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NOTES ON THE SCALE INSECT SUBTRIBE KUWANASPIDINA (HOMOPTERA: COCCOIDEA: DIASPIDIDAE)*

By SADAO TAKAGI

Abstract

TAKAGI, S. 1999. Notes on the scale insect subtribe Kuwanaspidina (Homoptera: Coccoidea: Diaspididae). *Ins. matsum. n. s.* 56: 95–150, 40 figs.

The kuwanaspidine pattern of marginal appendages is defined. Five genera are recognized and referred to the subtribe Kuwanaspidina, tribe Diaspidini. Seven new species are described from Malaysia, Japan, the Philippines, and India: *Kuwanaspis pectinata, Nikkoaspis berincangensis, N. sikokiana, Xiphuraspis ctenopyga, Medangaspis payunga* (gen. et sp. nov.), *Coronaspis malesiana*, and *C. malabarica*. Some species referred to the subtribe do not exactly conform to the kuwanaspidine pattern; a few of them are interpreted to have undergone atavistic modifications, and the others to have changed towards the advanced state of the Diaspidini. They are kept in the subtribe according to the view that an atavistic organism does not mean the revival of an ancestral taxon and that an incompletely derivative state alone is not sufficient for taxonomic change. *Kuwanaspis* and *Nikkoaspis* are closely related to each other, but the other genera appear to be isolated especially owing to a fairly wide variety of characters observed in the first instar larvae and also in the second instar males. It follows that the known forms are fragments from a once diversified large group, unless unrelated forms are included. Preliminary considerations are given to the question why marginal appendages change from taxon to taxon. A list of the Kuwanaspidina is prepared. *Chuaspis* Tao and Wong is synonymized with *Kuwanaspis*, and *C. shuichuensis* Tao and Wong with *K. bambusicola*.

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Contents

1. INTRODUCTION

Adult females of the family Diaspididae are generally provided with processes or appendages on the pygidial margin. In many species the appendages are differentiated in shape and function, and are arranged in a definite order. Certain forms are devoid of marginal processes of definite shape, yet referable to the Diaspididae on the basis of other features. It is postulated that the appendages originated from simple extensions of ventral derm and evolved from uniform elements to parts for specialized apparatus. In fact, some successive stages are recognized in the combination of appendages in each of two main divisions of the family, the tribe Diaspidini (subfamily Diaspidinae) and the subfamily Aspidiotinae [for a scheme of these stages, see Takagi, 1981, 1990b, 1995].

The majority of Diaspidini possess appendages composed of gland spines, trullae (lobes), of which the lateral pairs are divided into two lobules, and pore prominences (each associated with the orifice of a marginal macroduct). Other forms differ from them in the composition of appendages, yet cannot be excluded from the tribe in other features. They are classified into the subtribes Protodiaspidina and Kuwanaspidina under the tribe.

The Protodiaspidina are supposed to be primitive Diaspidini, because their pygidial appendages are composed of non-glanduliferous pectinae (plates) except for gland spines which are common to members of the subfamily Diaspidinae (Diaspidini and Lepidosaphedini) [for further information about this subtribe, see Takagi, 1993]. In the subfamily Aspidiotinae, *Thysanaspis* has non-glanduliferous pectinae alone, and may represent a very primitive stage of appendages in the subfamily (though this pattern is manifested not in the adult female but in the second larval instar in this pupillarial genus).

The subtribe Kuwanaspidina as represented by *Kuwanaspis* and *Nikkoaspis* also has non-glanduliferous pectinae in addition to gland spines, but differs from the Protodiaspidina in possessing strongly sclerotized trullae (except for *K. pectinata*, sp. nov.). The lateral trullae are divided into a variable number of lobules and the median trullae, too, are often divided. This variability in the number of lobules is exceptional in the family. The median trullae are widely separated from each other, with a pair of pectinae between. These characters are combined to constitute the kuwanaspidine pattern of pygidial appendages.

The occurrence of non-glanduliferous pectinae is common to the Protodiaspidina and the Kuwanaspidina, and the presence of trullae unites the Kuwanaspidina with the advanced subtribes (Diaspidina, Fioriniina, Chionaspidina, etc.) of the Diaspidini. The trullae are supposed to have arisen from pectinae situated at particular positions. Thus, the kuwanaspidine pattern of pygidial appendages can be evolutionarily transitional between the protodiaspidine pattern and the advanced pattern of the Diaspidini. It should be emphasized that the trullae are variable or unstable in the number of lobules in the kuwanaspidine pattern, whereas stable in the advanced pattern. The instability may suggest that the trullae are still in a primitive state.

Megacanthaspis was placed in the subtribe Kuwanaspidina by Borchsenius (1966), but it is referable to the Protodiaspidina, lacking trullae. *Pygalataspis miscanthi* was also placed in the subtribe by Tang (1986), but Takagi (1997b) found no positive evidence for this position. In the following lines five genera, *Kuwanaspis*, *Nikkoaspis*, *Xiphuraspis*, *Medangaspis* (gen. nov.), and *Coronaspis*, are recognized and referred to the Kuwanaspidina, and seven new species belonging to these genera are described. Some species referred to the subtribe do not exactly conform to the kuwanaspidine pattern, but they are supposed to represent modifications of that pattern. This subtribe has generally been understood to comprise bamboo-feeders, but two of the five genera are associated with dicotyledons.

2. DESCRIPTIONS OF NEW TAXA

Terms. 'Pygidial lobes' and 'plates' have commonly been used by authors, but in this paper 'trullae' and 'pectinae' are adopted in place of them.

Abbreviations. Abd I–abd VIII: first to eighth abdominal segments.

Depositories of holotypes. FRIM: Forest Research Institute of Malaysia, Kepong, Selangor, Malaysia. ZSI: Zoological Survey of India, 535, M-Block, New Alipur, Calcutta 700 053, India. SEHU: Laboratory of Systematic Entomology, Faculty of Agriculture, Hokkaidô University, Sapporo, 060-8589, Japan.

2.1. *Kuwanaspis pectinata*, sp. nov.

Material. Collected at the Gombak Field Research Centre, University of Malaya, Ulu Gombak, Selangor, Malaya, Malaysia, on *Gigantochloa scortechinii* (bamboo, Poaceae; identified by Mr K. M. Kochummen, FRIM), 27 Nov. 1988 [88ML-388].

Holotype. Adult female, deposited in FRIM.

Habit. Females occurring on the lower surface of the leaves along the midrib; test slender, cylindrical, tinged with light brown, exuvial casts brown (Fig. 25). No male tests recognized.

Recognition characters (adult female, based on about 20 specimens) (Fig. 1). Body cylindrical, about 3–4 times as long as wide in slide-mounted specimens, attaining about 1mm in length; lateral margins nearly parallel, with no intersegmental notches; pygidium (interpreted to be composed of abd VI and succeeding segments, though not defined from abd V by a distinct intersegmental line) roundish along margin. Two pairs of pectinae at apex of pygidium between a pair of gland spines, followed on each side of pygidium by 2 or 3 pectinae, 1 gland spine, 2 or 3 pectinae, and 1 gland spine successively; 1 marginal gland spine on abd V. Macroducts in single segmental rows along posterior borders of abd I–V; about 13–18 macroducts on each side of pygidium, forming indistinct oblique or longitudinal rows; 1 macroduct situated medially near apex of pygidium; some lateral macroducts scattered on abd I–V mainly on ventral surface; about 30–40 macroducts in a row across ventral surface of abd I. A transverse group of 5–9 small tubercular gland spines on each side of abd I on ventral surface just posteriorly to the transverse row of macroducts, the groups of both sides almost continuous medially; a group of 7–13 similar gland spines on ventral surface of abd II mesally to the lateral macroducts. Antennae separated from each other by a space nearly as wide as mouth-parts, each composed of a small tubercle and a fleshy seta, often with another seta, which is usually fine and a little shorter. Anterior spiracles each with 1–3 (usually 2) trilocular disc pores; posterior spiracles without disc pores; both pairs of spiracles with microducts scattered posteriorly. Perivulvar disc pores in 5 groups, 2–4 medians, 3–8 anterolaterals, and 3–5 posterolaterals. Anus subbasal, accompanied anteriorly with a pair of thick curved scleroses situated on boundary between abd V and VI and set close together.

Remarks. This species differs from the other known species of *Kuwanaspis* in having no sclerotized appendages recognizable as trullae. In other characters, however, it cannot be excluded from the genus. On the other hand, it is also very similar to some Protodiaspidina, especially *Megacanthaspis leucaspis*, and may be supposed to be a species of *Megacanthaspis*. However, the five described species of *Megacanthaspis* are associated with Lauraceae (Takagi, 1981), whereas *Kuwanaspis* species occur mainly on bamboos. The view is adopted that *K. pectinata* represents a modified form of *Kuwanaspis* [for further discussion, see 4.1.].

2.2. *Nikkoaspis berincangensis*, sp. nov.

Material. Collected on Gunung Batu Berincang (2,031m) [Mt. Brinchang], at an altitude of about 1,900m, Pahang, Malaya, Malaysia, on *Bambusa magica* (bamboo, Poaceae; identified by Mr K. M. Kochummen, FRIM), 16 Oct. 1986 [86ML-214].

Holotype. Adult female, deposited in FRIM.

Habit. Females occurring on the leaf blade near the base, usually on the lower, but sometimes also on the upper, surface; test white, broadly expanded posteriorly (Figs. 26, 27). Males occurring on the lower surface of the leaves along the midrib; test felt-like in texture, tricarinate on dorsal surface (Figs. 28–30).

Recognition characters (adult female, based on about 10 specimens) (Figs. 2, 3). Body attaining about 1.3mm in length, elongate pyriform, broadest across base of abdomen; pygidium (composed of abd VI and succeeding segments) broadly roundish along margin; prepygidial segments, especially abd I–V, lobed laterally. Trullae in 2 pairs; median trullae unilobed or bilobulate, and the second divided into 2–5 (usually 3 or 4) lobules, all these lobes and lobules being of the same size, nearly as long as adjacent pectinae, elongate, bluntly pointed apically, and notched subapically on one or either side. Median trullae widely separated from each other, with a pair of pectinae between; 1 broad pectina mesally to second trulla (on abd VII); 7 or so pectinae on abd VI, and some also on V. Marginal gland spines well developed, much longer than trullae and pectinae; 1 laterally to median trulla; 1 or 2 laterally to second trulla (on abd VII), and also at anterior angle of pygidium (on abd VI) and on abd V. Dorsal macroducts occurring laterally to submarginally on metathorax and abd I–V, also submedially and medially on II–V along posterior borders of the segments (median macroducts often lacking on II and sometimes also on V); about 38–57 macroducts on each side of pygidium, forming indistinct oblique or longitudinal rows or bands; 1 macroduct marginally between median trullae. Ventral macroducts occurring laterally on metathorax and abd I, and also in a transverse row across abd I. Small tubercular gland spines on ventral surface: about 9–17 in a transverse row on each side of abd I and about 12–20 submarginally on II. Antennae separated from each other by a space nearly as wide as mouth-parts, each composed of a small tubercle and 2 setae, of which one is often very fine. Anterior spiracles each with a loose cluster of 5–8 trilocular disc pores, posterior spiracles without disc pores; both pairs of spiracles with microducts scattered posteriorly. Perivulvar disc pores in 5 groups, 10–20 medians, 14–25 anterolaterals, and 17–24 posterolaterals. Anus subbasal.

Remarks. This species is referred to *Nikkoaspis* on account of its body shape, habit, and collection site [see 6.: under *Nikkoaspis*]. It may be close to *N. simaoensis* described from Yunnan, China, but disagrees with the description of the latter (Hu, 1988) mainly in having only two pairs of trullae (three pairs in *N. simaoensis*), in lacking pectinae on the fourth abdominal segment, and in the elongate marginal gland spines.

2.3. *Nikkoaspis sikokiana*, sp. nov.

Material. Collected on Siraga-yama (1,470m), at an altitude of about 1,000m, Kôti-ken, Sikoku [Kôchi Pref., Shikoku], Japan, on *Sasa* sp. (dwarf bamboo, Poaceae), 10–11 Nov. 1964.

Holotype. Adult female, deposited in SEHU.

Habit. Females occurring on the leaves: on the upper surface of the midrib, or on the lower surface of the blade near the base; test white, convex dorsally. Males occurring on the lower surface of the leaves, attached to the lateral sides of the midrib; test felt-like, tricarinate dorsally.

Recognition characters (adult female, based on about 20 specimens) (Figs. 4, 5). Body attaining 1.7mm in length, pyriform, broadest across base of abdomen; prepygidial segments little lobed laterally; pygidium (interpreted to be composed of abd VI and succeeding segments, though not defined from abd V by a distinct notch marginally on each side) broadly round along margin. Trullae in 2 pairs; median trullae unilobed, the second divided into 2–4 (usually 2) lobules, all these lobes and lobules being of the same size, nearly as long as adjacent pectinae, elongate, bluntly pointed apically, and notched subapically on one or either side. Median trullae separated from each other by a wide space occupied by a pair of pectinae; 1–2 (usually 1) gland spines laterally to median trulla; 1–3 (usually 2) pectinae mesally to second trulla; then, a continuous series of pectinae, with about 15–35 gland spines intermingled, occurring as anteriorly as abd III; all these gland spines longer than pectinae. Some (up to about 30) small tubercular ventral gland spines on each side of basal part of abdomen (abd I and II). About 44–94 dorsal macroducts on each side of pygidium, forming indistinct oblique or longitudinal rows or bands; 1–5 macroducts medially near apex of pygidium, and 1–3 macroducts often present medially in front of anus. Numerous dorsal macroducts on prepygidial abdominal segments laterally to submarginally and also along posterior borders. Ventral macroducts numerous in a broad transverse band across base of abdomen (abd I and II). Antennae separated from each other by a space nearly as wide as mouth-parts, each composed of a small tubercle and 2 setae, of which one is usually very fine. Anterior spiracles each with a compact group of about 10–35 trilocular disc pores, posterior spiracles without disc pores; both pairs of spiracles with microducts scattered posteriorly. Perivulvar disc pores in 5 groups, 7–28 medians, 13–39 anterolaterals, and 16–38 posterolaterals. Anus a little anterior to centre of pygidium.

Remarks. This species is very close to *Nikkoaspis shiranensis*, but definitely differs from the latter in the marginal gland spines longer than the pectinae and projecting beyond the apices of the latter throughout the third to fifth abdominal segments and pygidium. In *N. shiranensis* the marginal gland spines, except those occurring just laterally to the median and second trullae, are as long as or shorter than the pectinae (so that they may easily be overlooked when overlapping with pectinae) (Fig. 6). Furthermore, *N. sikokiana* is usually provided with two pectinae between the median and second trullae, whereas *N. shiranensis* with one pectina and only rarely with two in this space.

In the morphological characters *Nikkoaspis sikokiana* can be the immediate ancestor of *N. shiranensis*. The material examined of the former makes the only record of the genus from the island of Sikoku, whereas the latter is distributed in southern Sakhalin, southern Kurile Islands, Hokkaidô, Honsyû, and Kyûsyû [for records in Sakhalin and the Kuriles, see Danzig, 1980]. This situation suggests that *N. sikokiana* survives in isolation from *N. shiranensis*. The supposed ancestor-descendant relationship, however, is left pending, because there are at least two other species which may be closely related to *N. shiranensis* [see 6.].

2.4. *Xiphuraspis ctenopyga*, sp. nov.

Material. Collected in the grounds of the Forest Research Institute of Malaysia, Kepong, Selangor, Malaya, Malaysia, on *Dendrocalamus* sp. (bamboo, Poaceae; identified by Mr K. M. Kochummen, FRIM), 14 June 1990 [90ML-2].

Holotype. Adult female, deposited in FRIM.

Habit. Females and males occurring on the upper surface of the leaves. Female test elongate, very narrow, with a median ridge, brown, exuvial casts darker than secretionary part (Fig. 32). Male test similar, but much shorter than the completed female test, the median ridge narrowly white.

Recognition characters (adult female, based on about 15 specimens) (Figs. 7, 8). Body slender; when fully grown attaining about 1.6mm in length, more than 6 times as long as wide, the meso- and metathorax becoming especially elongate, and these segments and basal 2 abdominal segments sclerotized dorsally; cephalothorax and basal 2 abdominal segments nearly parallel-sided; pygidium (interpreted to be composed of abd VI and succeeding segments, though not defined from abd V by an intersegmental line) narrow and nearly elongate triangular. Median trullae unilobed and sometimes bilobulate, the second bilobulate, all these lobes and lobules being of the same size, elongate, bluntly pointed apically, notched on each side. Median trullae separated from each other by a pair of well-developed pectinae; median and second trullae separated from each other by a wide space, 1 broad pectina occurring mesally to the second trulla; then, a series of similar pectinae occurring as anteriorly as abd III, diminishing in size on anterior segments, a few of them occurring on abd VI sometimes sclerotized and more or less trulla-like in shape. About 30–40 marginal gland spines occurring on each side of abdomen, intermingled with trullae and pectinae, extending as anteriorly as abd I, where the series ends with some short gland spines occurring within margin; 1 or 2 spiniform processes (gland spines?) sometimes discernible mesally to median trulla, overlapping with the pectina situated there. About 20–40 dorsal macroducts occurring in median region of pygidium, forming a longitudinal group, which is not always sharply defined from other macroducts occurring around; some dorsal macroducts occurring along margin of abdomen and on posterior borders of abd III–V. Antennae set rather close together, each composed of a low tubercle and 2 fleshy setae. Anterior spiracles each with 4–6 trilocular disc pores, posterior spiracles without disc pores; both pairs of spiracles with microducts scattered posteriorly. Perivulvar disc pores absent. Anus subbasal.

Remarks. This species is remarkable in having a median group of dorsal macroducts on the pygidium. This group occupies a broad median space between the anus and the apex of the pygidium, ending with a macroduct occurring between the median trullae. A similar median group of macroducts occurs in *Xiphuraspis spiculata* (*=Chionaspis spiculata*), the type-species of the genus. *Xiphuraspis ctenopyga* is quite different from *X. spiculata* in having differentiated marginal appendages. In the latter species the appendages are represented by a series of 'longish acuminate processes (7 or 8 on each side) of which the median two are longer and stouter than the others' (Green, 1919). In spite of this difference, which appears too great, the new species is referred to *Xiphuraspis* in accordance with a view adopted in this paper concerning atavistic modifications of pygidial appendages [for the view, see 4.1.]. The first instar larva of *X. ctenopyga* possesses many 'verrucose plates' on the dorsal surface (Figs. 20, 31) [3.1.]. This character is so peculiar that I have no doubt that it has generic value. An examination of the first instar of *X. spiculata* for the occurrence of verrucose plates, therefore, is indispensable for proceeding with the generic problem of *X. ctenopyga*. I have examined no specimens of *X. spiculata*, which is known to me through the original description (Green, 1919) and the redescription given by Borchsenius and Williams (1963). However, examinations of the adult female will give no more information helpful in clarifying the relationship between the two species.

This species is similar to *Kuwanaspis elongata* from Taiwan in the narrow pygidium and the well-developed pygidial appendages, but definitely differs from the latter in lacking perivulvar disc pores. The figure of *K. elongata* accompanying the original description (Takahashi, 1930) suggests the presence of a mid-pygidial group of macroducts. *K. elongata*, therefore, should also be examined for the presence of verrucose plates in the first instar and for its possible position in *Xiphuraspis*.

2.5. *Medangaspis payunga*, sp. nov.

Material. Collected in the grounds of the Forest Research Institute of Malaysia, Kepong, Selangor, Malaya, Malaysia, on *Actinodaphne pruinosa* (Lauraceae; identified by Mr K. M. Kochummen, FRIM; local name for *Actinodaphne* spp.: Medang payung, literally meaning umbrella laurels), 21 Nov. 1986 [86ML-511].

Holotye. Adult female, deposited in FRIM.

Habit. Females and males occurring on the lower surface of the leaves. Adult female wholly covered with larval exuvial casts (Figs. 33, 34). Male tests felt-like, white, curved up so that the posterior end is directed above (Fig. 35–37).

Recognition characters (adult female, based on about 15 specimens) (Fig. 9). Pupillarial, with dermal secretionary organs much reduced. Body cylindrical; mounted specimens about 300–320μm long, narrowly elliptic, with no intersegmental notches on lateral margins; pygidium (interpreted to be composed of abd VI and succeeding segments) well sclerotized dorsally throughout (thus well demarcated from abd V), round along margin. Marginal appendages of pygidium rather reductive, yet median trullae still recognizable, always unilobed, sclerotized, conical, incised subbasally on one or either side, with a pair of pectinae between, followed on each side of pygidium by 1 gland spine, 3 pectinae, 1 gland spine, and 1 rudimentary pectina successively (the last occurring on abd VI). Four small submarginal dorsal ducts on each side of pygidium, as large as or a little larger than ventral microducts. Microducts and gland spines occurring submarginally on ventral surface of prepygidial part of body, forming together a longitudinal row on each side: 1 or 2 microducts laterally to mouth-parts, 1–3 microducts and 2 or 3 gland spines between anterior and posterior spiracles, 1–3 microducts and 1–3 gland spines laterally to posterior spiracle (on metathorax), 1 microduct and 1 gland spine on abd I–V each. Another ventral microduct on each side of pygidium. Antennae separated from each other by a space a little narrower than mouth-parts, each with a fleshy seta. Both pairs of spiracles without disc pores. Perivulvar disc pores absent. Anus a little posterior to centre of pygidium.

2.6. *Medangaspis*, gen. nov.

Type-species. *Medangaspis payunga*, sp. nov.

Because only the type-species is known, the description of it given above should substitute for a generic description. The dermal features of the adult female are simplified undoubtedly in association with the pupillarial mode of life. The marginal appendages of the pygidium are apparently reductive, but they still hold the kuwanaspidine pattern (except for the absence of lateral trullae): they are composed of trullae, pectinae and gland spines, and the median trullae are separated from each other by a pair of pectinae. This pattern is also represented in the second instar female, which differs from the adult female in having three pectinae (instead of one) on the sixth abdominal segment.

2.7. *Coronaspis malesiana*, sp. nov.

Material. Collected in Sabah, Malaysia, and Luzon, the Philippines:

Sabah. Danum Valley Conservation Area, Ulu Segama, Tawau, on *Spatholobus oblongifolia* (Fabaceae), 23 Oct. 1988 [88ML-189]; Sepilok, Sandakan, on *Lophopetalum beccarianum* (Celastraceae) and *Reissantia indica* (Celastraceae), 31 Oct. 1988 [88ML-236, -238] (the host plants were identified at the Forest Research Centre, Sabah).

Luzon. Grounds of the University of the Philippines at Los Baños, Laguna, on *Celtis luzonica* (Ulmaceae; identified by Dr Edwino S. Fernando, University of the Philippines at Los Baños), 24 Nov. 1992 [92PL-25].

Holotype. Adult female, mounted from 88ML-189, deposited in FRIM.

Habit. Females occurring on the upper surface of the leaves along the margin; test elongate, with a median ridge, dirty brown, pale brown or nearly white (Figs. 38, 39). Males occurring on the lower surface of the leaves; test felt-like in texture, white, with a median carina (Fig. 40).

Recognition characters (adult female, based on about 15 specimens mounted from 88ML-189, several specimens from 88ML-236, about 15 specimens from 88ML-238, and 6 specimens from 92PL-25) (Fig. 10). Body elongate, fusiform, attaining about 1.3mm in length, membranous except for pygidium, which is weakly sclerotized, rather narrow, nearly triangular, and slightly roundish along the margin (the boundary between the pygidium and prepygidial abdomen is clear between abd V and VI in the median to submedian area; in the submarginal to marginal area, however, this boundary becomes obscure and the pygidium appears to include abd IV and V). Asymmetric when fully grown: the side facing towards the middle of the leaf is more or less expanded laterally, while the opposite side, lying just on the extreme margin of the leaf, tends to be undergrown especially on the ventral surface of the prepygidial abdominal segments (so that, in slide-mounted specimens, the lateral region of the dorsal surface turns around to take the ventral position). Trullae in 2 pairs; median trullae unilobed, separated from each other by a space a little narrower than one of them, oblong, bluntly pointed apically, and notched once or twice on each side; second trullae bilobulate, each lobule similar to median trulla. A marginal process, pointed or divided apically, occurring just mesad of second trulla, with a macroduct basally; 3 serrate, sclerotized processes on abd VI, the mesal two of them each with a macroduct basally; 3 similar but broader processes on abd V, the mesal and sometimes also the middle of them with a macroduct basally; another similar process on abd IV at the posterolateral angle of the segment, with a macroduct basally. A pair of slender, spiniform processes between median trullae, often projecting beyond the apices of the trullae. Marginal gland spines well developed, much longer than other marginal processes: 4 single gland spines on each side of pygidium, belonging to abd V–VIII (the mesalmost occurring just laterally to median trulla); numerous similar gland spines on abd II–IV, with some much shortened ones mingled on II and III; short gland spines also on abd I. Dorsal macroducts arranged in submedian rows on prepygidial abdomen along posterior borders of segments and scattered in submarginal region through metathorax and abdomen; a few or several median macroducts occurring on abd IV and often on V, and sometimes also on II and III; some macroducts on abd VI in a longitudinal band, which is sometimes divided into a submedian and a submarginal group. Antennae set close, prominent, having 3–6 conical processes and 1 or sometimes 2 fleshy setae. Small ducts laterally to mouth-parts and also between anterior and posterior spiracles. Anterior spiracles each with a group of trilocular disc pores, posterior spiracles each with a smaller group. Perivulvar disc pores in 5 groups. Anus subbasal.

The examined specimens are variable in the numbers of dermal secretionary organs. The spiracular disc pores, perivulvar disc pores, dorsal macroducts, and prepygidial gland spines are comparatively numerous in the specimens from the Danum Valley [88ML-189] (Fig. 10), and fewer in the specimens from Sepilok [88ML-236, -238]; the specimens from Los Baños [92PL-25] are intermediate between them. The numbers of some secretionary organs are given below for the specimens mounted from 88ML-189 and 88ML-238.

88ML-189. Spiracular disc pores: about 5–16 at anterior spiracle, 2–10 at the posterior. Perivulvar disc pores: 5–10 medians, 10–17 anterolaterals, 13–24 posterolaterals. Long gland spines: 4–12 on abd III, 6–12 on IV. Dorsal macroducts in the longitudinal band on Abd VI: about 15–25.

88ML-238. Spiracular disc pores: 2–7 at anterior spiracle, 1–5 at the posterior. Perivulvar disc pores: 2–10 medians, 4–11 anterolaterals, 4–11 posterolaterals. Gland spines: 3-6 on abd III and IV each. Dorsal macroducts in the longitudinal band on abd VI: about 8–13.

[Remarks are given under 2.8.].

2.8. *Coronaspis malabarica*, sp. nov.

Material. Collected in southern India: Anaimalai, at an altitude of 750m, Tamil Nadu, on an undetermined plant, 3 Dec. 1978 [78IND-282]; Periyar Tiger Reserve, at an altitude of about 900m, Kerala, on an undetermined plant (same species as the host plant of 78IND-282), 19 Dec. 1978 [78IND-405], and on *Zanthoxylum ovalifolium* (Rutaceae; identified by Dr Philomina Kuriachan, Dept. of Botany, University of Kerala), 21 Dec. 1978 [78IND-422]. The undetermined host plant [78IND-282, -405] smelled spicy when twigs were cut off. I believe that it is *Murraya koenigi* (Rutaceae), which is used for seasoning herb in India.

Holotype. Adult female mounted from 78IND-282, deposited in ZSI.

Habit. Females occurring on the upper surface of the leaves along the margin; test elongate, brown. Males occurring on the lower surface of the leaves; test felt-like, white, obscurely tricarinate.

Recognition characters (adult female, based on about 15 specimens mounted from 78IND-282 and about 10 from 78IND-422) (Fig. 11). Very similar to *C. malesiana*, differing mainly in the following characters: 1) The pygidium is broader and more roundish along the margin; 2) the sclerotized spiniform processes occurring between the median trullae are shorter than in *C. malesiana*, and are applied to the base of a membranous slender process which occurs between them and projects beyond the apices of the median trullae; 3) two or three marginal macroducts are associated with the serrate marginal processes of the fifth abdominal segment; 4) no median macroducts occur on prepygidial abdominal segments. The body, when fully grown, is more or less asymmetric as in *C. malesiana*. Spiracular disc pores: about 10–26 at anterior spiracle, 2–13 at the posterior. Perivulvar disc pores: 4–9 medians, 8–18 anterolaterals, 11–17 posterolaterals. Long gland spines: about 3–8 on abd III and IV each. Dorsal macroducts in the longitudinal band (sometimes divided into a submedian and a submarginal group) on abd VI: about 10–20.

Remarks. The two new species described above are referred to *Coronaspis*, of which the type-species, *C. coronifera* (=*Chionaspis coronifera*), is known to me only through the original description (Green, 1905) and the figures prepared by Ferris (1937, Fig. 2). It seems that Green and Ferris studied full-grown adult females with pygidial appendages 'set back on the ventral surface and scarcely projecting the margin' and prepygidial segments 'densely chitinous, with exception of penultimate segment' (quotations from Green). The type-species, therefore, requires a further examination based on younger adult females for detailed characters. I have little doubt, however, that the two new species are congeneric with *C. coronifera*. They agree with Green's description and Ferris' figures in some characters including the coronate antennae. They are easily distinguishable from *C. coronifera* in the prepygidial segments remaining membranous and in having perivulvar disc pores. The genus *Coronaspis* was referred to the Lepidosaphedina (=Lepidosaphedini in my classification) by Balachowsky (1954) and to the Chionaspidina by Borchsenius (1966). The view is adopted in this work that it belongs to the Kuwanaspidina. The marginal appendages of the pygidium in *C. malesiana* and *C. malabarica* are not exactly of the kuwanaspidine pattern, but may be understood to represent a modification of it [for further discussion, see 4.1.].

3. LARVAL INSTARS AND TESTS

3.1. First instar larvae (Figs. 18–22)

The first instar larvae of the species examined (including some undescribed species of *Kuwanaspis*) agree in the antennae having a single terminal seta, in the tarsi without well-developed ventral seta, in having submedian dorsal setae on the thoracic and abdominal segments, in lacking submedian ventral setae on the first to fifth abdominal segments, and, in most species, in having three pairs of submedian dorsal ducts on the thoracic segments. The combination of these characters is common to many other Diaspidini.

The antennae are five-segmented in *Kuwanaspis*, *Nikkoaspis*, and *Xiphuraspis*, whereas six-segmented in *Medangaspis* and *Coronaspis*, thus differing between the genera associated with Poaceae (mainly bamboos) and those feeding on dicotyledons. In the first three genera the intermediate segments are often deeply constricted and the antennae may appear to have more than five segments. In fact, Howell and Tippins (1973) described the first instar antennae of *Kuwanaspis howardi* as six-segmented. The exact number of segments can be known by the presence of membranous joints. However, such joints are not always visible, and in the exuvial cast the whole antennae are sclerotized, leaving no membranous joints. In *Kuwanaspis hikosani* the fourth and fifth segments are tightly connected together and, thus, the antennae appear to be four-segmented.

The three pairs of submedian dorsal ducts occurring on the thorax are usually very small, and may easily be overlooked. In *Kuwanaspis pectinata* (Fig. 18), however, I have failed to find them. On the other hand, in *Medangaspis payunga* (Fig. 21) they are enlarged, and there is another pair of enlarged ducts laterally to the anus. Unlike many other diaspidids, this species lacks enlarged ducts on the head instead. It is also remarkable in having shortened antennae (with the terminal segment especially shortened) and shortened tibiotarsi.

The first instar larvae of *Coronaspis malesiana* and *C. malabarica* (Fig. 22) are provided with well-developed, sclerotized processes or trullae and serrate processes or pectinae on the caudal margin, whereas those of the other genera have only small, pointed processes or no discernible processes.

The first instar larva of *Xiphuraspis ctenopyga* (Fig. 20) is quite peculiar in possessing 'verrucose plates' (as called in the present paper) on the dorsal surface (I have observed the plates also on the bodies of embryonic larvae within the mother's body). These plates are variable in size, irregularly round or elliptic, and studded with flat wart-like patches. More than 100 plates are strewn over the body except on the anterior and posterior ends, the marginal area, and a narrow median area. SEM observations have revealed no further details of the plate structure (Fig. 31).

3.2. Second instar females

The second instar females of the examined species are similar to the adult females in the pygidial appendages and differ in having much fewer ducts as usual in diaspidids (in *Medangaspis payunga*, which is pupillarial, the adult female, too, has a small number of ducts). In each species the exuvial cast assumes a definite shape, which may be species-specific and useful for identification (Figs. 23, 24).

3.3. Second instar males (Figs. 12-17)

Howell and Tippins (1973) in their study on the second instar male of *Kuwanaspis howardi* showed that this stage is quite different in dermal characters from the adult and second instar females. They stated that 'three or four ducts sharing a common orifice' are present on each of 'segments 6 and 5'. They applied to these ducts the term 'communal ducts' originally proposed by Tippins (1970) for one of the two types of modified ducts observed in the second instar males of *Fiorinia* species. Matile-Ferrero (1990) criticized the term as incorrect and proposed the replacing term 'cratère glandulifère'. Her term, 'glanduliferous crater' in English, is adopted in this paper. The second instar male as exemplified by *Kuwanaspis howardi* may be referred to as the *howardi* type. It should be mentioned, however, that in *K. howardi* the glanduliferous craters belong to the sixth and seventh abdominal segments and not to the fifth and sixth as described by Howell and Tippins (1973).

The second instar males of 12 species of *Kuwanaspis* and 3 species of *Nikkoaspis* examined in connection with the present study belong to the *howardi* type except for one undescribed species of *Kuwanaspis* (the second instar male of this species has no glanduliferous craters, but in other characters it is not much different from the *howardi* type and may represent a variation of that type). The glanduliferous craters usually occur on the sixth and seventh abdominal segments, but in two undescribed species of *Kuwanaspis* and two species of *Nikkoaspis* (*N. shiranensis* and *N. sikokiana*) they are restricted to the seventh segment. The number of ducts composing a glanduliferous crater also varies and may decrease to only two as exemplified by *N. sikokiana* (Fig. 13).

Medangaspis and *Coronaspis* represent other types of the second instar male. This stage in *Medangaspis payunga* (Fig. 15) entirely lacks pygidial appendages, and is quite dissimilar to the second instar female as well as to the adult female in other characters, too. In *Coronaspis malesiana* (Fig. 16) and *C. malabarica* (Fig. 17) it is provided with well-developed trullae and rather rudimentary pectinae but otherwise remarkably different from the female. In all these species, however, there is no modified duct peculiar to the second instar male.

Sexual dimorphism in the second instar is much less pronounced in *Xiphuraspis ctenopyga*, in which the second instar male and female and the adult female are all very much alike in the marginal appendages and differ in the number and arrangement of ducts and other minor details. Thus the second instar male of this species (Fig. 14) is 'homomorphic' (agreeing in the principal pattern of characters) with the female in contrast with the 'heteromorphic' second instar males of the other kuwanaspidines examined.

3.4. Female tests (Figs. 25–27, 32, 38, 39)

In SEM observations on the female test of *Nikkoaspis shiranensis* I found no trace of regular movements of the insect body (Takagi, 1990a). This is also true in the species of *Kuwanaspis*, *Nikkoaspis*, *Xiphuraspis*, and *Coronaspis* examined in the present study. Growth patterns are prominent in some of them, but there has been observed no regular transverse running of wax filaments (Figs. 27, 32B, 32C, 39).

4. DISCUSSIONS

4.1. Modified marginal appendages and their implications in taxonomy

In some species referred to the Kuwanaspidina the marginal appendages do not exactly conform to the kuwanaspidine pattern defined in the introduction. *Kuwanaspis pectinata* has no sclerotized processes recognizable as trullae, the appendages being composed of pectinae and gland spines as in the Protodiaspidina. Its similarity to *Megacanthaspis leucaspis*, Protodiaspidina, is especially impressive. But it is a bamboo-feeder like other species of *Kuwanaspis*, and is closely similar to the latter in characters other than the absence of trullae. It is referred to *Kuwanaspis* on the supposition that the absence of trullae is secondary. In the kuwanaspidine pattern the median trullae are situated just laterally to the median pair of pectinae. In *K. pectinata* these trullae are apparently replaced by another pair of pectinae. The second trullae are also absent and may have been replaced as well, but they cannot be located among the pectinae occurring on the seventh abdominal segment, because those pectinae are few as compared with kuwanaspidines with well-developed trullae. The replacement is atavistic on the postulation that in the evolutionary course of diaspidids the trullae originated from pectinae occurring at particular sites.

The pygidial appendages of *Xiphuraspis spiculata*, the type-species of the genus, are composed of simple membranous processes, of which some are gland spines [see under 2.4.]. *Xiphuraspis ctenopyga* possesses well-developed appendages definitely of the kuwanaspidine pattern, and, nevertheless, is placed in *Xiphuraspis* on the basis of other characters, especially the presence of a median group of macroducts on the pygidium. Although the supposed relationship between the two species is to be verified (or refuted) by an examination of the first instar of *X. spiculata* [see 2.4.; for the very peculiar character in the first instar of *X. ctenopyga*, see 3.1.], the state of appendages in *X. spiculata* can be an extreme modification, involving atavism, of the kuwanaspidine pattern. As stated in the introduction, very primitive diaspidids are supposed to have had simple marginal processes, which were precursors of differentiated appendages.

The supposition that atavism is involved in the state of appendages in *K. pectinata* and *X. spiculata* is based also on the view that, in general, genetic potential for manifesting ancestral phenotypes is not lost for a long geological time in evolving organisms. These years I have forwarded this view at describing various diaspidids. I, therefore, do not repeat the discussions in this paper.

The problem here is how to treat atavistic organisms in taxonomy. Should *K. pectinata* be referred to the Protodiaspidina and *X. spiculata* to another primitive group? The lineage leading to *K. pectinata* should once have been provided with good trullae, and potential for manifesting them (now an ancestral feature) may not be lost in the genetic system* of *K. pectinata*. The ancestors of *X. spiculata* must once have been like *X. ctenopyga*, and potential for manifesting a complete kuwanaspidine pattern may still be retained. Hampé's (1959)

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* Or, to be more exact, 'multiple inheritance systems' according to Jablonka, E. and Lamb, M. J., 1995 (Epigenetic Inheritance and Evolution: the Lamarckian Dimension, Oxford U. P., xii+346pp.).

experimental chicken embryos developed limb bones similar to those of *Archaeopteryx* (for a criticism, see Müller, 1989), but their genetic system was nothing else than that of *Gallus gallus*. Odd second instar males of some diaspidid species are apparently atavistic [my recent paper on this subject: Takagi 1998], but the adult females show no trace of atavism and indicate the proper taxonomic positions of the species. In *K. pectinata* and *X. spiculata* the supposedly atavistic changes are restricted to the appendages. If an organism is atavistic in its whole phenotype and in all stages of development — a purely theoretical situation — the recognition of atavism will be impossible. But, given the considerations outlined above, even a completely atavistic organism does not mean the revival of any ancestral taxon.

K. pectinata, agreeing with other species of *Kuwanaspis* in general characters except the absence of trullae and in host association, can remain in the genus. It should be emphasized, however, that *K. pectinata* shows how closely the Kuwanaspidina are related to the Protodiaspidina. *X. spiculata*, apparently related to *X. ctenopyga*, should also be a kuwanaspidine. I agree with Borchsenius and Williams (1963) in their view that *X. spiculata* is distinct but allied to *Kuwanaspis* [also see 4.2.].

The two new species of *Coronaspis* have no typical pectinae. The pair of slender processes occurring between the median trullae can be homologous with the median pectinae in the kuwanaspidine pattern, and the pointed or serrate marginal processes occurring on the lateral sides may also be modified pectinae. Macroducts are associated with some of the lateral processes, that is, marginal macroducts are differentiated. Especially in this last character the two species are similar to advanced Diaspidini.

The view is adopted that *Coronaspis* should belong to the Kuwanaspidina. The median pectinae persist in the modified shape, and the serrate processes are still reminiscent of pectinae rather than round or angular pore prominences. The species of the genus have changed apparently in the direction to advanced Diaspidini, but the change is incomplete. In other words, they have not yet effected an evolutionary breakthrough sufficient for taxonomic change.

Two other kuwanaspidine species, *Kuwanaspis bambusicola* and *K. tanzawensis*, also have no well-shaped pectinae. The median pectinae are modified into conical processes, and the lateral pectinae are replaced by tubercular or slightly serrate prominences accompanied with macroducts. These prominences are little different from the pore prominences occurring in advanced Diaspidini. These two species, therefore, may be excluded from *Kuwanaspis* to form another genus, but they are connected through *K. neolinearis* to other species of *Kuwanaspis* in the state of the pygidial appendages. They hold to the kuwanaspidine pattern in one character, the persistence of median pectinae (which are, however, modified in shape) [for further discussion, see 6.: under *Kuwanaspis*].

4. 2. Relationships among the kuwanaspidine genera

In the diaspidid ontogeny the adult female forms the nucleus of adaptive evolution (Takagi, 1990c), whereas the first instar larva, the earliest stage in the postembryonic development, is expected to be relatively stable phylogenetically in its morphological characters. The first instar larvae examined in the present study agree in some characters, which are common to many other Diaspidini, but are various in other characters [3.1.].

Kuwanaspis and *Nikkoaspis*, represented by the type-species and other species, are very similar not only in the adult female but also in the first instar larva, and there is no doubt that they are closely related. They once have been synonymized. In the present study they are recognized as different genera, but rather tentatively, and the generic problem of the '*Kuwanaspis-Nikkoaspis* complex' is left pending [see 6.: under *Nikkoaspis*].

Xiphuraspis ctenopyga is also very similar to *Kuwanaspis* species in the adult female. In contradiction to this, it is quite peculiar in possessing a number of 'verrucose plates' in the first instar [3.1.]. The function of these plates is unknown, but they imply specialization rather than primitiveness. In other characrters of the first instar *X. ctenopyga* is not much different from *Kuwanaspis*. If the supposition that this species is congeneric with *X. spiculata*, the type-species of the genus, is correct [see 2.4.], *Xiphuraspis* should be a specialized form allied to *Kuwanaspis*.

Medangaspis payunga is pupillarial, with the pygidial appendages of the adult female somewhat reductive. In spite of this, it shows an unmistakable kuwanaspidine pattern, and is referable to the Kuwanaspidina. In the first instar, however, it is distinct from the other genera of the subtribe, and does not seem to be particularly related to any of them.

Coronaspis, based on the two new species, is ambiguous about the pattern of its pygidial appendages. It is referred to the Kuwanaspidina on the supposition that its appendages represent another modified kuwanaspidine pattern [4.1.]. However, in the first instar it is remarkably different from all the other genera of the subtribe, possessing well-developed trullae and other appendages, and there is no evidence that it is closely related to any of them.

The second instar males examined are also strikingly different among the genera except between *Kuwanaspis* and *Nikkoaspis* [3.3.]. In *Xiphuraspis ctenopyga* the second instar is homomorphic between the male and female, whereas in the other species it is heteromorphic. The heteromorphic second instar males examined differ in the presence or absence of glanduliferous crater and are various especially in the state of the abdominal margin.

In the Diaspidini, homomorphism and heteromorphism in the second instar sometimes occur even in a group of species which are very closely related so far as based on the adult females. Homomorphic second instar males are not especially useful in phylogenetic research. In contrast, heteromorphic second instar males supply information of great value, because they are, in my view, principally atavistic in their patterns of characters. However, in some cases I have observed these years, they show atavistic characters in various degrees and in various modifications, and thus are mutable even between closely related species [my recent paper on this subject: Takagi, 1998]. Therefore, heteromorphic second instar males are sometimes very useful in distinguishing species, but, in phylogenetic research, a comparison of them based simply on resemblance and difference will be misleading.

In spite of all these considerations, there is in the present study no contradiction between the heteromorphic second instar males and the first instar larvae concerning the generic relationships they suggest: the *Kuwanaspis-Nikkoaspis* complex, *Medangaspis*, and *Coronaspis* are isolated from each other.

4.3. To the question why appendages so change from taxon to taxon

Trulla-like appendages or incipient trullae have been observed in a few species of the Protodiaspidina (Takagi, 1993), but fully sclerotized trullae appear in the Kuwanaspidina and are variously shaped in other diaspidids, which are more advanced than the Kuwanaspidina in the organization of appendages. Strong median trullae in advanced diaspidids are supposed to be an effective implement in peeling the upper epidermal layer of the host plant or in burrowing into it, being used as a knife or saw when the insect makes oscillatory or rotative movements in forming the test (Takagi, 1990c).

In the Protodiaspidina the test is secreted rather than constructed around the immobile insect body and becomes larger following the growth of the body. Kuwanaspidines do not make oscillatory movements in forming the test [3.4.]. *Kuwanaspis* and *Xiphuraspis* form an elongate female test, which becomes much longer than the insect body. Apparently the insect moves backwards when making an extension to the test under construction and forwards when depositing eggs behind the body within the completed test. The assumption is adopted that the trullae are used as a claw in this type of movements. Also in *Nikkoaspis* and *Coronaspis* the completed female test is distinctly longer than the insect body, and the trullae may be used likewise. If the 'claw assumption' is correct, the use of the trullae must have been altered in advanced diaspidids for the cutting of the plant epidermal tissue.

The gland spines, occurring in the Diaspidinae, are wax-secreting organs. Wax for constructing the test is supplied by the ducts, and the gland spines may have a different or supplementary role. The pectinae are well developed in primitive forms in both the subfamily Diaspidinae (Protodiaspidina; Kuwanaspidina) and the subfamily Aspidiotinae (*Thysanaspis*; Leucaspidini). They are replaced by pore prominences in advanced Diaspidinae and reformed to glanduliferous pectinae (which undoubtedly have the same role as the gland spines and, in fact, are often modified into spiniform processes) in advanced Aspidiotinae. Pectinae also occur in the Conchaspididae; they are well developed in *Fagisuga* and *Asceloconchaspis*, whereas much reduced in *Conchaspis*. In this family, too, the reduction of pectinae seems to be associated with active movements of the insect in constructing the test, which is dome-like and very large relative to the insect body (Takagi, 1992, 1997a). It follows that the pectinae have their function in immobile or relatively inactive species (as a possibility, working as a sensory organ to perceive the inner wall of the test under secretion) in both the families. In *Conchaspis* they are much reduced but persist, and may still be useful in the active movements of the insect body.

If all this is correct as a generalization, individual cases are too variable to explain. Why have the trullae been replaced by pectinae in *Kuwanaspis pectinata* (if this species is really an atavistic form of *Kuwanaspis*)? Why have the appendages been so much modified in *Xiphuraspis spiculata* (if this species is really congeneric with *X. ctenopyga*)? Is there any significance in the modified appendages of the *Coronaspis* species in connection with the habit to occur on the extreme leaf margin? All these questions as well as many others find no answer.

5. CONCLUSION

The subtribe Kuwanaspidina as composed in the foregoing sections is a small group, yet is not uniform. A few members of this group display very primitive states of appendages probably owing to atavistic change, and several others have a tinge of advanced Diaspidini. Thus the Kuwanaspidina may approximate some forms which existed in relatively early stages of diaspidine evolution.

The kuwanaspidines examined show a fairly wide variety of characters in the first instar larvae and also in the second instar males. The diversity in these larval stages implies two possibilities: the known forms of the subtribe are fragments from a once diversified, large group (*Xiphuraspis ctenopyga* shows this possibility), or the subtribe as composed in the present paper includes phylogenetically unrelated forms, in which the appendages have converged to the kuwanaspidine pattern. The former possibility requires for its acceptance discoveries of other surviving forms that will connect the isolated genera.

The Kuwanaspidina are not restricted to bamboos and other Poaceae. The dicotyledon-associated forms are notable, because Diaspidini have evolved mainly on dicotyledons and only partly on monocotyledons and gymnosperms. Their presence in the subtribe is significant, if not indispensable, for the view that the lineage or lineages leading to the extant advanced forms of the Diaspidini must have passed the stage with appendages of the kuwanaspidine pattern.

Especially interesting is the occurrence of glanduliferous craters in the second instar males of *Kuwanaspis* and *Nikkoaspis*, because this type of modified duct is common to many species of the Fioriniina (including *Pseudaulacaspis* and other non-pupillarial genera), one of the advanced subtribes of the Diaspidini. In the adult female, however, the Kuwanaspidina and the Fioriniina do not appear to be closely related.

In conclusion, the subtribe Kuwanaspidina is worthy of study from the viewpoint of the evolution of advanced Diaspidini. In this connection, discoveries of further dicotyledon-associated forms referable to the subtribe are especially expected.

6. An annotated list of Kuwanaspidina

Diaspidinae: Diaspidini: Kuwanaspidina

I. *Kuwanaspis*

Kuwanaspis MacGillivray, 1921 [type-species: *Chionaspis hikosani* Kuwana, 1902].

Tsukushiaspis Kuwana, 1928 [type-species: *Tsukushiaspis pseudoleucaspis* Kuwana, 1923=*Leucaspis bambusae* Kuwana, 1902].

Lepidosaphoides Lindinger, 1930 [type-species: *Leucaspis bambusae* Kuwana, 1902].

Chuaspis Tao and Wong, 1982 [type-species: *Tsukushiaspis neolinearis* Takahashi, 1930], syn. nov.

The synonyms *Tsukushiaspis* and *Lepidosaphoides* are purely nomenclatural and settled, but *Chuaspis* involves biological problems. In erecting this genus Tao and Wong (1982) emphasized that the median pectinae are 'conical shaped instead of serrated' in the type-species, *Kuwanaspis neolinearis*, and referred to the genus a new species, *Chuaspis shuichuensis*, which has tubercular prominences in the place of lateral pectinae in addition to the conical processes occurring in the place of median pectinae. The modified lateral pectinae in *C. shuichuensis* are similar to pore prominences in advanced Diaspidini, so that they are derivative for a kuwanaspidine and may justify the exclusion of this species from *Kuwanaspis*. But, so far as the state of pectinae is concerned, *C. shuichuensis* is connected to other species of *Kuwanaspis* through *K. neolinearis*, the type-species of *Chuaspis*, which possesses a few but rather well-shaped pectinae on the lateral sides of the pygidium. Moreover, some species have spiniform median pectinae and, nevertheless, also well-developed lateral pectinae [see under *Kuwanaspis linearis* in this list]. There seems to be no good reason to recognize *Chuaspis* as a distinct genus, so far as the type-species is concerned. Also *C. shuichuensis*, which is regarded as identical with *Kuwanaspis bambusicola*, should tentatively be retained in *Kuwanaspis* [see 4.1.; also see *Kuwanaspis bambusicola* in this list].

Borchsenius (1966) mentioned 14 species as members of *Kuwanaspis*. Since then five other species have been described in the genus. *Chuaspis shuichuensis* is transferred to *Kuwanaspis* but synonymized with *K. bambusicola* in this list. One species is added in this paper. Some undescribed species are also at hand. After all, about 30 species (and undoubtedly more than 30 species) of *Kuwanaspis* are distributed mainly in tropical to warm-temperate eastern Asia. However, five species (*K. annandalei*, *K. arundinariae*, *K. bambusicola*, *K. elongata*, and *K. tanzawensis*) are referred to the genus only tentatively.

Rao (1953) described *Kuwanaspis longissima* from India, but this species is a member of *Takahashiella* or *Acanthomytilus*, s. lat., of the tribe Lepidosaphedini. Based on the description it seems to be identical with *A. vermiformis* (=*Chionaspis vermiformis* Takahashi, 1930).

1. *Kuwanaspis annandalei*

Chionaspis annandalei Green, 1919 ['Paresnath Hill, 2500 ft, Bihar', India, on '*Dendrocalamus*'].

This species was described only briefly. It may be very close to or even identical with *K. bambusicola* [see under *Kuwanaspis bambusicola* in this list].

2. *Kuwanaspis arundinariae*

Kuwanaspis arundinariae Takahashi, 1938 ['Hattsukan, near Mt. Niitaka' and 'Taiheizan', Taiwan, on '*Arundinaria*'].

According to the original description, this species is characteristic in 'the scale strongly convex dorsally', in the narrowly trapezoid body (if the figure [Fig. 2] is based on full-grown specimens), and in the median trullae and the lobules of the second very small and conical. One of the localities recorded, 'Mt. Niitaka' (now Yu-Shan), is the highest peak (3,950m) in Taiwan. This species may be a peculiar montane form of *Kuwanaspis* or referable to another genus.

3. *Kuwanaspis bambusae*

Leucaspis bambusae Kuwana, 1902 ['Kokura, Kiushiu', Japan, on 'bamboo'].

Chionaspis pseudoleucaspis Kuwana, 1923 [replacing name for *Chionaspis bambusae* (Kuwana, 1902) transferred from *Leucaspis*, preocuppied by *Chionaspis bambusae* Cockerell, 1896, now *Unachionaspis bambusae*].

This species is now widely distributed in the world, but may be native to warm-temperate eastern Asia including Japan and China.

4. *Kuwanaspis bambusicola*

Mytilaspis bambusicola Cockerell, 1899 ['Campinas, Brazil', on 'bamboo'].

Chuaspis shuichuensis Tao and Wong, 1982 ['Shuichu, Nantau Hsien, Taiwan', on '*Bambusa stenostachya* cv.'], syn. nov.

This species has been recorded from scattered localities in the world (Brazil; the Azores; Senegal; Algeria; Sumatra, Indonesia; Yunnan and Guangdong, continental China). I have examined specimens collected in Nepal (Kathmandu Valley, at altitudes of 1,300-1,540m). *Chuaspis shuichuensis* from Taiwan is hardly distinguishable from *K. bambusicola* so far as based on the original description and accompanying figures. It is possible that the insect recorded by Ferris (1921) from Taiwan under the name *Chionaspis annandalei* is also this species. *Kuwanaspis tanzawensis* occurring in central Honsyû, Japan, is closely related to *K. bambusicola*, which is, therefore, probably native to eastern Asia.

Balachowsky (1954) discussed the generic position of *K. bambusicola*, and retained it in *Kuwanaspis* in spite of the 'atrophied' pectinae ('l'atrophie presque totale des peignes latéraux entre les épines glandulaires'). Now the problem concerns the species group comprising *K. bambusicola* and *K. tanzawensis* [see 4.1.; also see under *Kuwanaspis* in this list].

5. *Kuwanaspis bambusifoliae*

Tsukushiaspis bambusifoliae Takahashi, 1934 ['Mt. Hichisei near Taihoku', Taiwan, on '*Bambusa* sp.'].

6. *Kuwanaspis daliensis*

Kuwanaspis daliensis Hu, 1983 ['Dali, Yunnan', continental China, on '*Phragmites* sp.'].

7. *Kuwanaspis elongata*

Tsukushiaspis elongata Takahashi, 1930 ['Suisha', Taiwan, on '*Bambusa* sp.'].

This species is very similar to *Xiphuraspis ctenopyga*. The presence of mid-pygidial dorsal macroducts is especially noteworthy. However, the figure accompanying the original description shows that the mid-pygidial macroducts do not form a large median group as in *X. ctenopyga* [also see 2.4.].

8. *Kuwanaspis elongatoides*

Kuwanaspis elongatoides Tang and Wu, in Tang, 1986 ['Maanshan City, Anhui Province', continental China, on '*Bambusa* sp.'].

According to the original description, this species is similar to *K. elongata*. The accompanying figure shows, however, that it differs from the latter in lacking mid-pygidial dorsal macroducts [see *Kuwanaspis elongata* above].

9. *Kuwanaspis foliosa*

Kuwanaspis foliosus Wu, 1986 ['Huangshan, Anhui', continental China, on '*Indocalamus migoi*'].

10. *Kuwanaspis hikosani*

Chionaspis (?) *hikosani* Kuwana, 1902 ['Hikosan, Kiushiu', Japan, on '*Phyllostachys bambusoides*'].

Takahashi (1942) described '*Kuwanaspis hikosani* Kuwana, var. *hongkongensis*' from Hong Kong. Tang (1986) recorded *K. hikosani* from other areas of continental China (Zhejiang, Anhui, and Fujian Provinces), and mentioned 'v. *hongkongensis*' in the synonymic list. Howell and Tippins (1973) states that *K. hikosani* 'occurs in great numbers in Georgia but males are unknown'.

11. *Kuwanaspis howardi*

Chionaspis howardi Cooley, 1898 ['Department of Agriculture, Washington, D. C.', U. S. A., on 'East Indian bamboo'].

This species was described from North America and has been recorded from Crimea, Caucasus, Japan, continental China, etc. It is closely related to *K. bambusae*, and may be native to warm-temperate eastern Asia as well.

12. *Kuwanaspis linearis*

Chionaspis linearis Green, 1922 ['Peradeniya', Sri Lanka, on 'a small species of Bamboo'].

Takahashi (1942) recorded '*Kuwanaspis linearis* Green' from Singapore and Kuala Lumpur, but did not redescribe it. Green (1922) states that the pectinae occurring between the median trullae are spiniform and very slender ('Spiniform squames very slender'), and depicts them as a pair of needle-like processes. Specimens which nearly agree with the original description and figures are at hand from Malaya (Taipin; Air Terjun Kota Tinggi) and Sabah (Sandakan).

Green (1937), however, states: 'My figure of *linearis* (loc. cit. [Green, 1922]) is faulty, in that it omits the fimbriate squamulae, which are actually present between the median pair of lobes (trullae)'. The specimens mentioned above are, therefore, referable to *K. linearis* only on the supposition that this statement is erroneous or refers to another species.

Other forms at hand, representing three species or more, are closely similar to the supposed *K. linearis*. All these species agree in having spiniform median pectinae and well-developed lateral pectinae.

13. *Kuwanaspis multiporus*

Kuwanaspis multiporus Tang, 1986 [continental China: 'Kunming, Yunnan Province on *Bambusa* sp.' and 'Nanning, Guangxi Province on *Asparagus plumosus*'].

14. *Kuwanaspis neolinearis*

Tsukushiaspis neolinearis Takahashi, 1930 ['Suisha, Taihoku', Taiwan, on '*Bambusa* sp.'].

Takahashi (1942) recorded this species from Singapore. Specimens referable to this species are at hand from Nepal (Ilam, Mechi, at an altitude of 750m; Sankranti, Kosi, 1,000m; Kathmandu, 1,400m) and Malaya (Tanah Rata, Cameron Highlands, 1,300m). Tao and Wong (1982) erected *Chuaspis* and designated *K. neolinearis* for the type-species [see under *Kuwanaspis* in this list].

15. *Kuwanaspis pectinata*, sp. nov.

16. *Kuwanaspis phragmitis*

Tsukushiaspis phragmitis Takahashi, 1931 ['Suo, Chippon, Daichikko near Daibu', Taiwan, on '*Phragmites* sp.'].

17. *Kuwanaspis suishana*

Tsukushiaspis suishana Takahashi, 1930 ['Suisha', Taiwan, on '*Bambusa* sp.'].

Takahashi (1942) recorded this species from Chiengmai, Thailand. Tang (1986) recorded it from continental China (Fujian and Sichuan Provinces). Specimens referable to this species are at hand from Nepal (Kathmandu Valley, at altitudes of about 1,300-1,400m) and Japan (Okinawa).

18. *Kuwanaspis takahashii*

Kuwanaspis takahashii Takagi, 1961 [Japan: 'Siro-Yama, Kagosima, Kyusyu, on an undetermined bamboo'].

19. *Kuwanaspis tanzawensis*

Kuwanaspis tanzawensis Takagi and Kawai, 1966 [Japan: 'Tanzawa, Kanagawa-ken, on *Sasa* sp.'].

This species is closely related to *Kuwanaspis bambusicola*, but is easily distinguishable from the latter in the arrangement of dorsal macroducts on the seventh abdominal segment: *K. tanzawensis* has a few macroducts just anteriorly to the marginal macroduct, whereas *K. bambusicola* has a row of macroducts, on this segment. They are also readily distinguishable in the second instar female: *K. tanzawensis* possesses on each of the fifth and sixth abdominal segments a submarginal macroduct situated near the marginal macroduct, whereas *K. bambusicola* has no submarginal macroduct (based on the material from Nepal [see under *Kuwanaspis bambusicola* in this list]). The generic position of these species remains problematical [see 4.1.; also see under *Kuwanaspis* in this list].

20. *Kuwanaspis vermiformis*

Tsukushiaspis vermiformis Takahashi, 1931 ['Taihoku, Tosei', Taiwan, on '*Bambusa stenostachya*, *Bambusa* sp., *Dendrocalamus latiflorus*'].

Takahashi (1942) recorded this species from Hong Kong, and Tang (1986) from other areas (Fujian; Guangdong) of continental China.

II. *Nikkoaspis*

Nikkoaspis Kuwana, 1928 [type-species: *Nikkoaspis shiranensis* Kuwana, 1928].

This genus was synonymized with *Tsukushiaspis* (=*Kuwanaspis*) by Takahashi (1934). The adult female of *Nikkoaspis shiranensis*, the type-species of the genus, is characterized by 'the abdominal area greatly expanded to form a flask-shape' (Kuwana, 1928). It has numerous macroducts on the dorsum and numerous pectinae around the abdomen, but these characters may be associated with the expanded abdomen. There is no other difference supposedly of generic value between *N. shiranensis* and many *Kuwanaspis* species. The body shape has generally been adopted as a feature having generic value, but recently it has been shown that this feature was overestimated in some cases. Species with an expanded abdomen are referable to *Nikkoaspis*, but this character alone does not afford a good basis for recognizing the genus as distinct [also see 3.1., 3.3., 4.2.].

N. shiranensis is common on the lowlands in northern Japan, where no species of *Kuwanaspis* is known, and occurs at higher altitudes in southern Japan, where its distribution is disrupted onto mountains (the known southernmost locality is Mt. Kirisima, Kyûsyû, where it was collected at an altitude of about 1,400m) [also see 2.3.: Remarks]. *N. sikokiana* was collected at an altitude of about 1,000m in Sikoku. The collection site of *N. berincangensis* is situated near the highest summit altitude in the Malay Peninsula. *N. simaoensis* was described from a mountainous area in southern Yunnan. So far as represented by these species, *Nikkoaspis* is predominantly montane in habitat (three other species are referred to the genus in the list below, but little is knowable about their habitats from the original descriptions). On the other hand, *Kuwanaspis* inhabits lowlands and mountains. Many *Kuwanaspis* species are linear in body shape and are apparently adapted to the surface structure of bamboo leaves, especially the parallel veins. *Nikkoaspis* species, with the abdomen extraordinarily expanded, occur on the basal part of the blade or, when associated with large-leaved dwarf bamboos (*Sasa* and allies), on the broad upper surface of the midrib. Several species of *Kuwanaspis* and *Nikkoaspis formosana*, however, occur on the stalks.

Nikkoaspis seems to have its own distribution pattern, and is not wholly the same as *Kuwanaspis* in habit. It may not be part of *Kuwanaspis*. Further species are expected to come from mountains of eastern Asia and to assure the status of *Nikkoaspis* (the mountainous region covering southern China and northern Indochina may be promising for finding such forms).

21. *Nikkoaspis berincangensis*, sp. nov.

22. *Nikkoaspis formosana*

Tsukushiaspis formosana Takahashi, 1930 ['Suisha', Taiwan, on '*Bambusa* sp.'].

This species is referred to *Nikkoaspis* rather tentatively. The original description is accompanied with no detailed figure and affords no good basis for determining the generic position of the species.

23. *Nikkoaspis hichiseisana*

Tsukushiaspis hichiseisana Takahashi, 1934 ['Mt. Hichisei near Taihoku', Taiwan, on '*Bambusa* sp.'].

According to the original description this species is closely allied to *Tsukushiaspis shiranensis* (=*Nikkoaspis shiranensis*).

24. *Nikkoaspis sasae*

Tsukushiaspis sasae Takahashi, 1936 ['Huchow, Chekiang', continental China, on '*Sasa* sp.'].

Based on the figure accompanying the description, this species is similar to *Nikkoaspis shiranensis* in the pygidial appendages.

25. *Nikkoaspis shiranensis*

Nikkoaspis shiranensis Kuwana, 1928 ['Yumoto, Nikko', Japan, on '*Sasa albomarginata* (Kumazasa)'].

26. *Nikkoaspis sikokiana*, sp. nov.

27. *Nikkoaspis simaoensis*

Nikkoaspis simaoensis Hu, 1988 ['Simao, yunnan (sic)', continental China, on 'a plant of Bambusoideae'].

III. *Xiphuraspis*

Xiphuraspis Borchsenius and Williams, 1963 [Type-species: *Chionaspis spiculata* Green, 1919].

28. *Xiphuraspis ctenopyga*, sp. nov.

29. *Xiphuraspis spiculata*

Chionaspis spiculata Green, 1919 ['Peria Ghat, N. Malabar, 2000 ft.', India, on '*Bambusa* sp.'].

IV. *Medangaspis*, gen. nov.

Medangaspis, gen. nov. [type-species: *Medangaspis payunga*, sp. nov.].

30. *Medangaspis payunga*, sp. nov.

V. *Coronaspis*

Coronaspis MacGillivray, 1921 [type-species: *Chionaspis coronifera* Green, 1905].

31. *Coronaspis coronifera*

Chionaspis coronifera Green, 1905 ['Galgammuwa, N. W. P.', Sri Lanka, on 'undetermined tree'].

32. *Coronaspis malabarica*, sp. nov.

33. *Coronaspis malesiana*, sp. nov.

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Fig. 1. *Kuwanaspis pectinata*, adult female, figured from a young specimen. B, antennae; C, ventral macroducts and gland spines on first and second abdominal segments; D, pygidium; E, F, pygidial margin, ventral surface (E, sixth and seventh abdominal segments; F, apex of pygidium). Scales: A, 100μm; D, 50μm; B, C, E, F, 10μm.

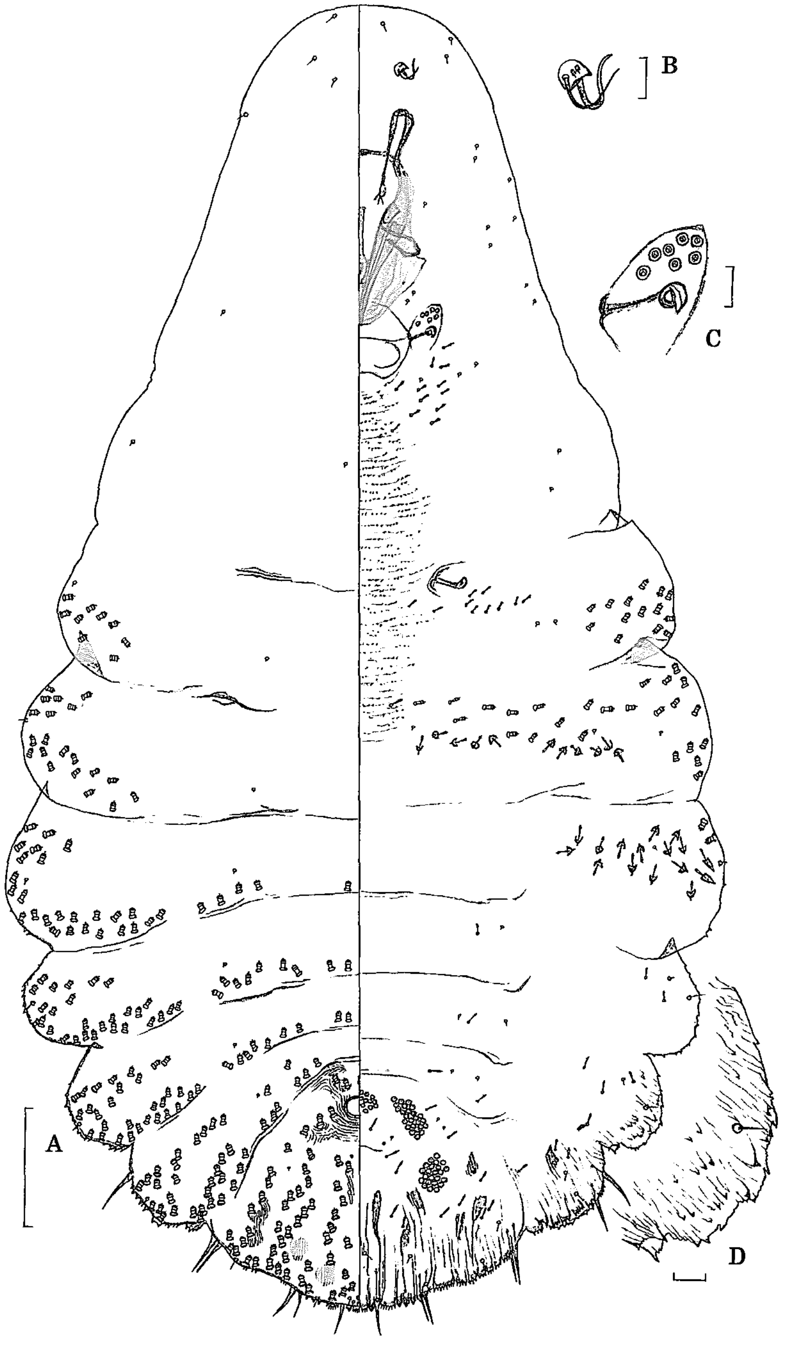

Fig. 2. *Nikkoaspis berincangensis*, adult female. B, antenna; C, anterior spiracle; D, fourth abdominal segment, ventral surface of lateral region. Scales: A, 100μm; B, C, D, 10μm.

Fig. 3. *Nikkoaspis berincangensis*, adult female, pygidium. Scale: 50μm.

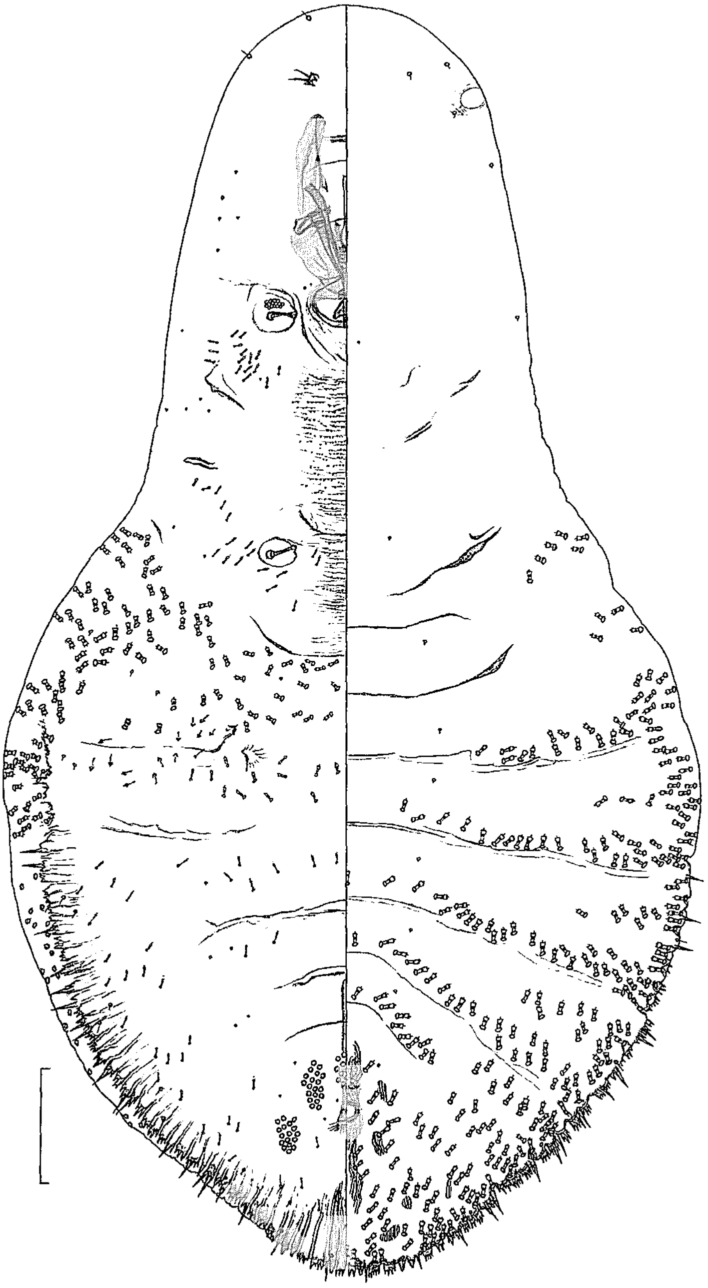

Fig. 4. *Nikkoaspis sikokiana*, adult female, figured from a young specimen. Scale: 100μm.

Fig. 5. *Nikkoaspis sikokiana*, adult female, pygidium. Scale: 50μm

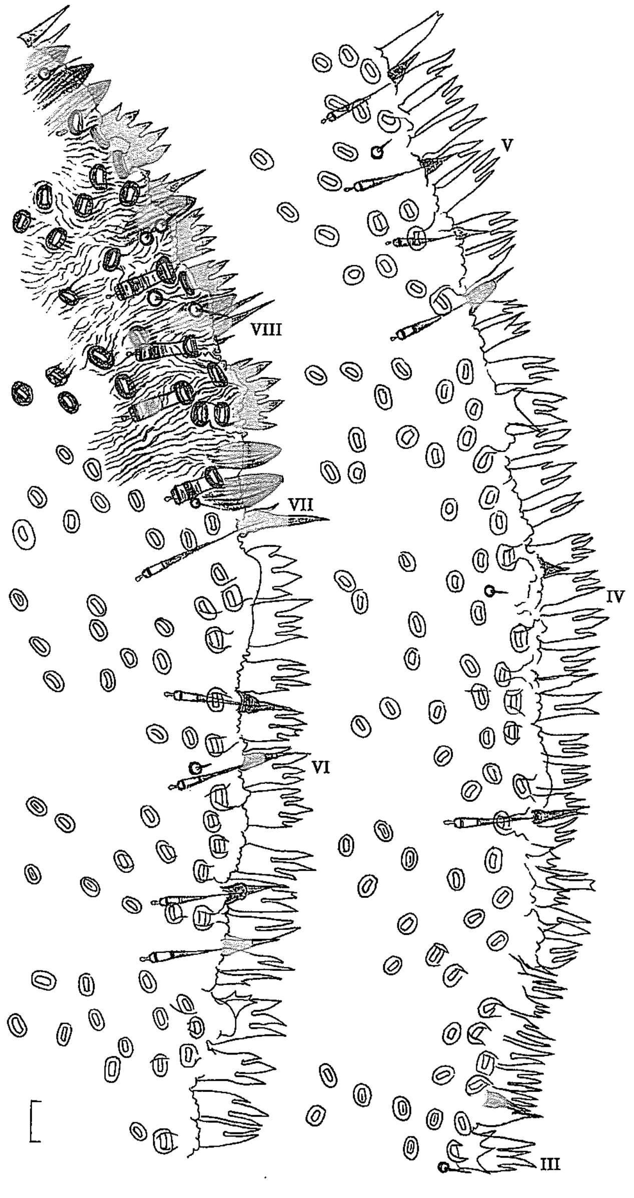

Fig. 6. *Nikkoaspis shiranensis*, adult female, abdominal margin, dorsal surface (showing appendages and especially gland spines intermingled with pectinae). III-VIII: third to eighth abdominal segments. Zenibako Coast, Otaru, Hokkaidô, Japan, on *Sasa palmata*. Scale: 10μm.

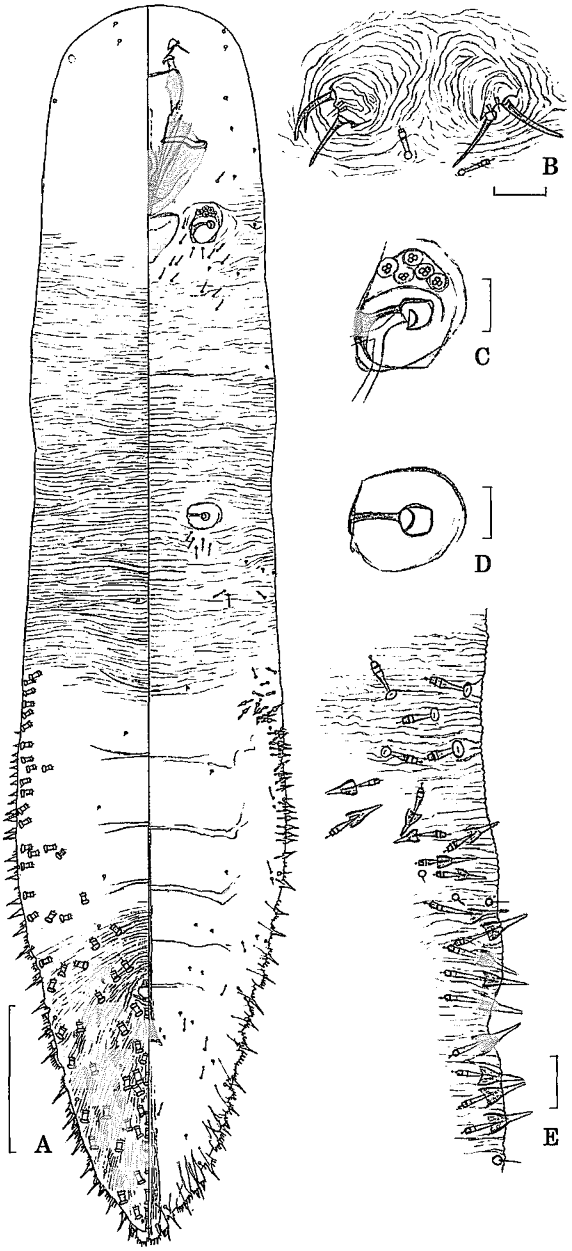

Fig. 7. *Xiphuraspis ctenopyga*, adult female, figured from a young specimen. B, antennae; C, D, anterior and posterior spiracles; E, lateral margin of first and second abdominal segments, ventral surface. Scales: A, 100μm; B, C, D, E, 10μm.

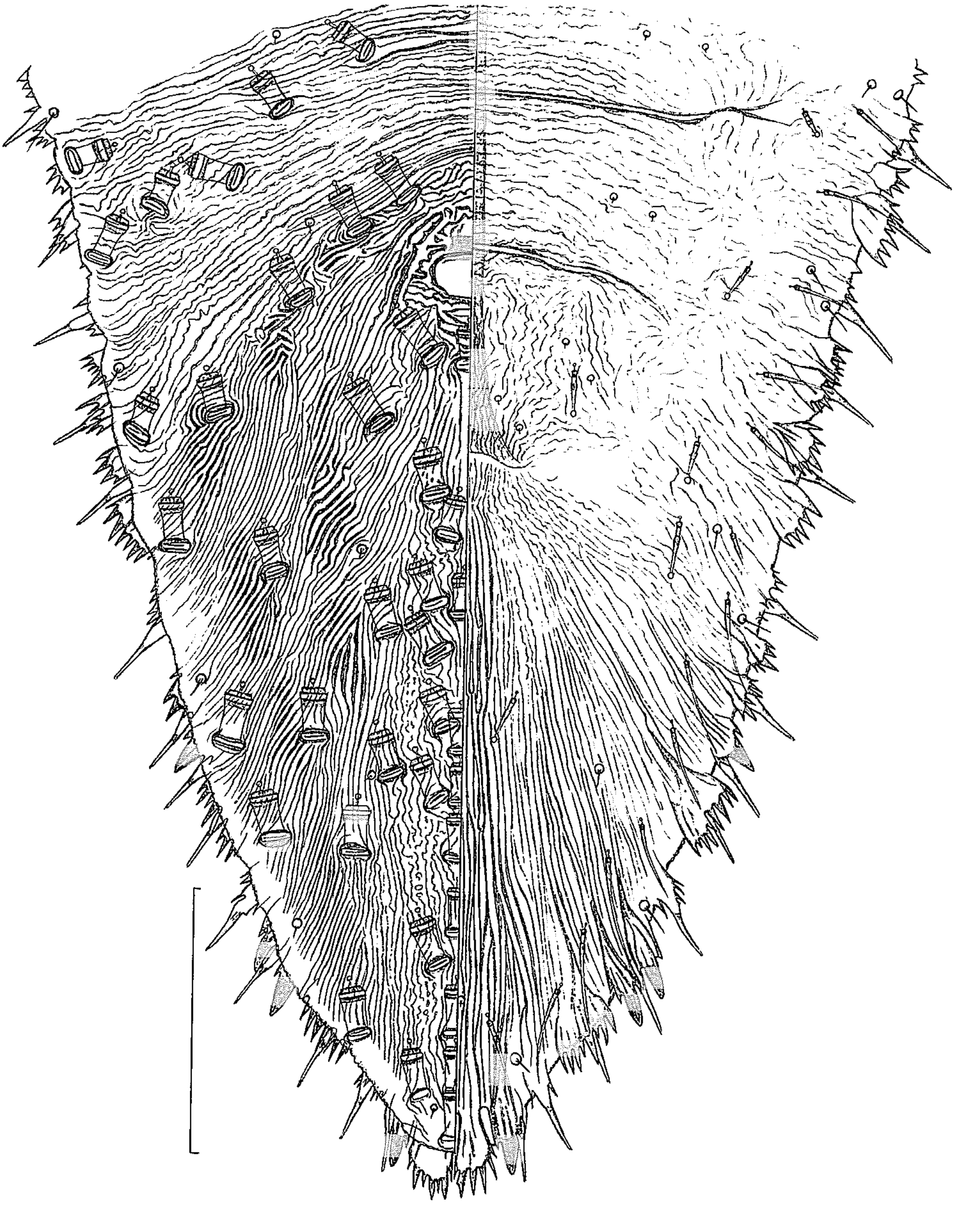

Fig. 8. *Xiphuraspis ctenopyga*, adult female, pygidium. Scale: 50μm.

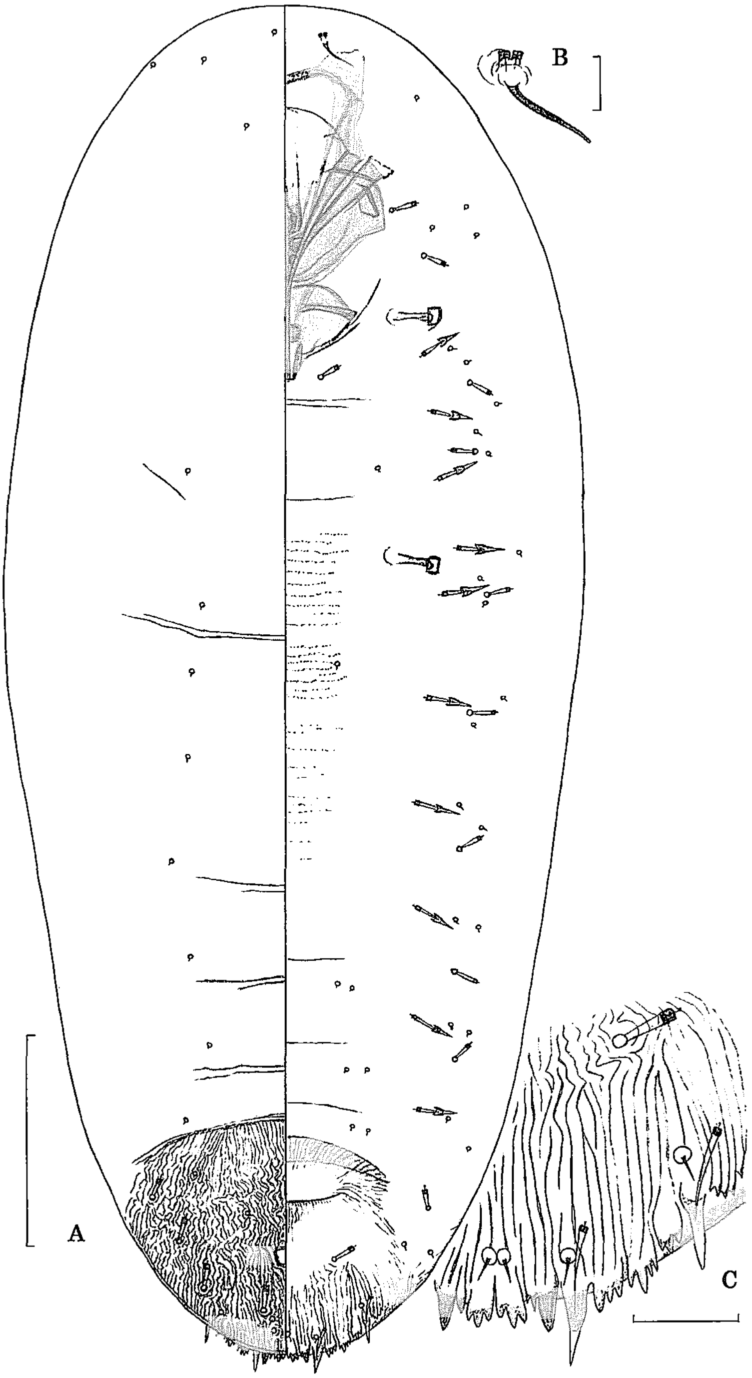

Fig. 9. *Medangaspis payunga*, adult female. B, antenna; C, pygidial margin, ventral surface. Scales: A, 50μm; B, 5μm; C, 10μm.

Fig. 10. *Coronaspis malesiana*, adult female [88ML-189]. B, antennae; C, D, pygidial margin, ventral and dorsal surfaces. Scales: A, 100μm; B, C, D, 10μm.

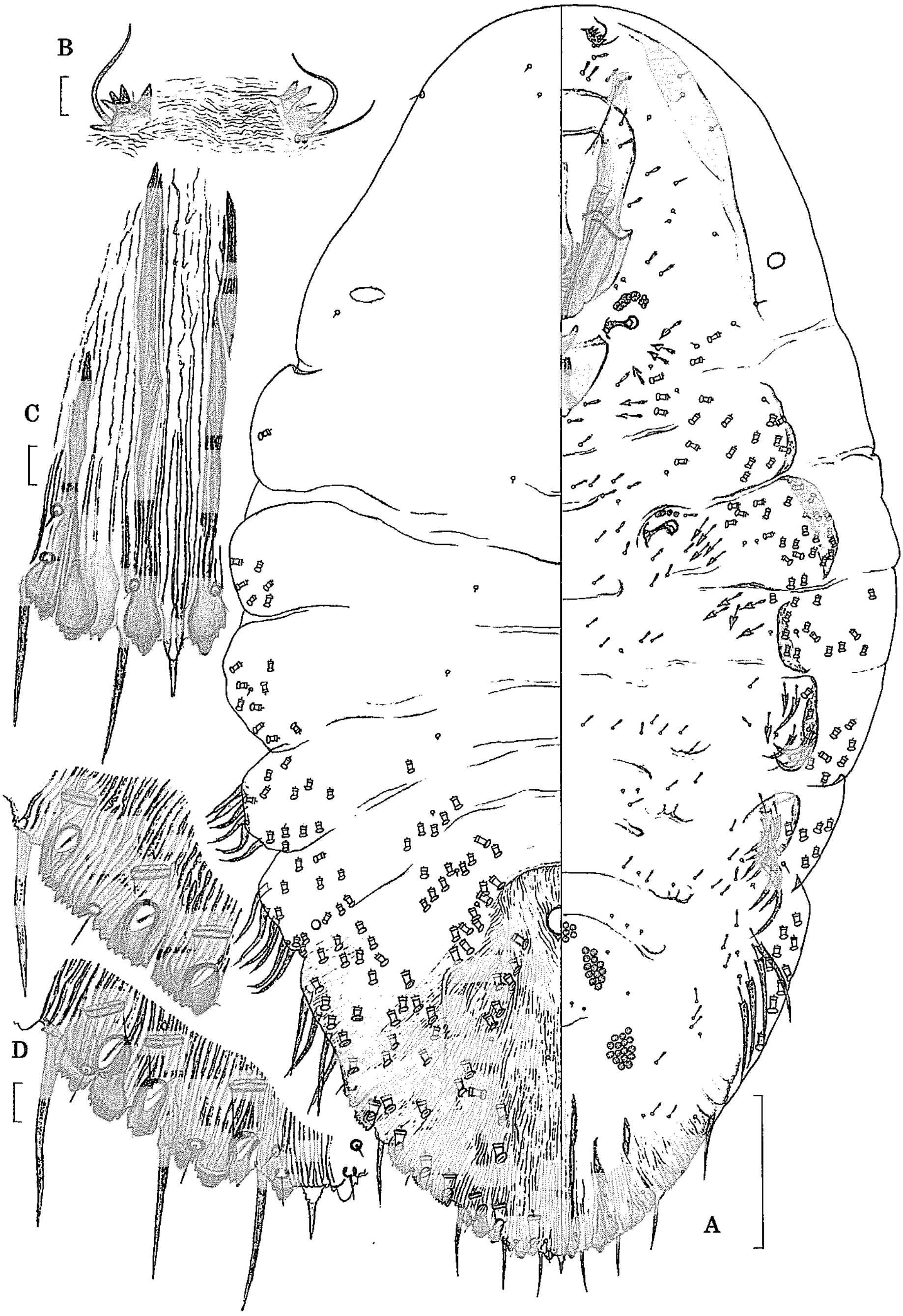

Fig. 11. *Coronaspis malabarica*, adult female [78IND-282]. B, antennae; C, pygidial apex, ventral surface; D, pygidial margin, dorsal surface (divided into two parts). Scales: A, 100μm; B, C, D, 10μm.

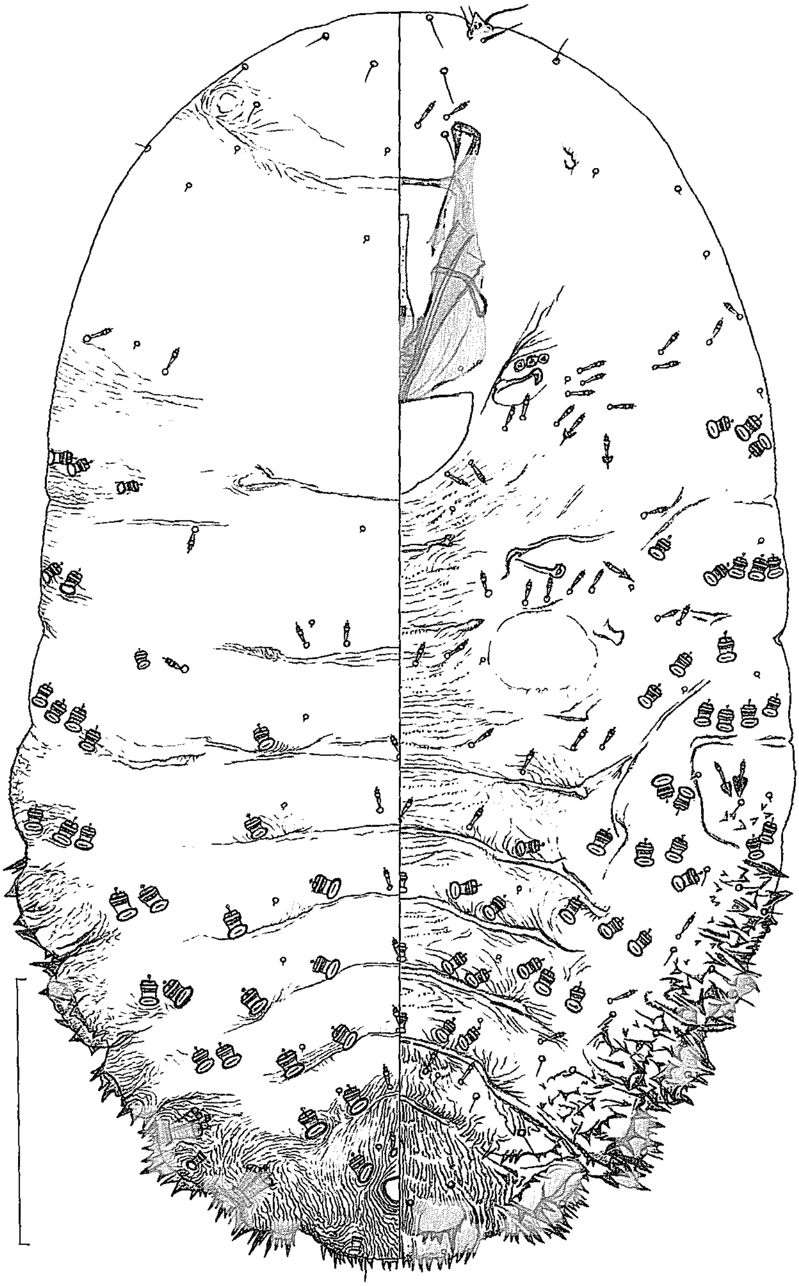

Fig. 12. *Nikkoaspis berincangensis*, second instar male. Scale: 100μm.

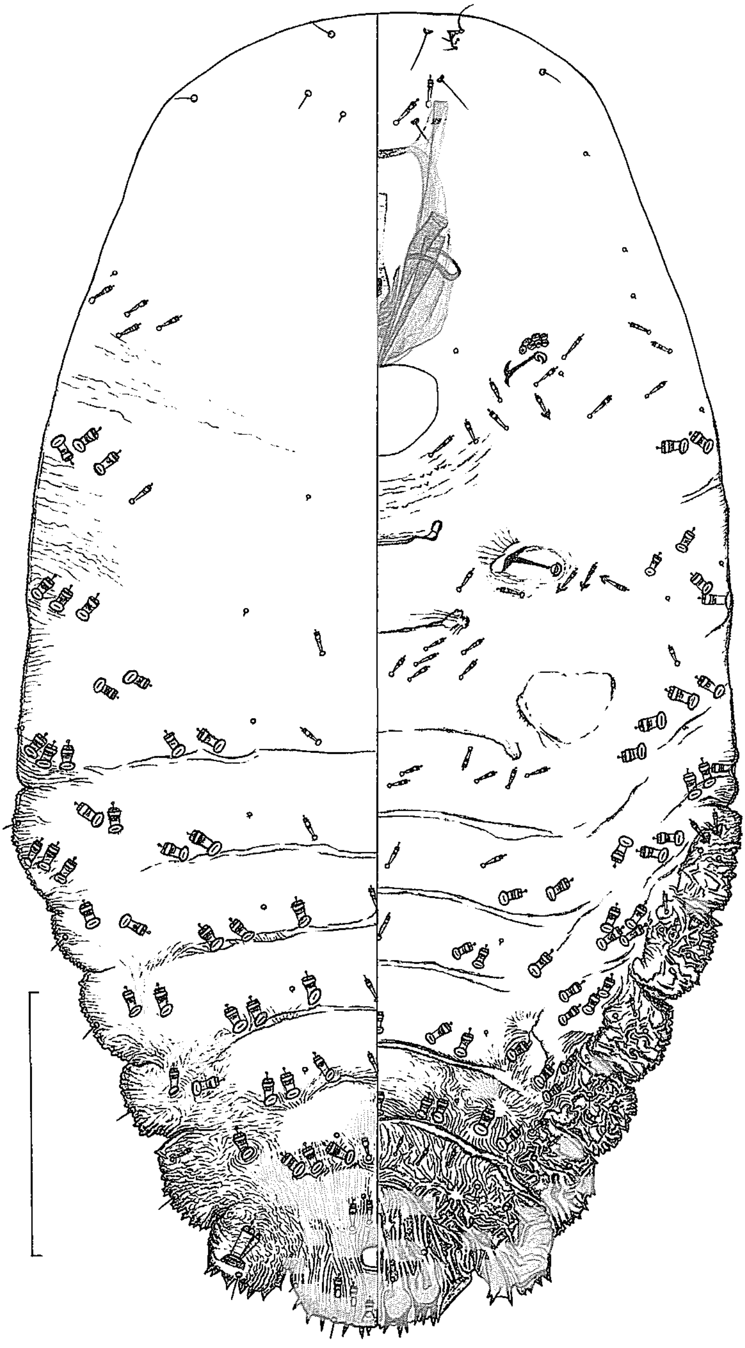

Fig. 13. *Nikkoaspis sikokiana*, second instar male. Scale: 100μm.

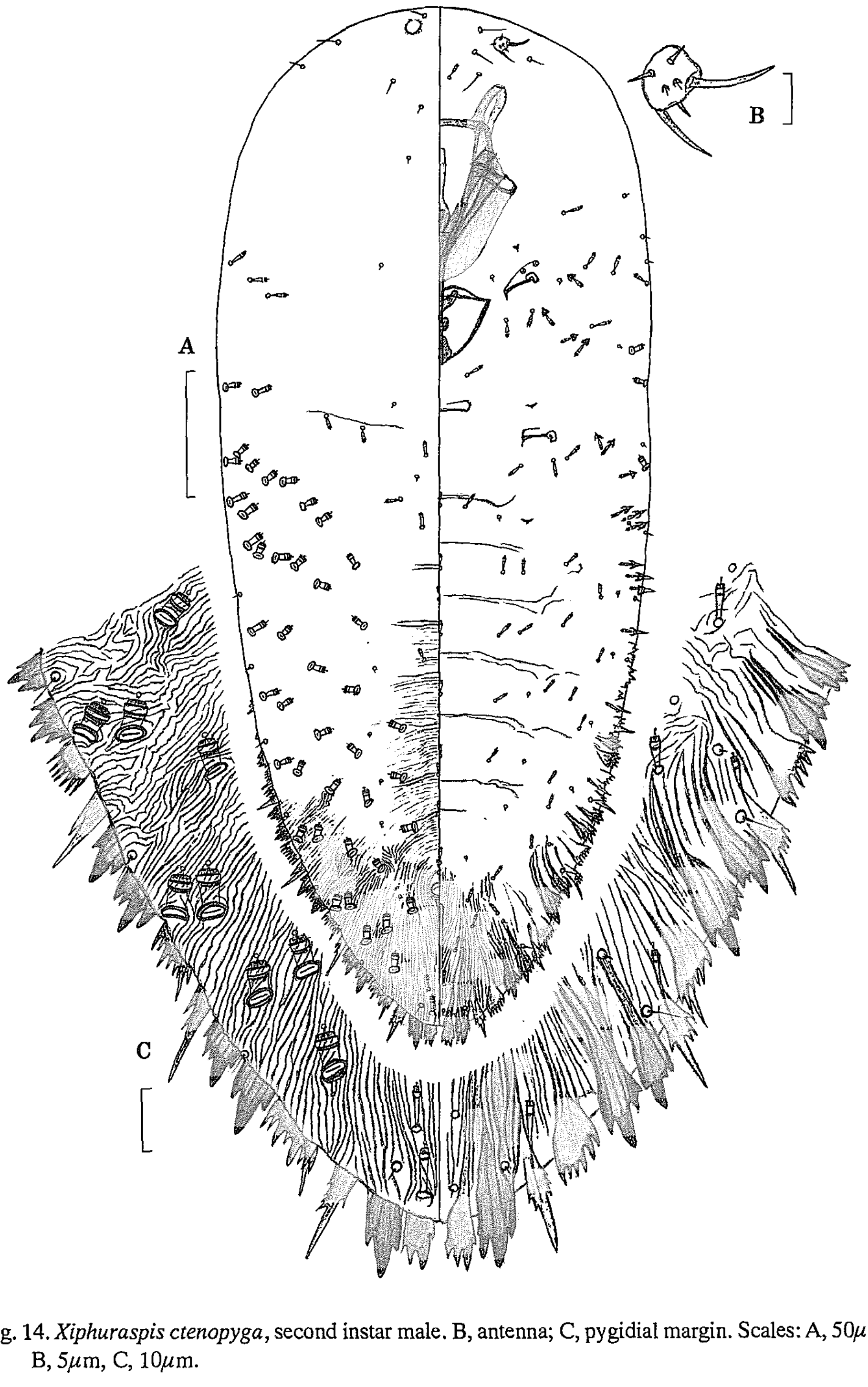

Fig. 14. *Xiphuraspis ctenopyga*, second instar male. B, antenna; C, pygidial margin. Scales: A, 50μm; B, 5μm, C, 10μm.

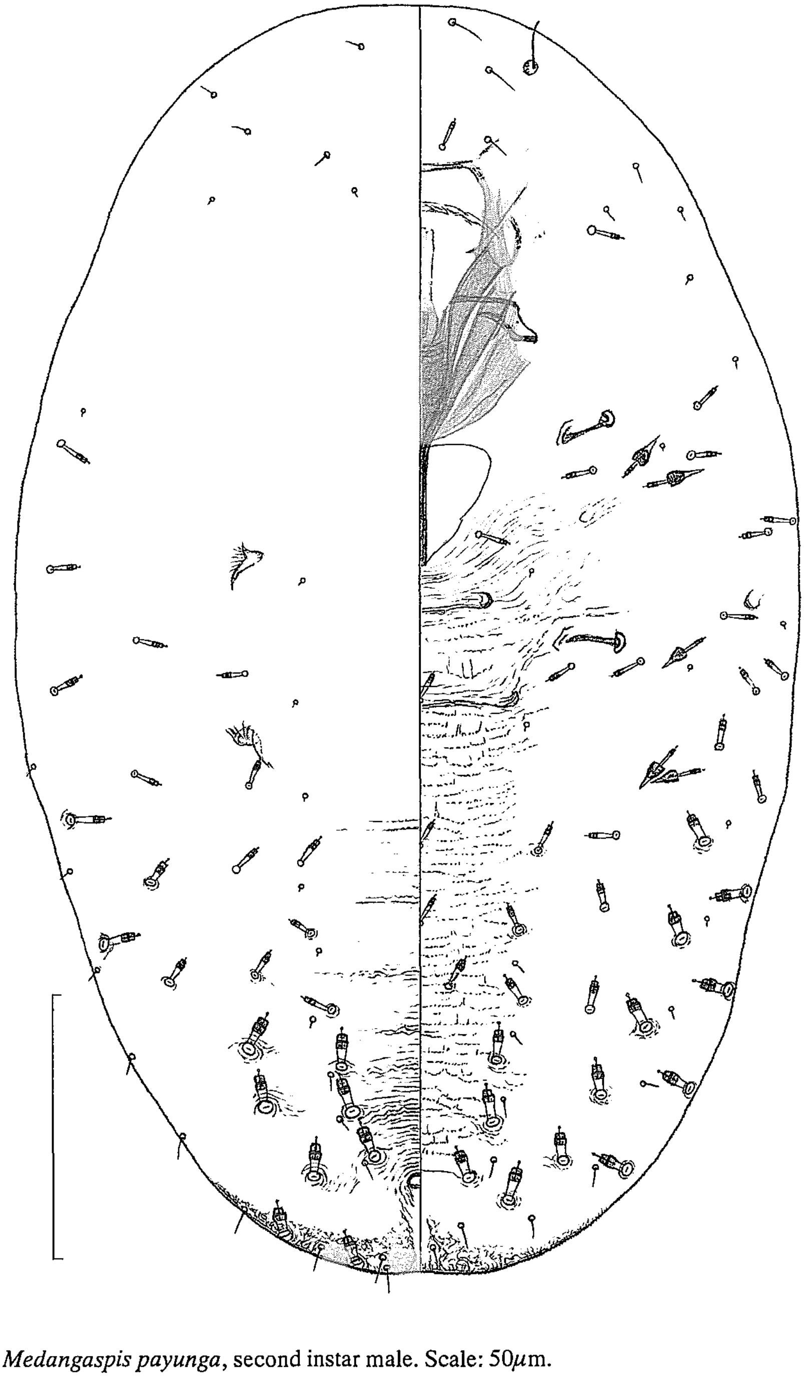

Fig. 15. *Medangaspis payunga*, second instar male. Scale: 50μm.

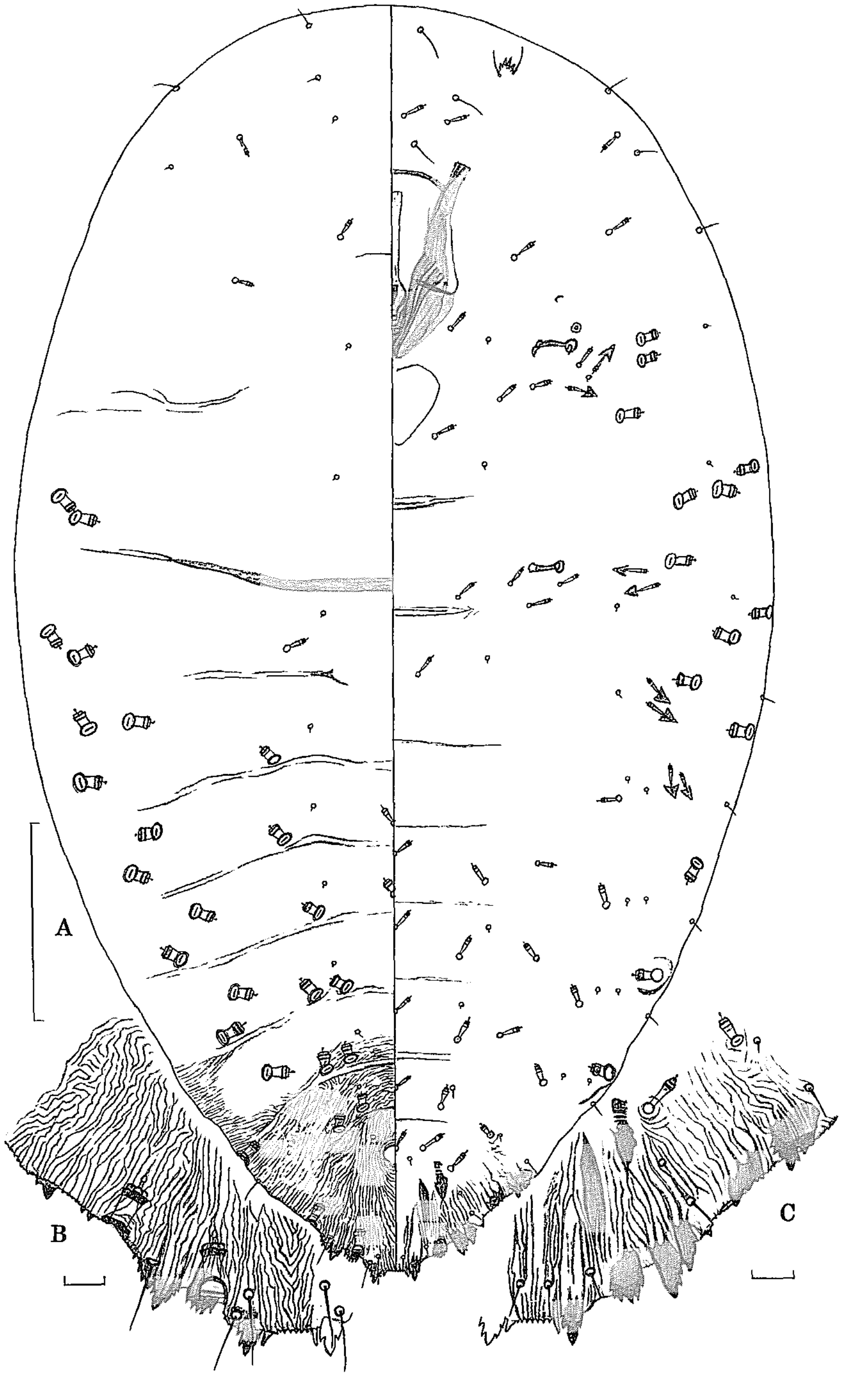

Fig. 16. *Coronaspis malesiana*, second instar male [88ML-238]. B, C, pygidial margin, dorsal and ventral surfaces. Scales: A, 100μm; B, C, 10μm.

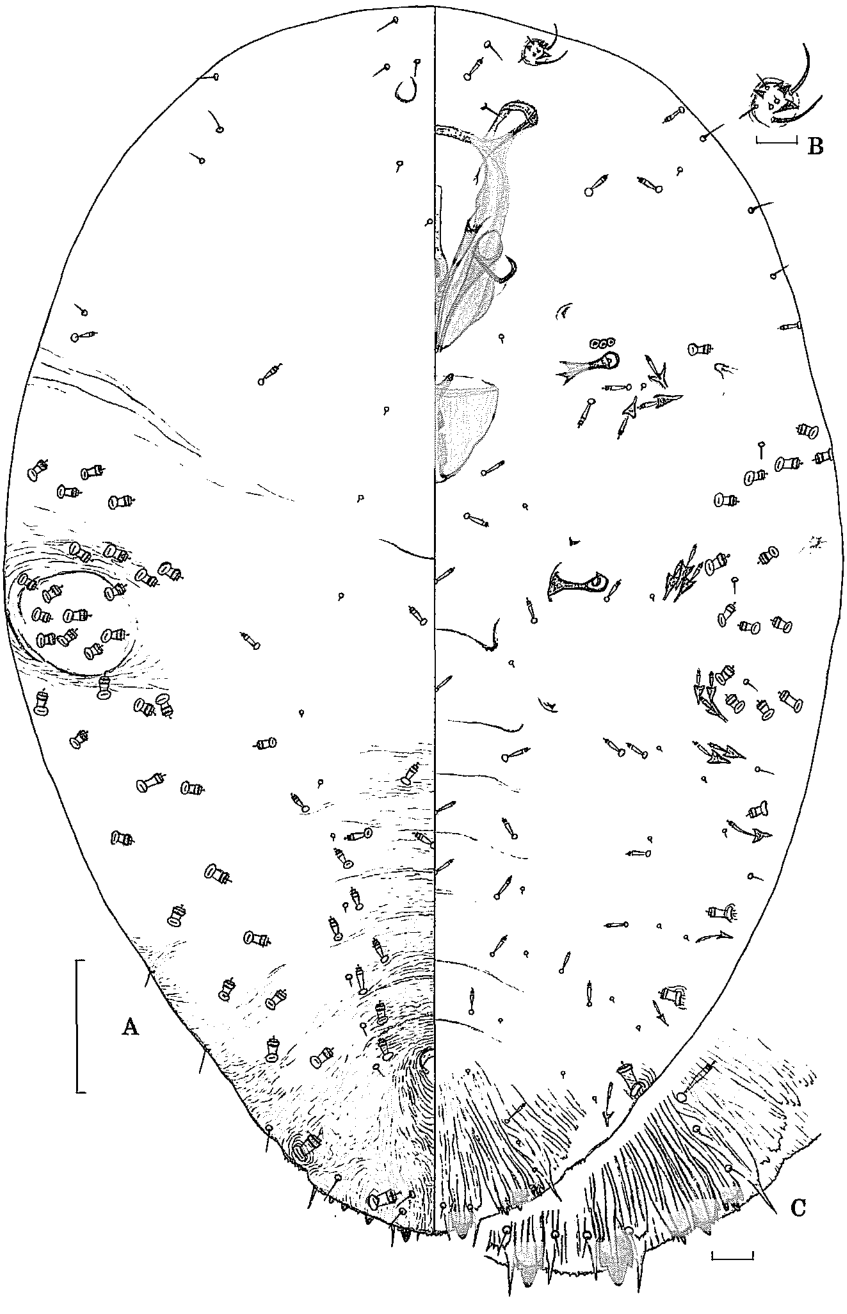

Fig. 17. *Coronaspis malabarica*, second instar male [78IND-405]. B, antenna; C, pygidial margin, ventral surface. Scales: A, 50μm; B, C, 10μm.

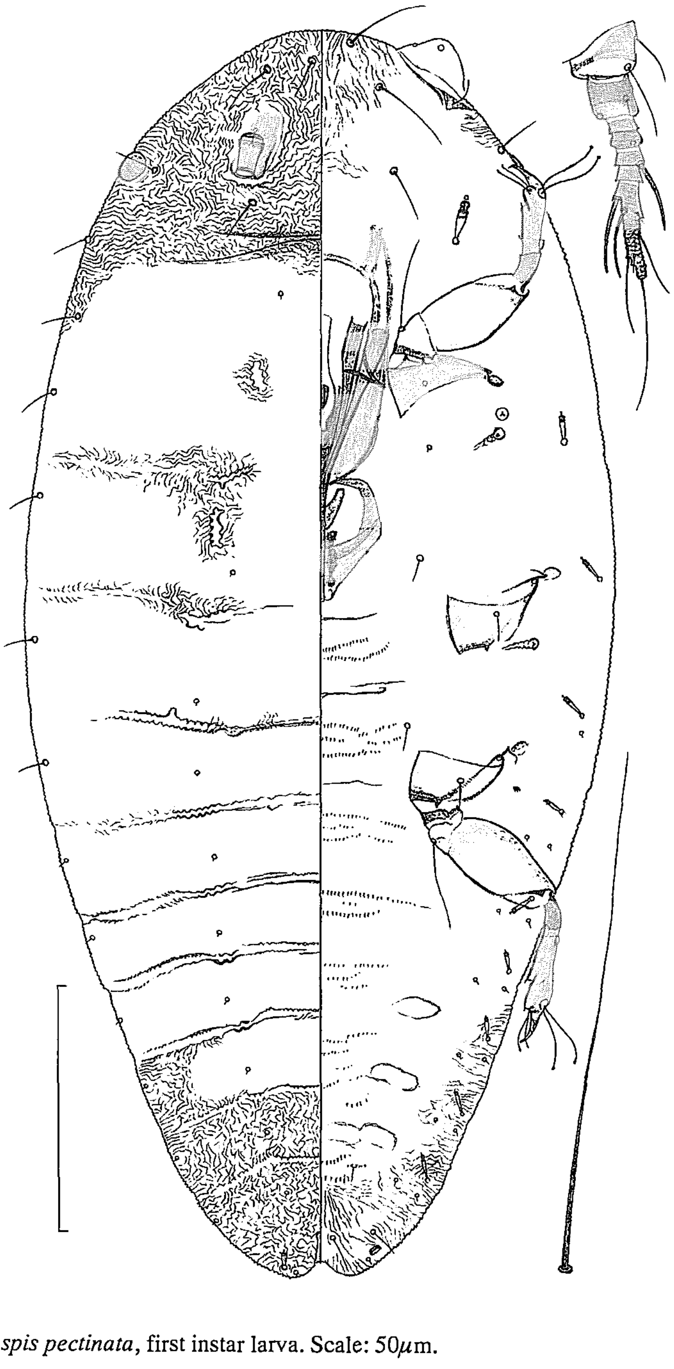

Fig. 18. *Kuwanaspis pectinata*, first instar larva. Scale: 50μm.

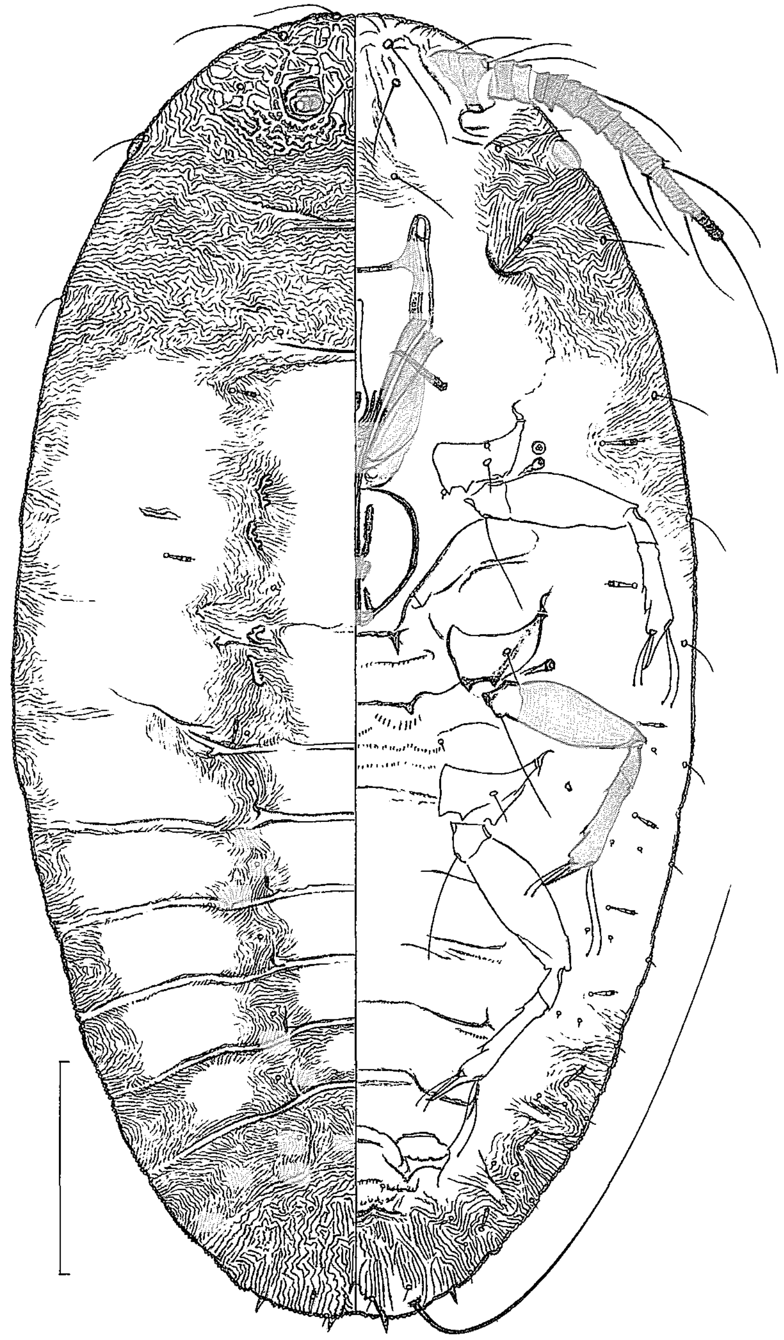

Fig. 19. *Nikkoaspis shiranensis*, first instar larva. Hamatonbetu, Hokkaidô, Japan, on *Sasa palmata*. Scale: 50μm.

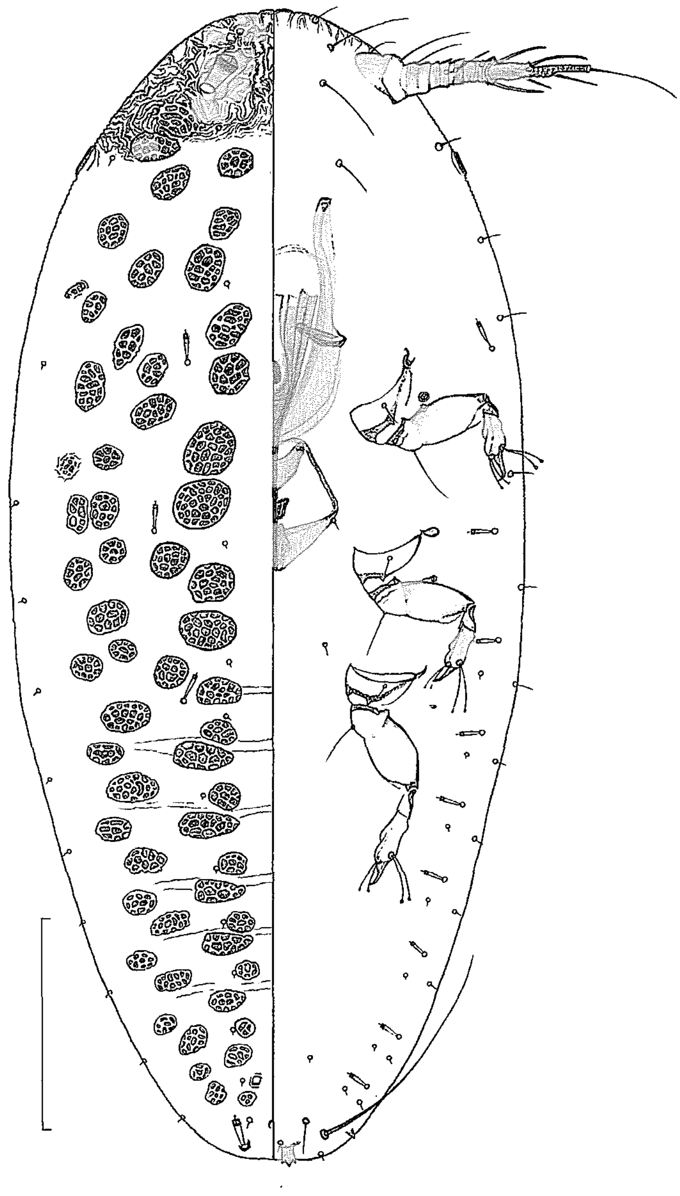

Fig. 20. *Xiphuraspis ctenopyga*, first instar larva. Scale: 50μm.

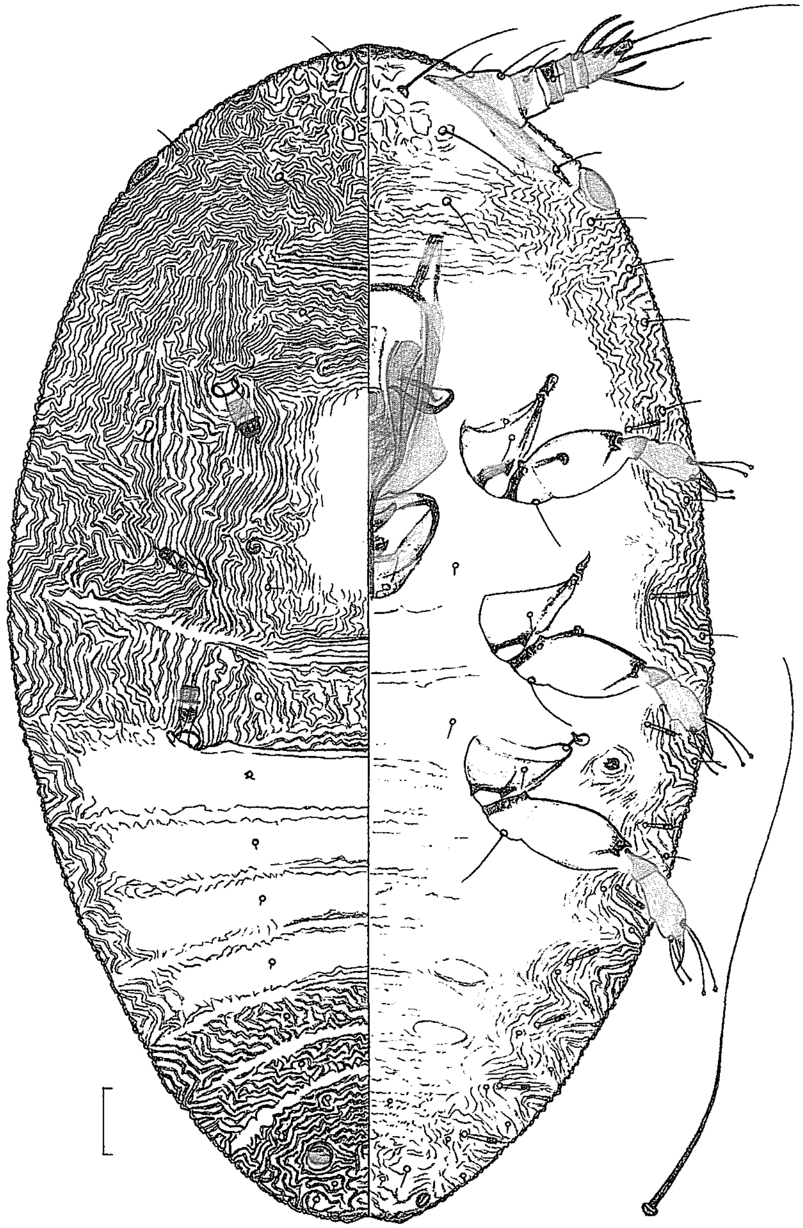

Fig. 21. *Medangaspis payunga*, first instar larva. Scale: 10μm.

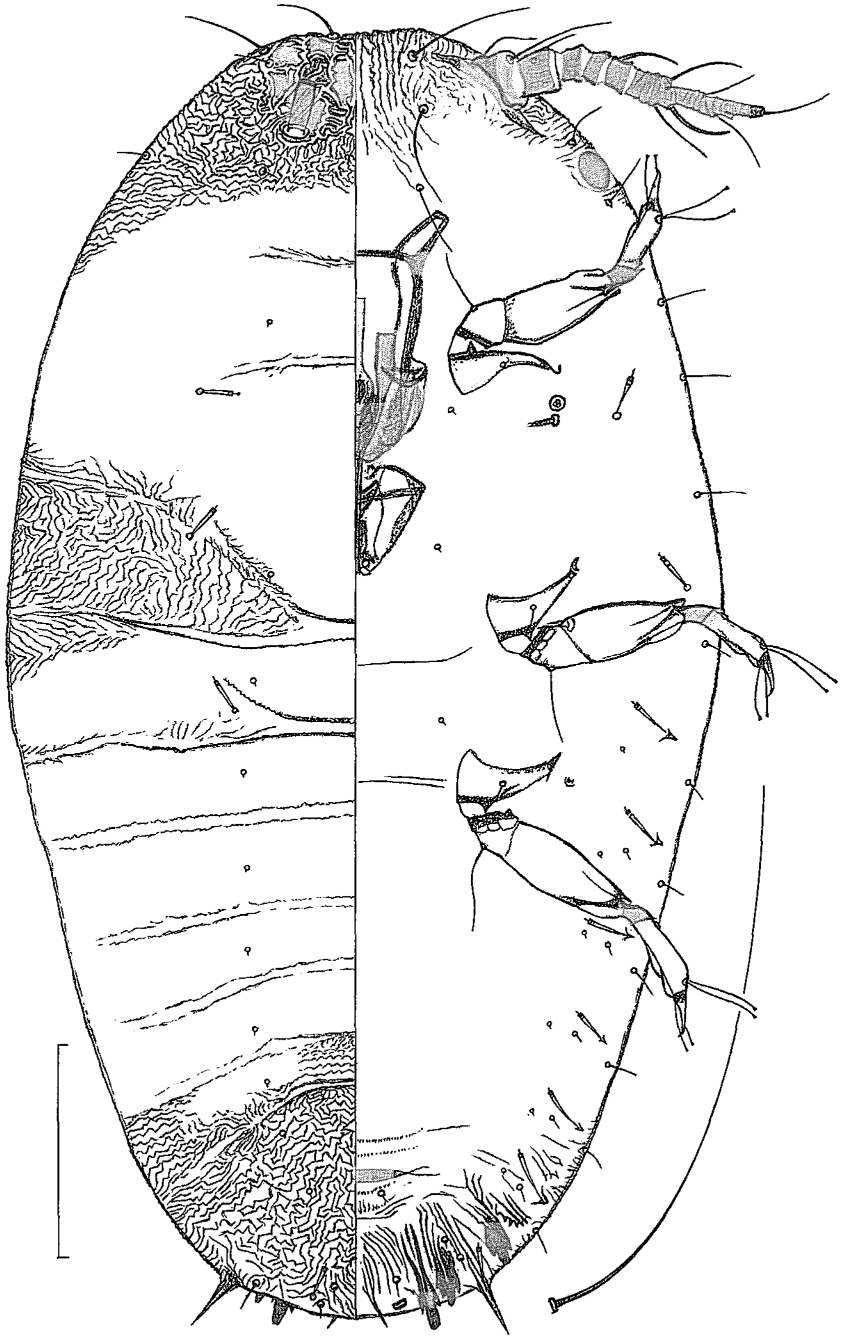

Fig. 22. *Coronaspis malabarica*, first instar larva [78IND-282]. Scale: 50μm.

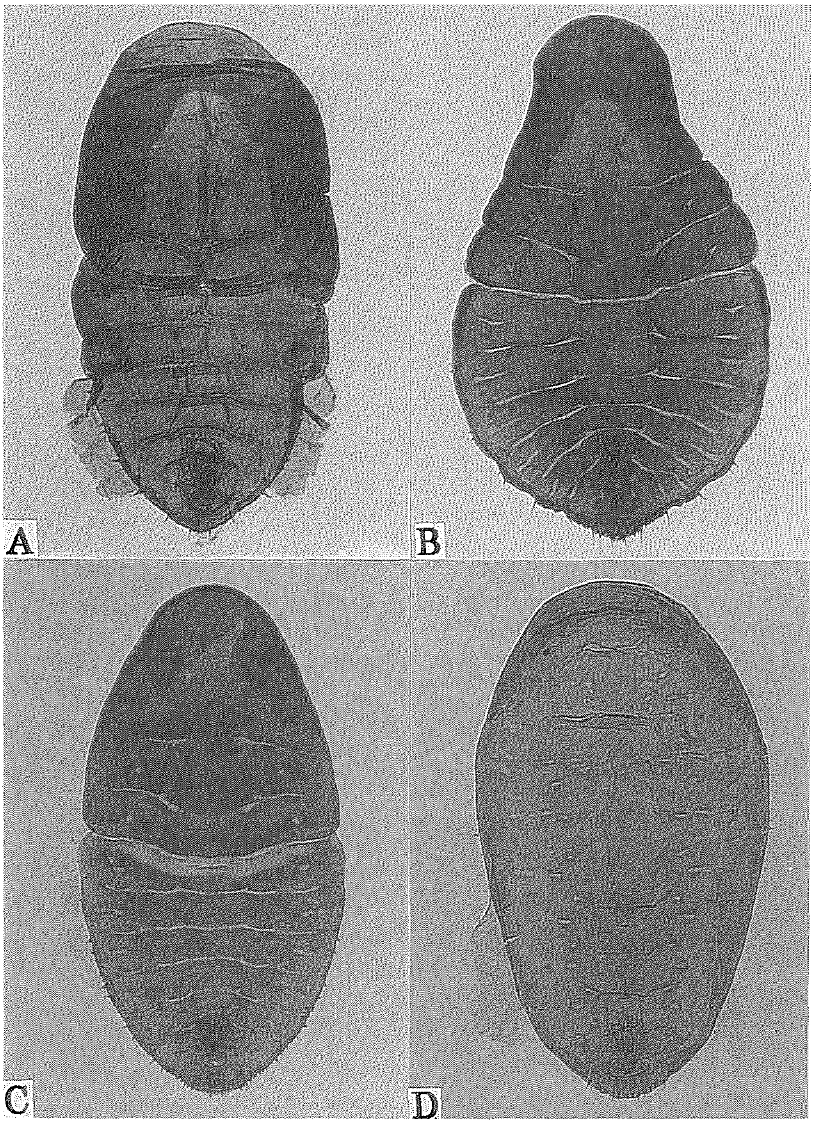

Fig. 23. Exuvial casts of second instar female. A, *Kuwanaspis pectinata*, 540μm long; B, *Nikkoaspis berincangensis*, 870μm long; C, *Nikkoaspis sikokiana*, 930μm long; D, *Medangaspis payunga*, 325μm long.

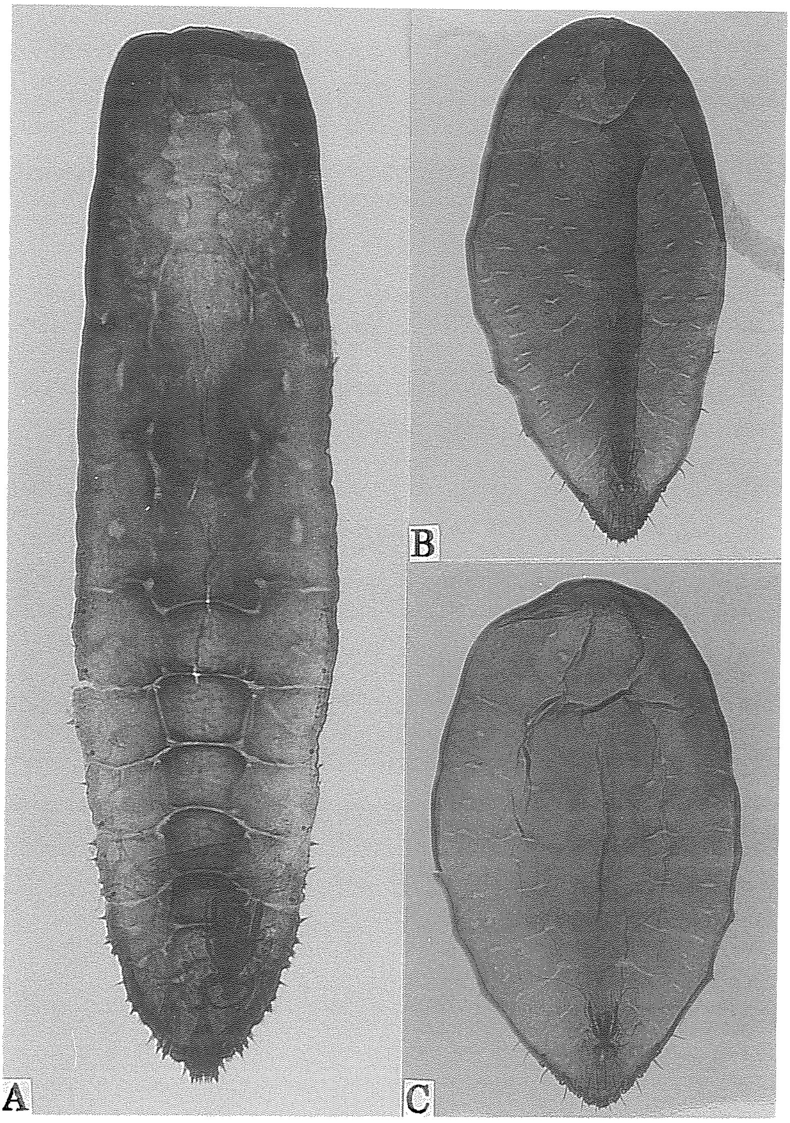

Fig. 24. Exuvial casts of second instar female. A, *Xiphuraspis ctenopyga*, 850μm long; B, *Coronaspis malesiana* [88ML-189], 1,180μm long; C, *Coronaspis malabarica* [78IND-282], 970μm long.

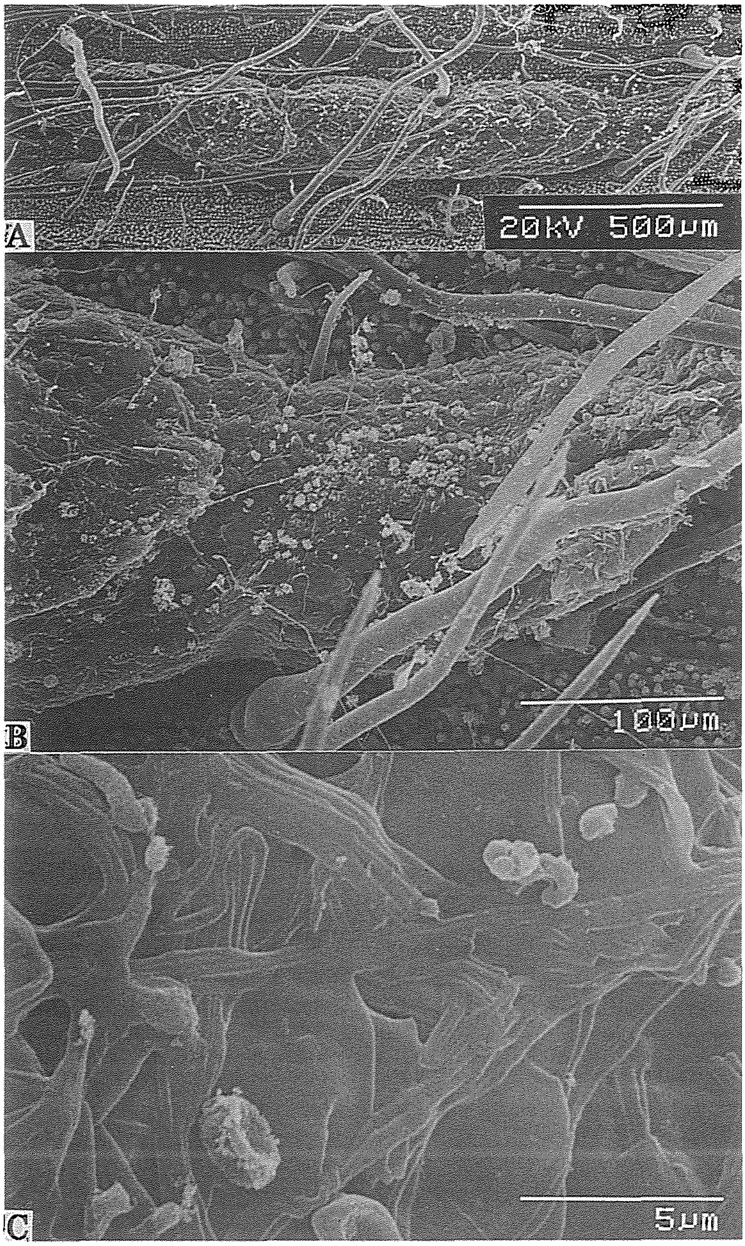

Fig. 25. *Kuwanaspis pectinata*, female test. A, test under construction; B, same, posterior end, showing a newly added part; C, part of dorsal surface.

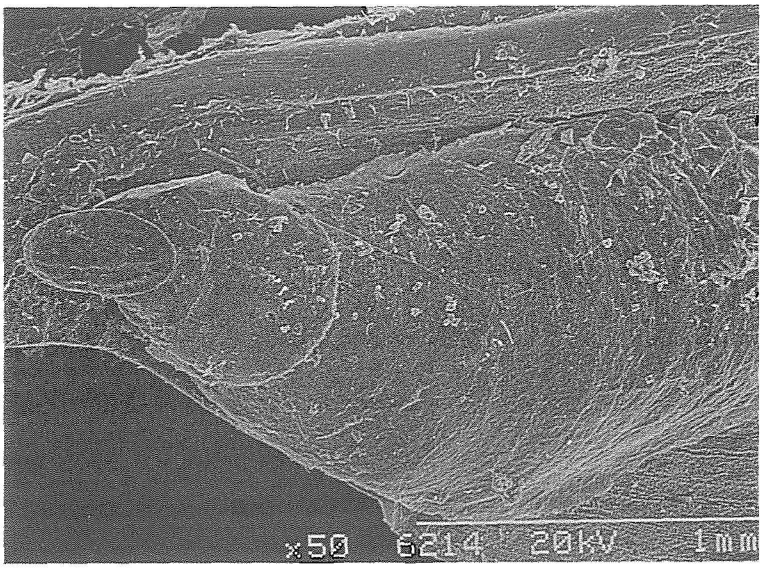

Fig. 26. *Nikkoaspis berincangensis*, female test.

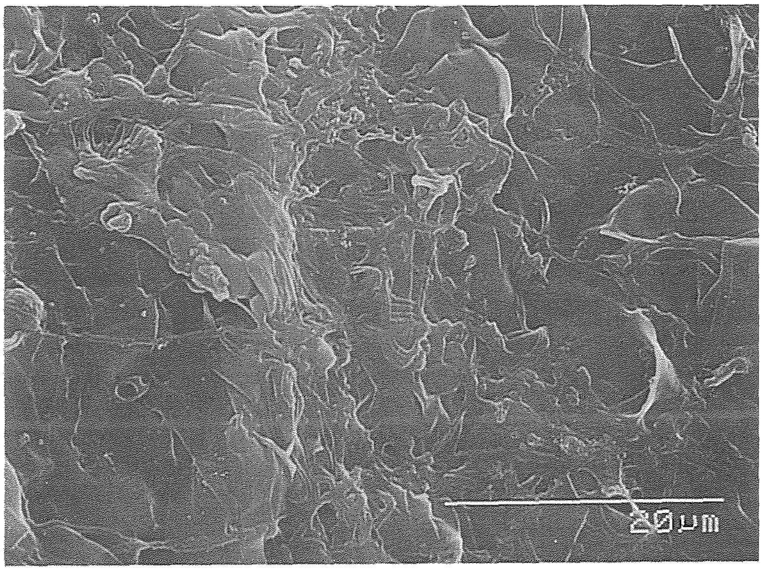

Fig. 27. *Nikkoaspis berincangensis*, female test. Part of dorsal surface.

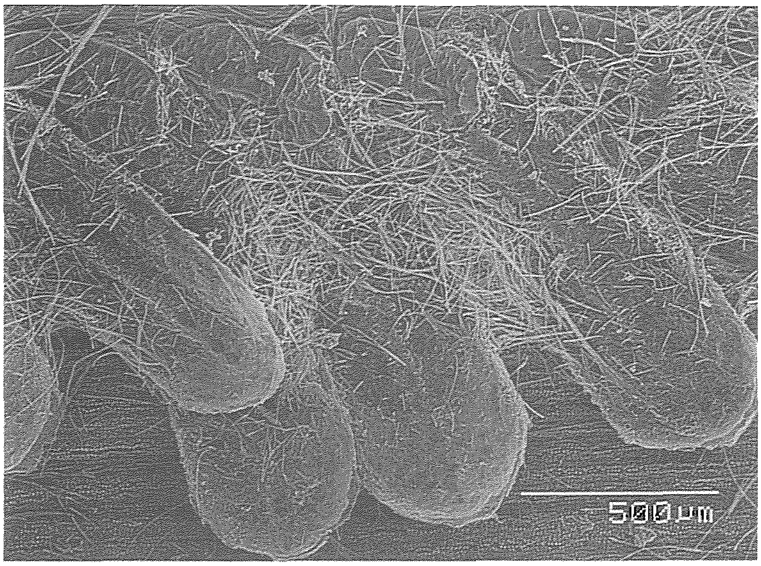

Fig. 28. *Nikkoaspis berincangensis*, male tests.

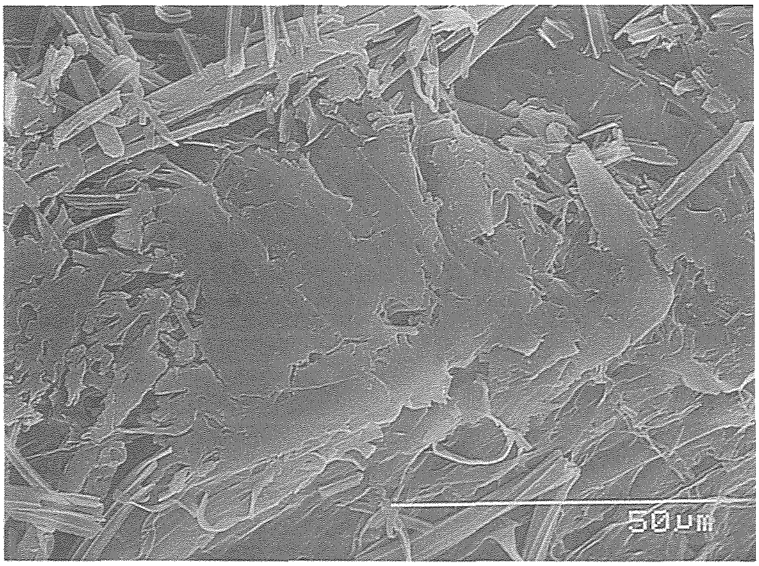

Fig. 29. *Nikkoaspis berincangensis*, male test. Part of median carina.

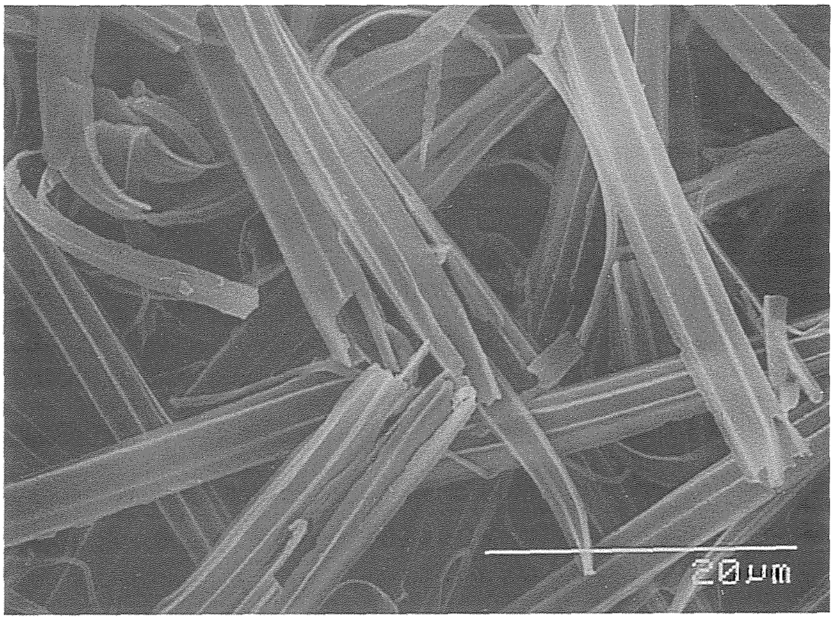

Fig. 30. *Nikkoaspis berincangensis*, male test. Wax filaments around first exuvial cast.

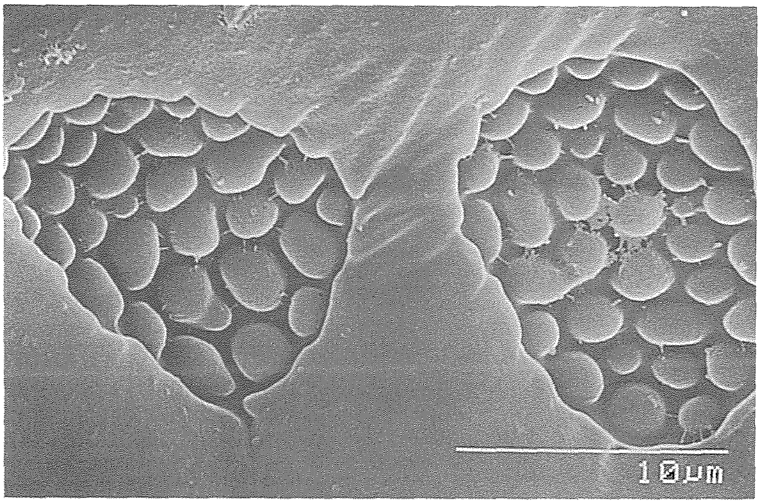

Fig. 31. *Xiphuraspis ctenopyga*, first instar larva. Verrucose plates.

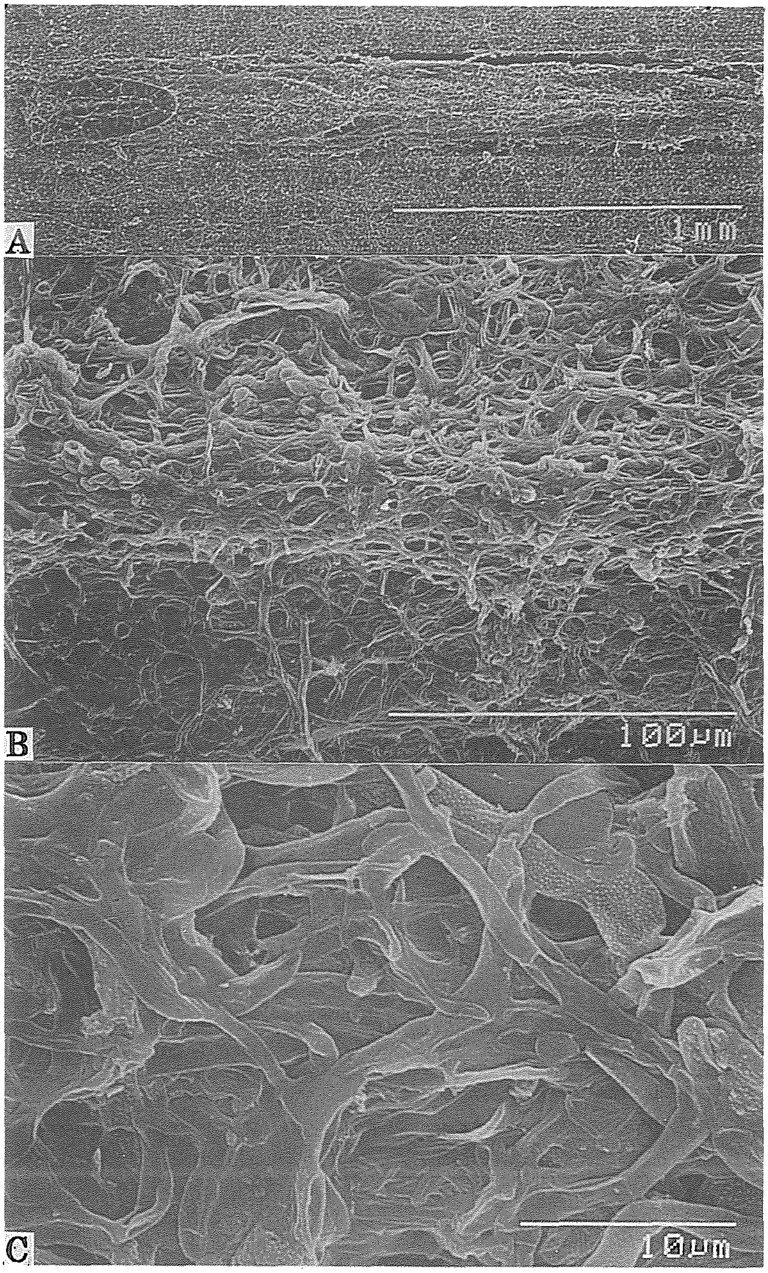

Fig. 32. *Xiphuraspis ctenopyga*, female test. A, dorsal view; B, part of median ridge; C, part of median ridge, details.

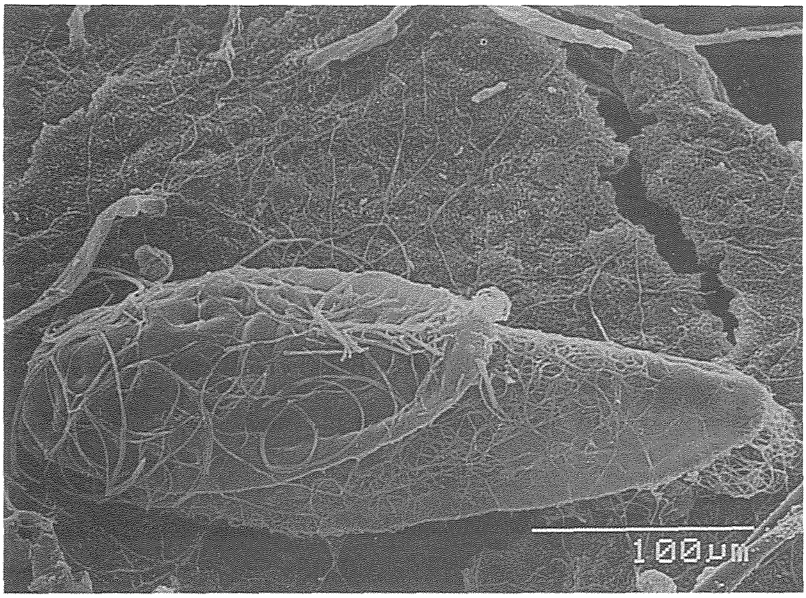

Fig. 33. *Medangaspis payunga*, female test.

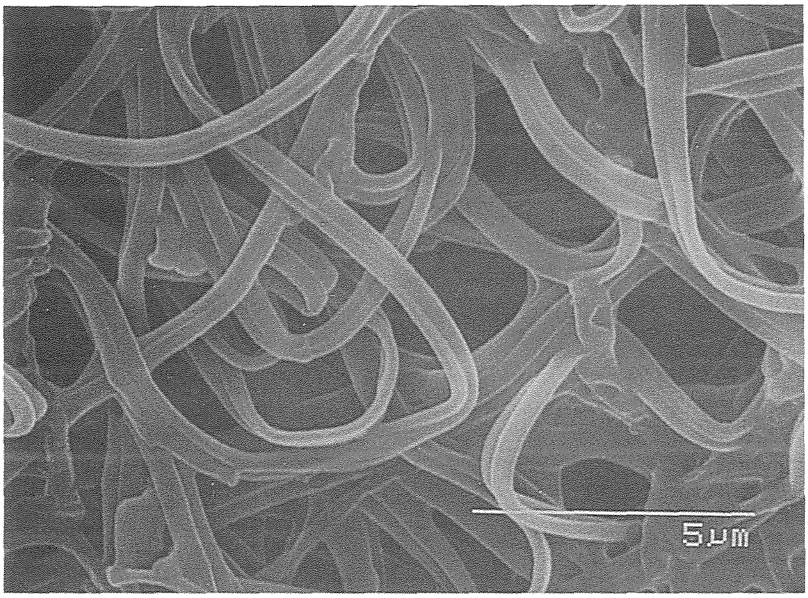

Fig. 34. *Medangaspis payunga*, female test. Wax filaments on second instar exuvial cast.

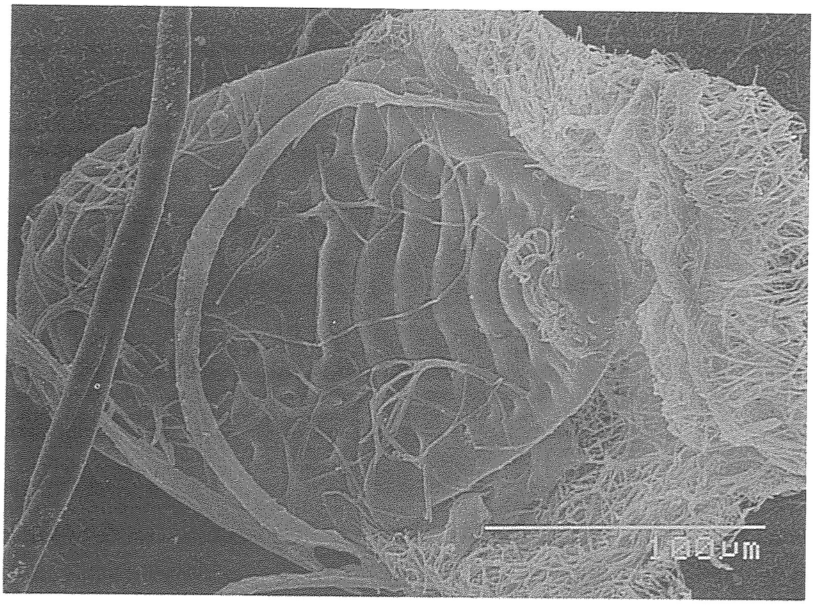

Fig. 35. *Medangaspis payunga*, male test. Dorsal view.

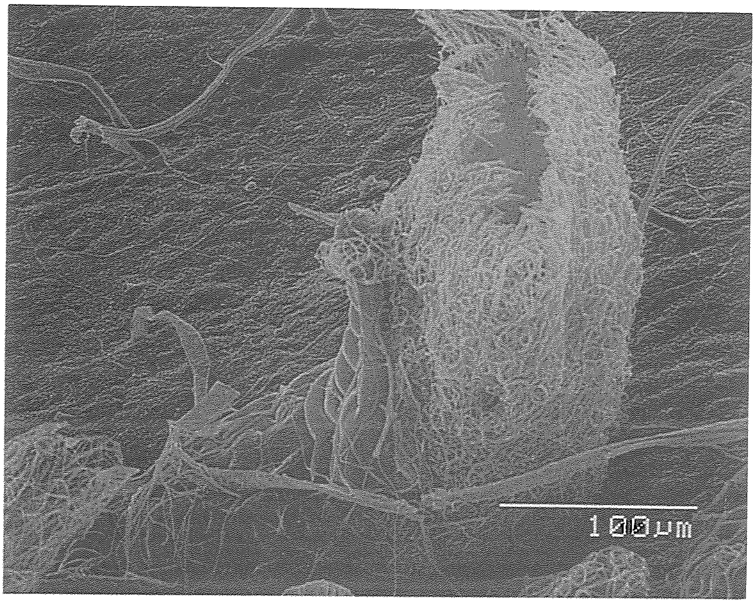

Fig. 36. *Medangaspis payunga*, male test. Lateral view.

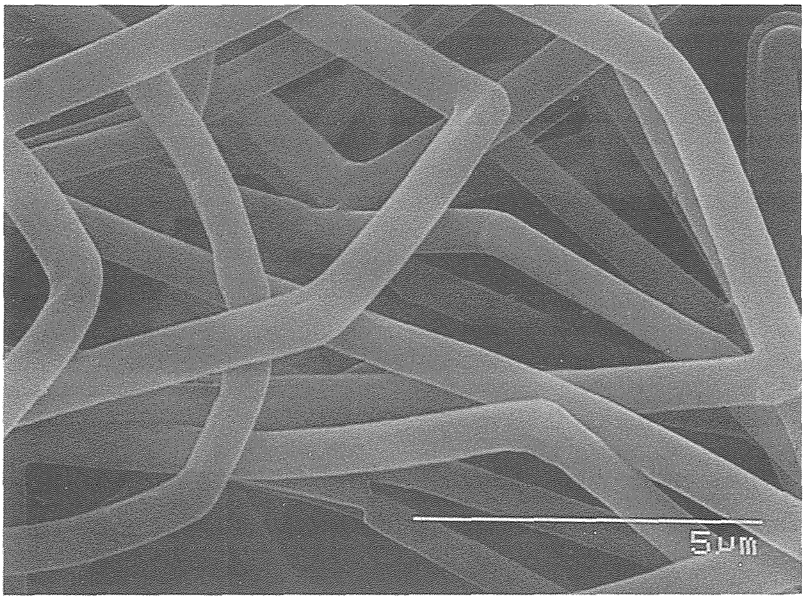

Fig. 37. *Medangaspis payunga*, male test. Wax filaments.

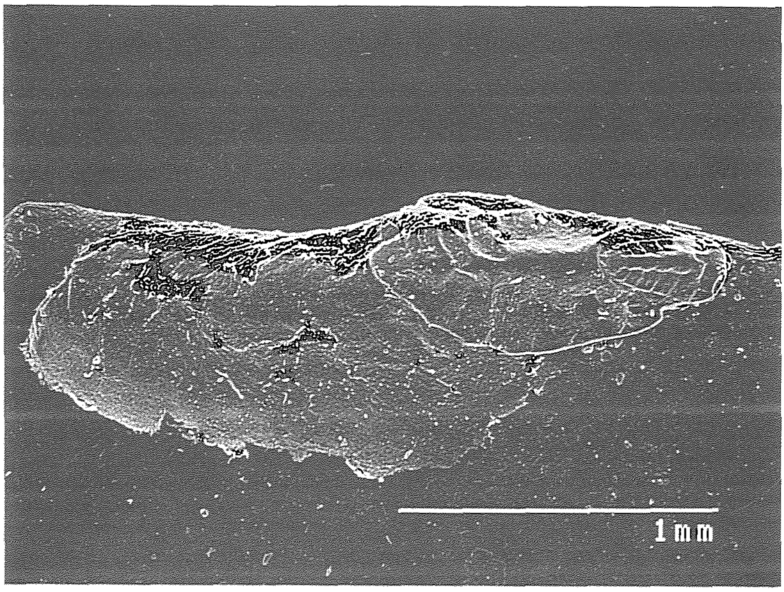

Fig. 38. *Coronaspis malesiana*, female test [88ML-238]. Dorsal view.

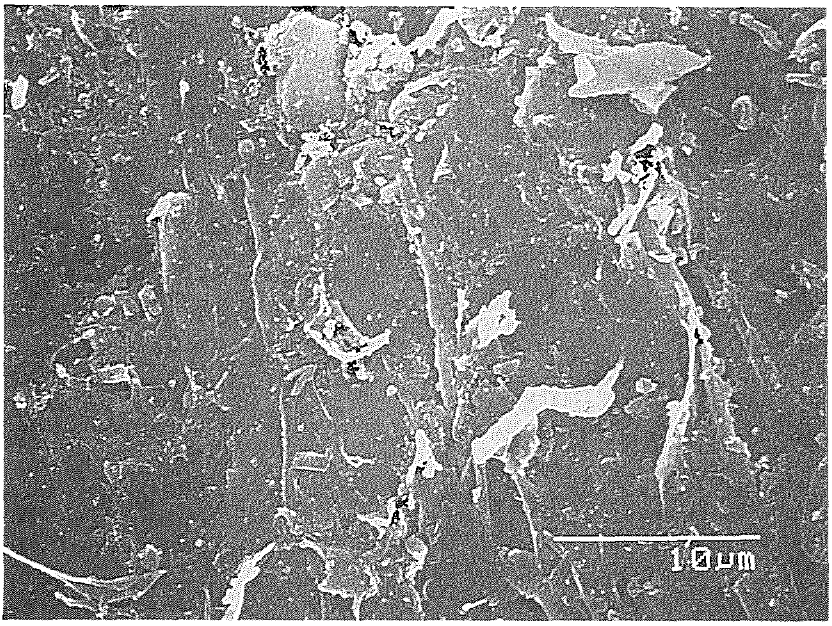

Fig. 39. *Coronaspis malesiana*, female test [88ML-238]. Part of dorsal surface.

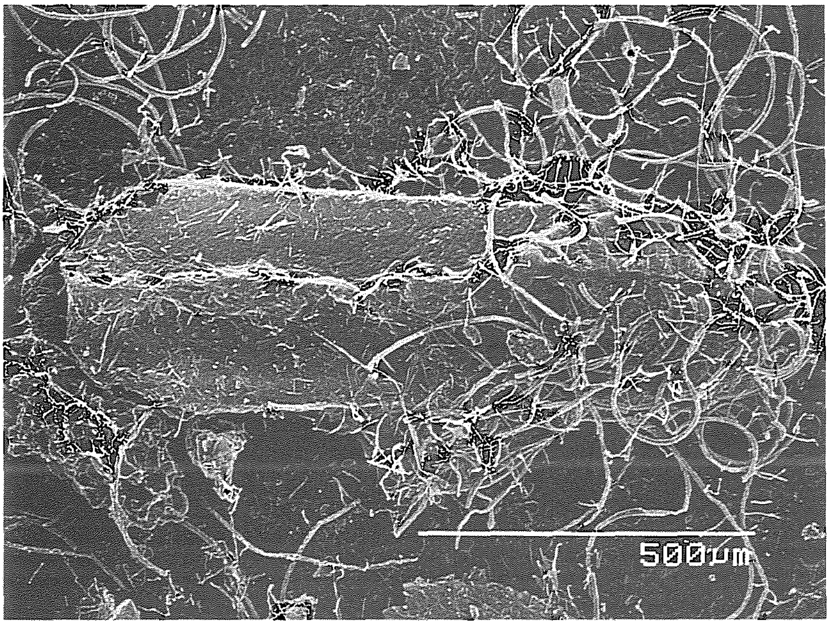

Fig. 40. *Coronaspis malesiana*, male test [88ML-238]. Dorsal view.