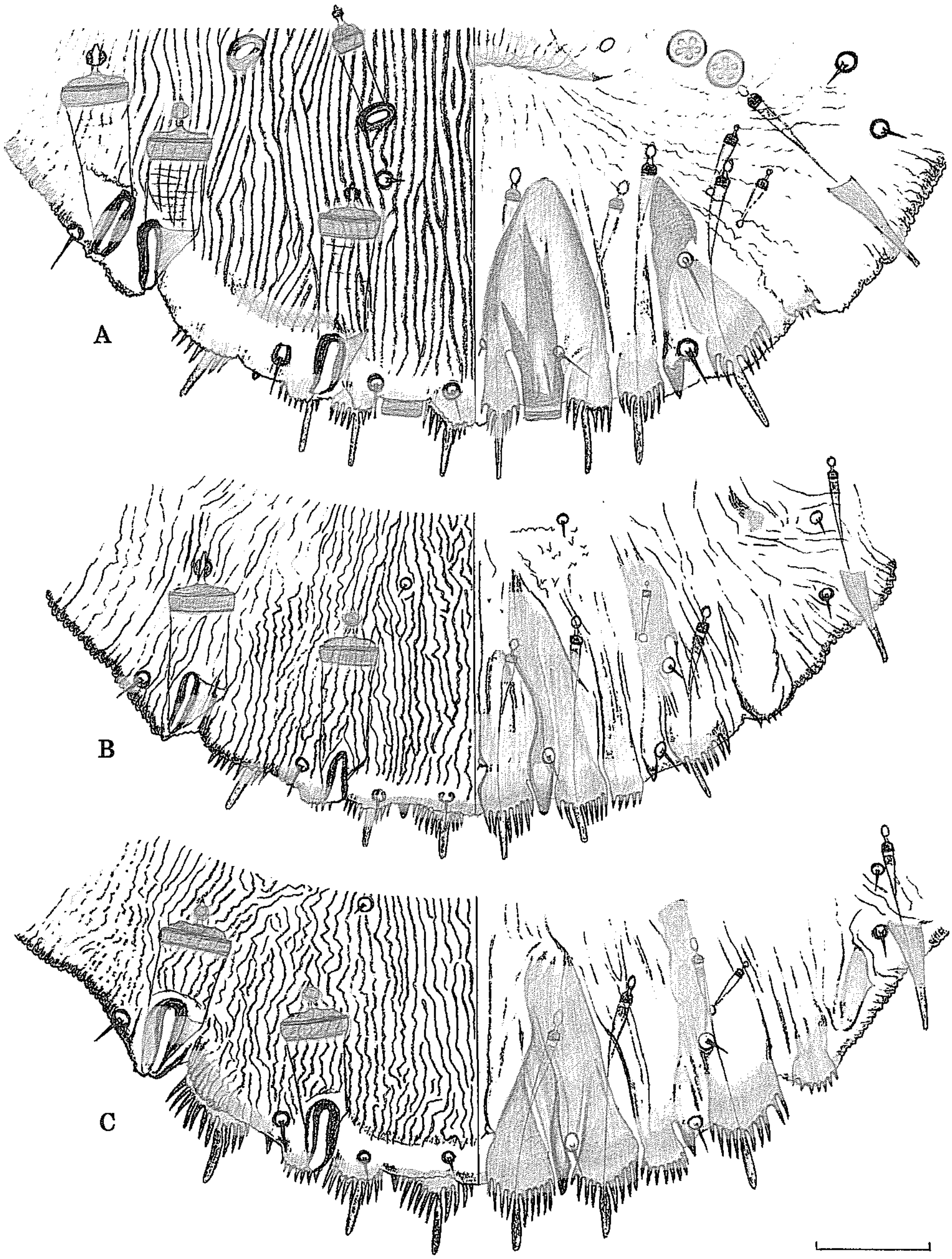

Fig. III-2. *Mempelaspis serpentina*, pygidial margins: A, adult female; B, second instar female; C, second instar male [91ML-231]. Scale: 10μm.

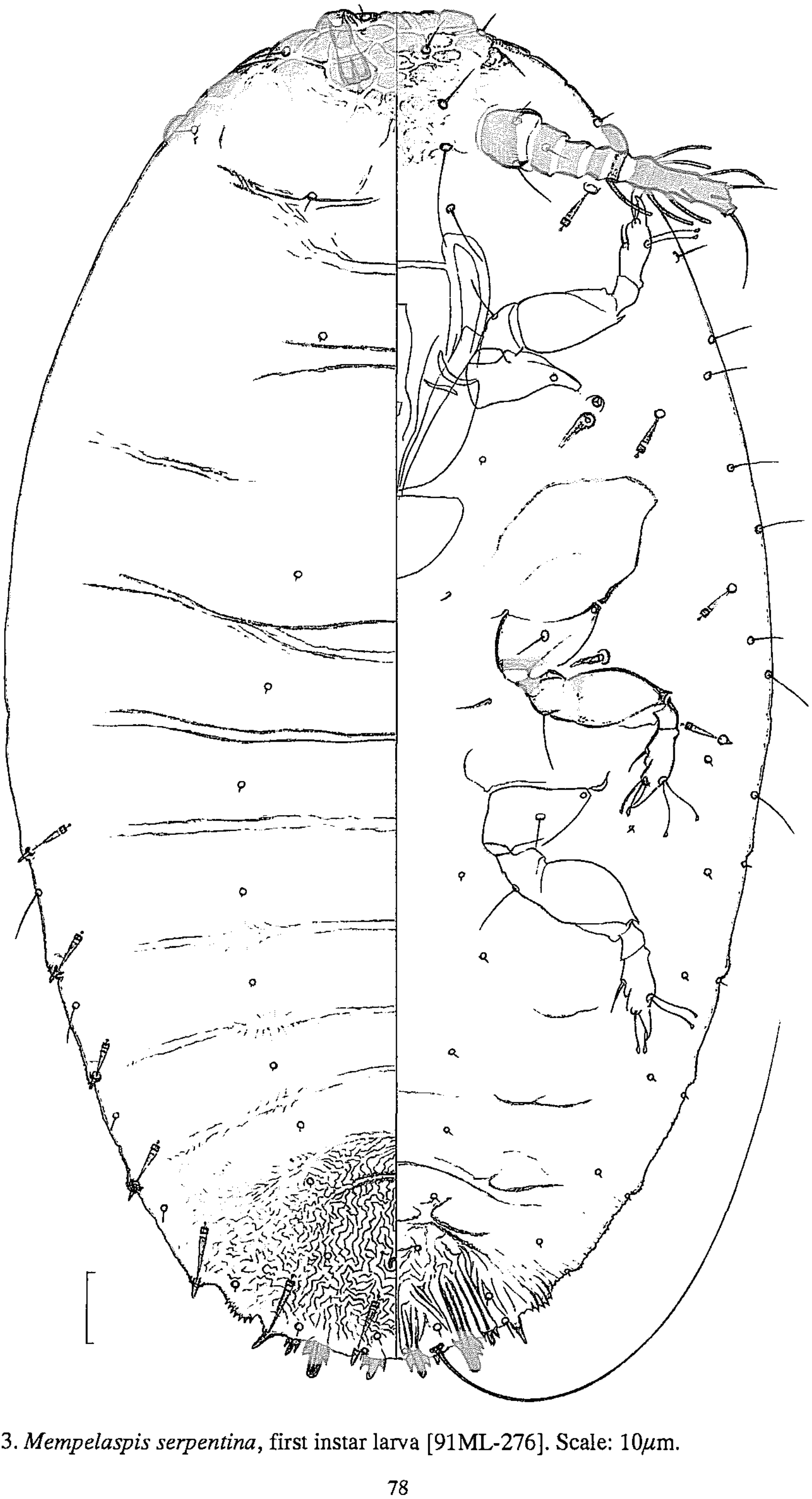

Fig. III-3. *Mempelaspis serpentina*, first instar larva [91ML-276]. Scale: 10μm.

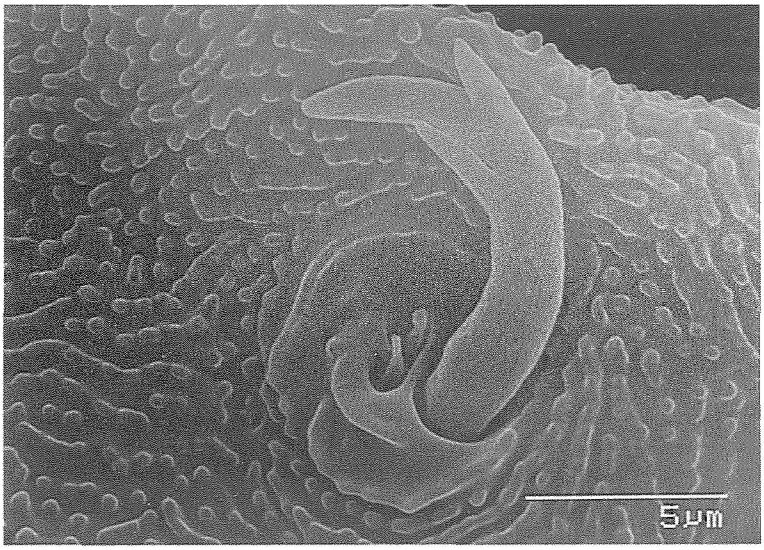

Fig. III-4. *Mempelaspis serpentina*, adult female: antenna [91ML-231].

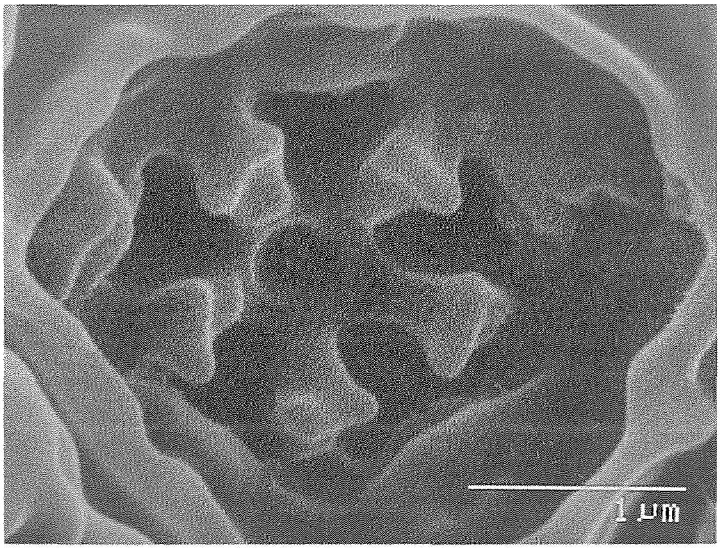

Fig. III-5. *Mempelaspis serpentina*, adult female: perivulvar disc pore [91ML-231].

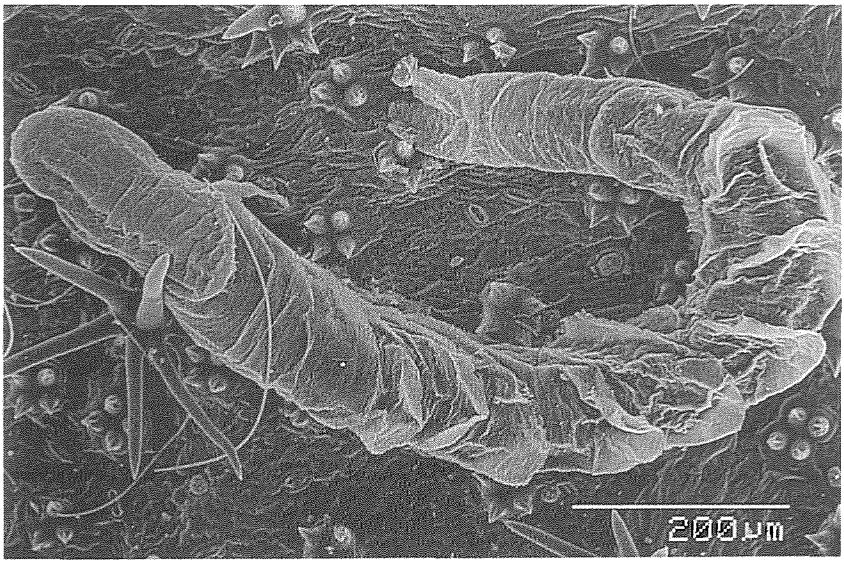

Fig. III-6. *Mempelaspis serpentina*, female test [91ML-231].

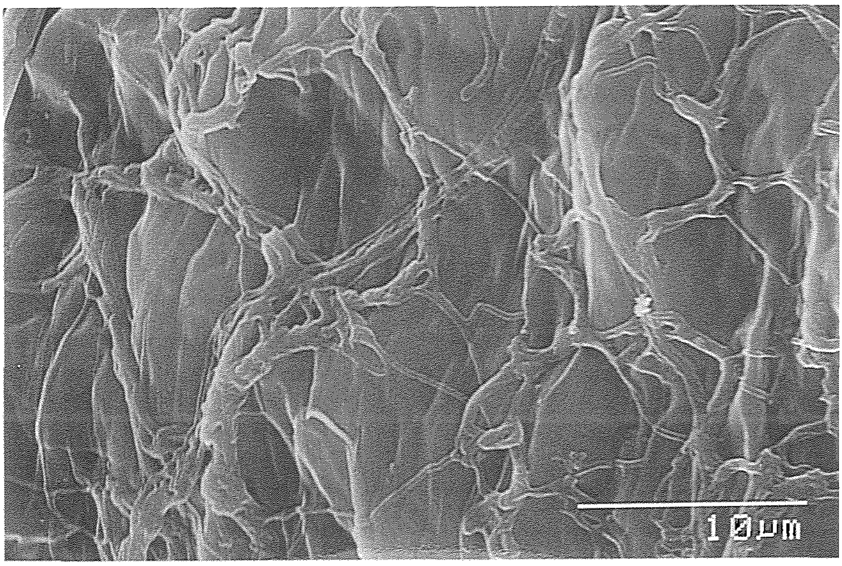

Fig. III-7. Same as Fig. III-6, penultimate section.

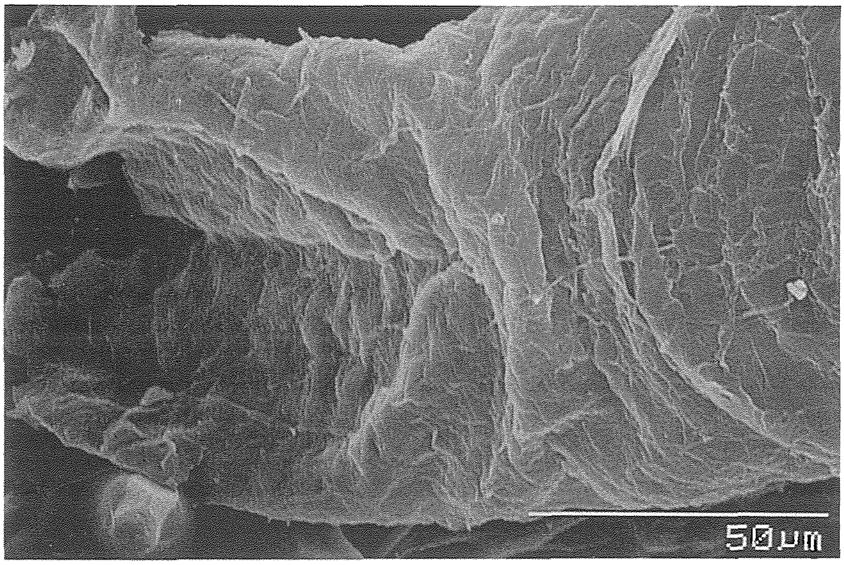

Fig. III-8. Same as Fig. III-6, posteriormost section.

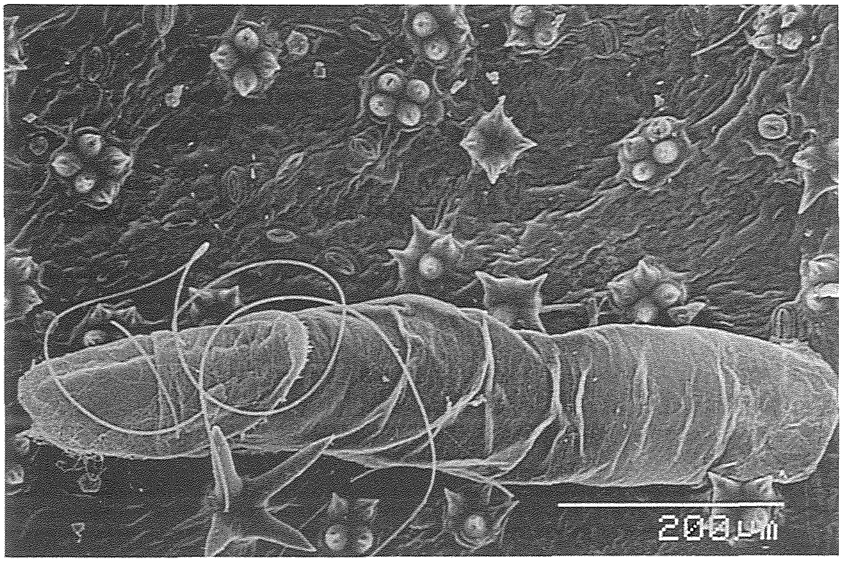

Fig. III-9. *Mempelaspis serpentina*, male test [91ML-231].

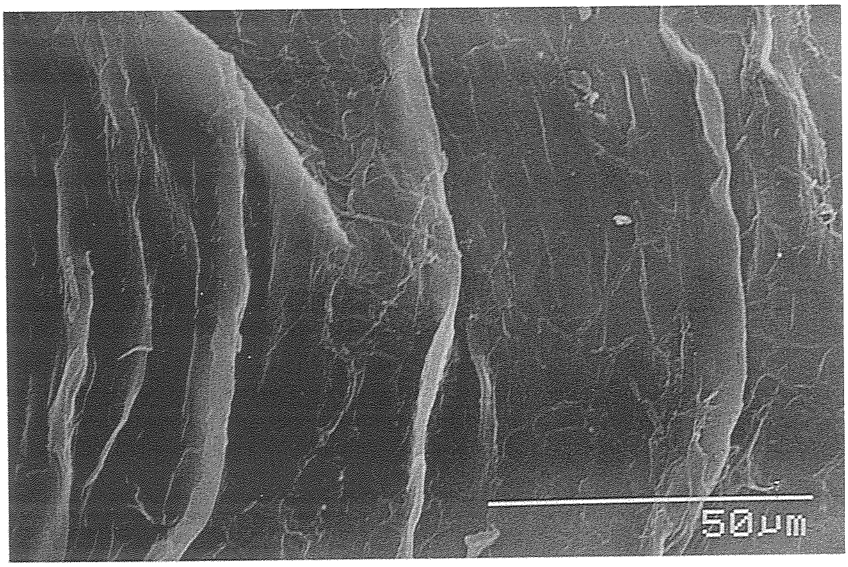

Fig. III-10. Same as Fig. III-9, part of dorsal surface.

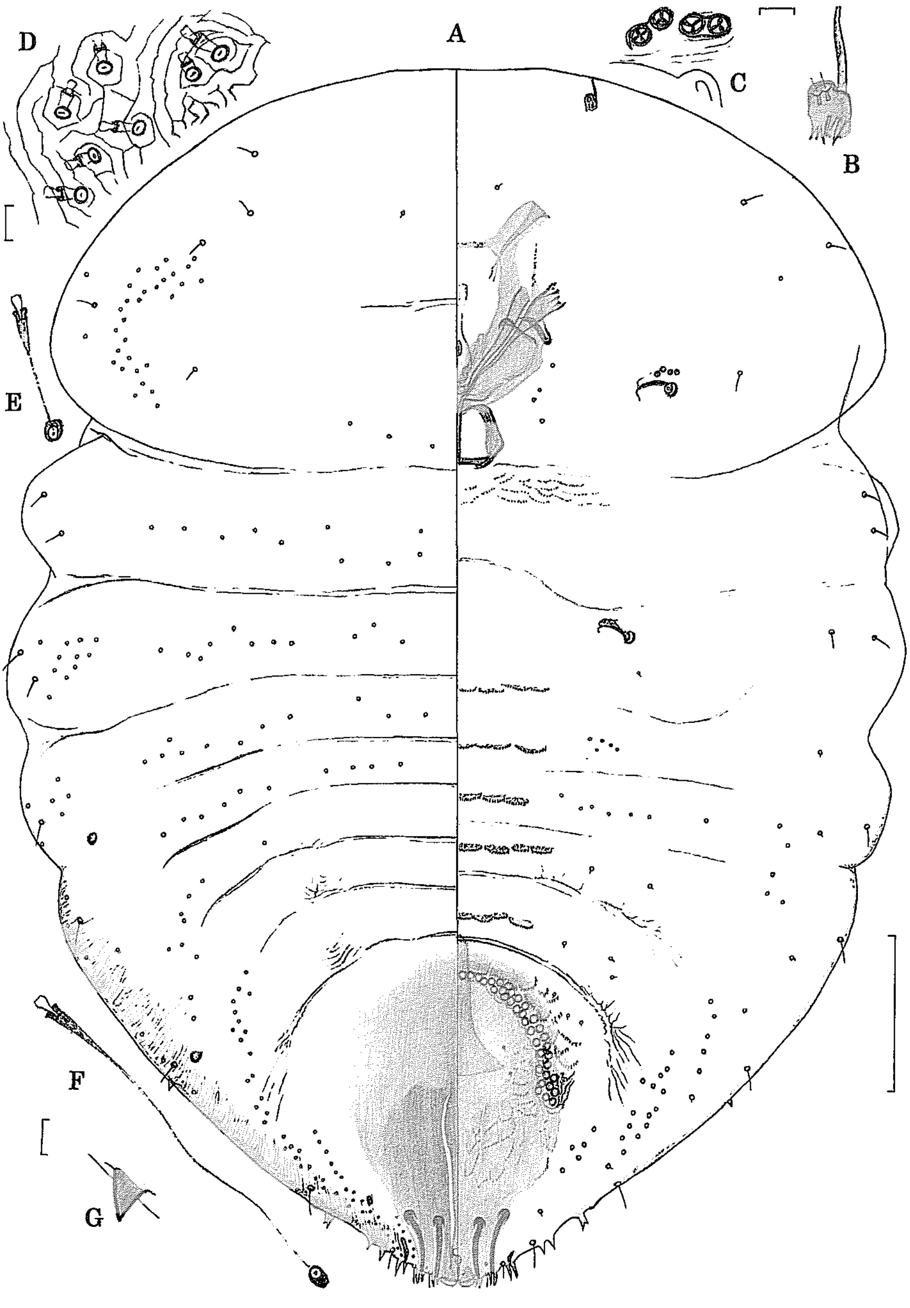

Fig. IV-1. *Icaraspidiotus chaetopterus*, adult female. B. antenna; C, disc pores associated with anterior spiracle; D, dorsal ducts on prothorax; E, dorsal duct on mesothorax; F, dorsal duct on pygidium; G, conical process on third abdominal segment. Scales: A, 100μm; B–G, 5μm.

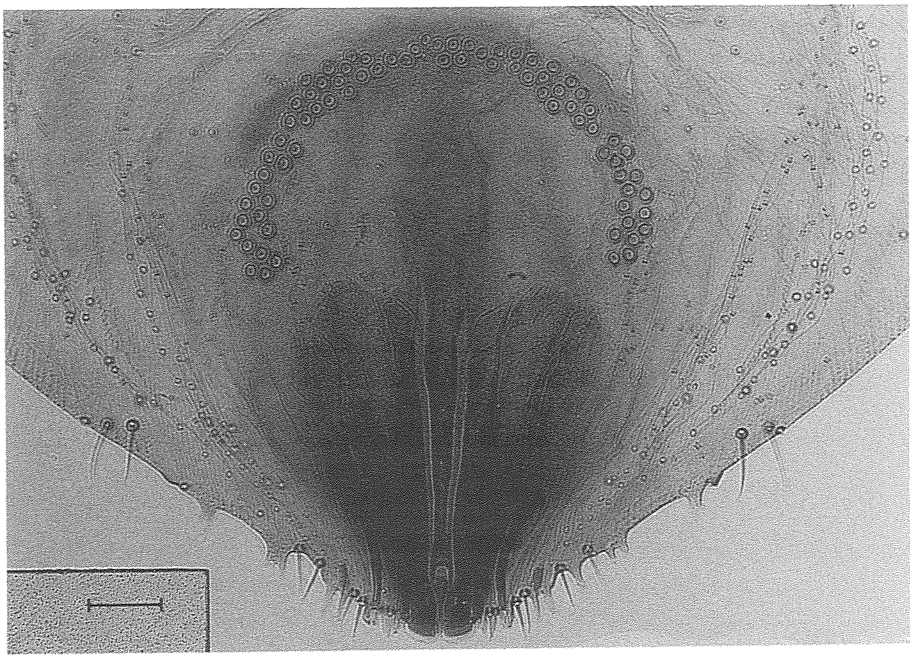

Fig. IV-2. *Icaraspidiotus chaetopterus*, adult female: pygidium. Scale: 25μm.

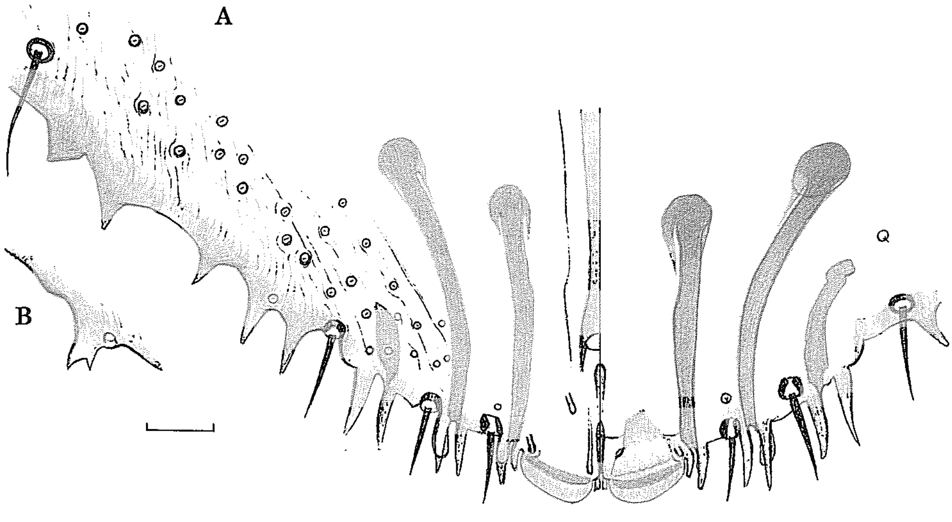

Fig. IV-3. *Icaraspidiotus chaetopterus*, adult female: pygidial margin. B, variation of conical process on fourth abdominal segment. Scale: 10μm.

Fig. IV-4. *Icaraspidiotus chaetopterus*, first instar larva, neonatal. Scale: 10μm.

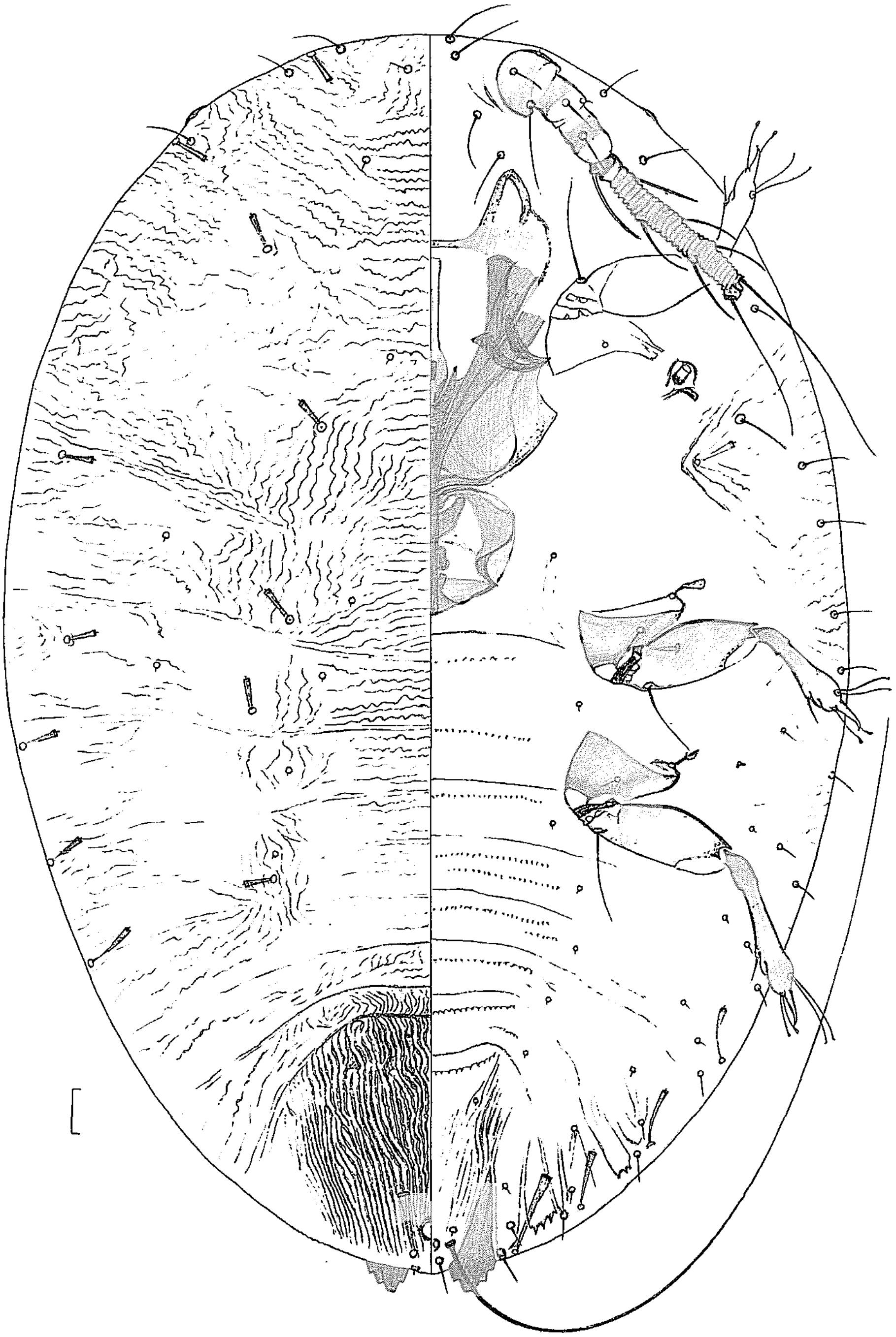

Fig. IV-5. *Pseudaonidia paeoniae*, first instar larva, neonatal. Tusima [Tsushima Is.], Nagasaki-ken, Japan, on azalea. Scale: 10μm.

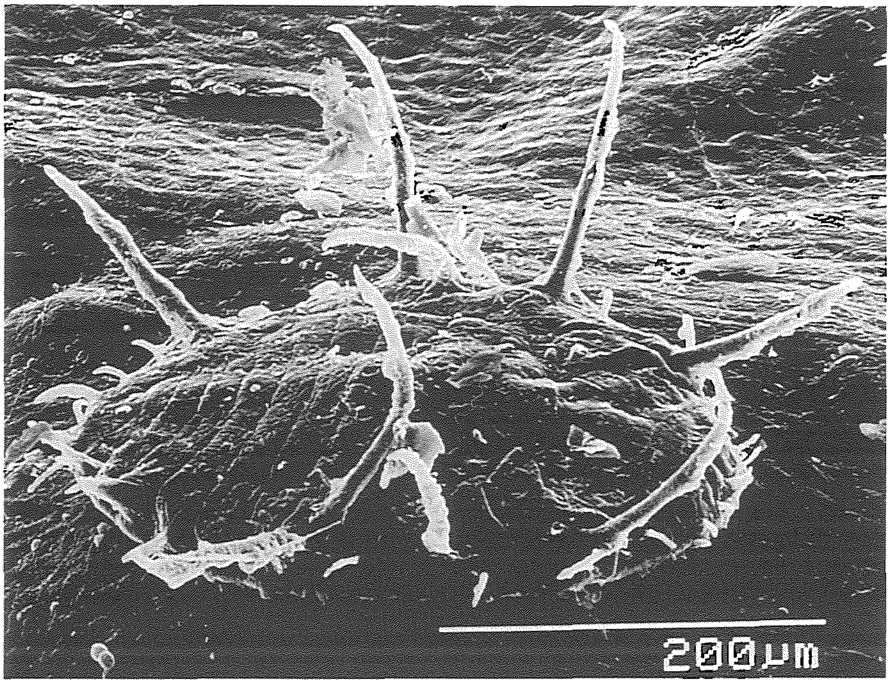

Fig. IV-6. *Icaraspidiotus chaetopterus*, first instar exuvial cast. (A few of the enormous marginal setae are lost).