INSECTA MATSUMURANA

NEW SERIES 49 : 1-67 DECEMBER 1993

PRIMITIVE DIASPIDINI (HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAO TAKAGI

Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia, Scientific Report No. 18.

Abstract

TAKAGI, S. 1993. Primitive Diaspidini (Homoptera : Coccoidea : Diaspididae). *Ins. matsum. n. s.* 49 : 1-67, 60 figs. (in 43 pls.).

Eight new species of scale insects are described from Malaysia, and 4 new genera, *Dungunia, Kyphosoma, Pentacicola* and *Thoa,* are erected to accept them. They agree in lacking lobes and in having nonglandular pectinae, gland spines, and 3-locular spiracular disc pores ; the 1st instar is characterized by having a pair of ducts or gland spines laterally to the anus. These genera, together with the temperate Asian *Megacanthaspis* and the American *Protodiaspis,* represent primitive Diaspidini and constitute the subtribe Protodiaspidina. The 2nd instar males examined form a roughly graded series in their divergence from the 2nd instar females, and the gradation is somewhat parallel to the evolutionary states of the adult females. Divergent types are similar to the 2nd instar males of some Chionaspidina ; on the other hand, one of them (represented by 2 species of *Pentacicola*) is very similar in several characters to the adult female and 2nd instar of *Ulucoccus,* a very primitive diaspidid, including geminate-type marginal ducts. Thus the subtribe connects the Chionaspidina with *Ulucoccus.* The 1st instar larvae of *Kyphosoma, Pentacicola* and *Thoa* are elaborately decorated dorsally, and it is noteworthy that in these genera the adult females are characterized by unusual dorsal growth.

Author's address. Systematic Entomology, Faculty of Agriculture, Hokkaidô University, Kita 9 Nisi 9, Kita-ku, 060 Japan.

Supported by Grants-in-Aid, Ministry of Education, Science and Culture, Japanese Government, No. 61041003, 62043003, 63041004, and 02041005.

Contents

INTRODUCTION

Scale insects of the family Diaspididae are generally characterized by having some distinct marginal processes or appendages on the pygidium, and broad divisions within the family are primarily based on the organization of these structures. The absence of these appendages has proved to be secondary in some cases.

Other forms in which appendages are wholly absent or only poorly represented show no trace of secondary loss, and yet are referable to the family based on other features. Beginning with this state, some successive stages in the organization of appendages are recognized in extant forms of diaspidids, and are interpreted to represent evolutionary stages within the family (Takagi 1981).

The 8 new species in 4 new genera described below are simple in the organization of pygidial appendages, having uniform pectinae alone besides gland spines, and, therefore, should be primitive. As discussed later, they are referable to the Diaspidini (sensu Takagi 1992). This tribe is a big one in the family, and as yet no classification scheme for it has found a general agreement. Diverse larval forms have been found, violating schemes based on the adult female, and no consistent explanation has been offered for them (Takagi, Tho and Khoo 1989). Obviously, primitive forms are important in systematics, and they are especially useful for this tribe in order to understand entangled larval forms.

NEW TAXA

The species described herein agree in some characters of taxonomic value. In the adult female there are no lobes on the pygidial margin; instead, there are pectinae ['plates' in authors] in addition to gland spines, which may be reduced to microducts; the spiracular disc pores are 3-locular; the macroducts appear to be of the '2-barred' type; the anus is situated close to the base of the pygidium; and the antennae are unisetose. In the 1st instar there is a pair of ducts or gland spines laterad of the anus.

Eight species belonging to 4 genera, all new, are described below. *Megacanthaspis*, with 5 species occurring in temperate eastern Asia, agrees with them in the general characters. All these species are among the smallest diaspidids.

Dungunia cnestis, sp. nov.

Material. Collected at Kuala Dungun, Terengganu, Malaya, on *Cnestis palala*, Jul. 18, 1990 [90ML-257]. Occurring on the undersurface of the leaves. Female test largely composed of thin, translucent exuvial casts, with a short white secretory part behind; male test with secretory part white, thin, elongate, and slightly carinate medially. Name-bearing specimen: adult female.

Adult female (based on 4 specimens not all in good condition) [Fig. 2]. Body plump; when mounted, nearly ovoid with both ends rounded; segmentation indistinct; head sclerotized along anterior margin; pygidium not well defined, dorsally represented by a weakly sclerotized area comprising abd VI–VIII. Pectinae and gland spines occurring along pygidial margin as follows: a pair of pectinae at apex of pygidium (on abd VIII), these pectinae being separated from each other by a space as broad as one of them, on each side followed by 1 gland spine, 3 pectinae, 1 gland

spine and 1 or 2 pectinae; beyond the last there is another gland spine (on abd VI). Sclerotized gland spines (with a membranous apical extension) occurring in a segmentally interrupted row on each side from head or prothorax to abd V, 20-31 in total. Macroducts rather small but not slender; about 40-55 strewn just laterally to the row of gland spines, the anteriormost occurring on anterior margin of head; dorsal macroducts dispersed on pygidium and around base of pygidium, about 6-8 on each side. Perivulvar disc pores present in 5 groups: 4-7 in median group, 6-9 in the anterolateral and 4-8 in the posterolateral; 30-38 in total. Anterior spiracle with 0-5 disc pores. Antennae set rather close to each other, each with a slender seta.

Second instar female (1 specimen and some exuvial casts) [Fig. 3]. Oblong. Pectinae and gland spines of pygidium as in adult female. Prepygidial gland spines: 2 or 3 laterally to anterior spiracle, 1 laterally to posterior spiracle and also on abd I-V each. No macroducts nor microducts present on both surfaces. Anus situated about centre of pygidium. Anterior spiracle with 1 disc pore. Exuvial cast mostly 0.50-0.56 mm long, about twice as long as wide.

Second instar male (2 specimens, both distorted on slide) [Fig. 4]. Oblong. Head with a pair of tubercles marginally (anteriorly to antennae). Pectinae similar to those in female, the median pectinae with a pair of slender processes (rudimentary pectinae?) between. Gland spines well developed on thorax and base of abdomen: 3 or 4 laterally to anterior spiracle, 2 laterally to posterior spiracle, 4 submarginally on base of abdomen; other gland spines small, 2 posterolaterally to the basal gland spines of abdomen, followed by marginal gland spines occurring singly on abd IV-VIII; the gland spine which occurs just laterally to the median pectina is accompanied by a few dentations basally. Macroducts rather large, rather abundant on dorsum of abdomen; some laterally to gland spines on thorax and base of abdomen. Modified macroducts (probably 'frame ducts') occurring singly along margin on abd II-VII. Microducts strewn ventrally. Anterior spiracle with 1 or 2 disc pores.

First instar larva (1 specimen and some exuvial casts) [Fig. 5]. Oblong. Antennae short, 5-segmented; segment V about as long as II-IV combined, not annulate. Enlarged dorsal ducts absent on head. Three pairs of submedian dorsal microducts on thoracic segments; a pair of minute ducts laterally to anus. Ventral microducts occurring along margin on thorax and abdomen, 9 on each side. A pair of small and sharp processes between caudal setae; another pair of processes laterally to the setae, larger and incised. Exuvial casts 0.27-0.32 mm long and 1.7-1.8 times as long as wide in female; 0.34-0.39 mm long and 1.7-2.0 times as long as wide in male.

Dungunia, gen. nov.

Name-bearing species: *Dungunia cnestis*, sp. nov.

This genus is represented by the name-bearing species alone, and characters of the species are not repeated here for a generic diagnosis. In the adult female, this species is hardly distinguishable generically from some species of *Protodiaspis*, in which, however, the dorsal ducts are small and slender. It is recognized as representing another distinct genus because of its host plant [Connaraceae] and 1st instar larval characters. *Protodiaspis* is associated with oaks [Fagaceae]; in the

1st instar it is especially characterized by having enlarged ducts laterally to the anus ('suranal ducts') and is uniform in having 6-segmented antennae (Ferris 1937 ; Howell and Tippins 1981). *D. cnestis* has suranal ducts, which are, however, minute ; it also differs from *Protodiaspis* in having 5-segmented antennae.

Kyphosoma kinabaluense, sp. nov.

Material. Collected on the Pinosuk Plateau, Kinabalu National Park, Sabah, alt. ca. 1,500-1,600 m, on *Lithocarpus* spp. [88ML-43, -63, -72] and *Castanopsis* sp. [88ML-50], Oct. 5-7, 1988. Occurring on the undersurface of the leaves. Female test [Figs. 29-31] with secretory part white, elongate, and with exuvial casts terminal and translucent ; the completed test is highly convex dorsally, the secretory part being compressed laterally and, in cross section [Figs. 32 & 33], very thick on the ridge thus formed. Male test [Figs. 36 & 37] with secretory part white, elongate, and tricarinate. Name-bearing specimen : adult female, from 88ML-43.

Adult female (based on 15 specimens from 88ML-43 and 15 from 88ML-50, not all of them being in good condition on slide owing to swollen body) [Figs. 1 & 6]. Body elongate, plump ; at full growth abruptly and highly swollen dorsally in thorax, then gradually decreasing in height toward posterior end. Derm remaining membranous and segmentation indistinct. Pygidium not well defined, the apical margin flatly roundish, with a pair of pectinae medially (on abd VIII) ; these pectinae are separated from each other by a space as broad as or broader than one of them, followed, on each side, by 2 pectinae occurring on abd VII, which are separated from the median pectina by a good space. Gland spines in segmentally defined groups : 3-7 (usually 4-6) posteriorly to anterior spiracle, 1 or 2 (1) anteriorly to posterior spiracle, 1-3 (2 or 3) laterally to posterior spiracle, and 6-11 submarginally on abd I ; several gland spines (usually 2 or 3) on abd II-VI each, forming together a segmentally interrupted row along margin ; 1 gland spine just laterally to median pectina and 1-3 (usually 1 or 2) just laterally to pectinae on abd VII. Rather large dorsal macroducts occurring medially on abd II-V, forming a transverse row on each segment, 1-6 (usually 5 or 6) on II, 4-8 on III, 5-8 on IV, and 3-7 on V ; other macroducts strewn on pygidium and also submedially on abd III (IV)-V, mostly smaller than the median macroducts. Small macroducts scattered laterally to the groups and row of gland spines. Antenna with a long seta. Anterior spiracle with 1-3 (usually 1 or 2) disc pores.

Second instar female (2 specimens and exuvial casts) [Fig. 7]. Elongate, broadest across metathorax. Pectinae as in adult female on abd VII and VIII ; rudimentary ones on VI. Gland spines : 2 just posteriorly to anterior spiracle, 1 laterally to posterior spiracle, 3 in an oblique or transverse submarginal row on abd I, and 1 on abd II-VIII each. Three dorsal macroducts occurring marginally on each side, bolonging to abd V-VII ; 6 smaller macroducts occurring singly on preceding segments just laterally to the row of gland spines. Antenna unisetose. Anterior spiracle with 1 disc pore. Anus situated about centre of pygidium. Exuvial cast fusiform, cleft laterally between metathorax and abd I, usually 0.55-0.59 mm long, 1.5-1.7 times as long as wide.

Second instar male (15 specimens, not all of them in good condition) [Fig. 8]. Elongate obovoid. Pectinae similar to those of female ; median pectinae well separated from each other, usually with a pair of narrow, fimbriate or pointed

membranous processes between. Gland spines: 1-4 (usually 3) just posteriorly to anterior spiracle, 1-2 (1) laterally to posterior spiracle, 2-4 (3) on abd I submarginally, 1-2 (1) on II and sometimes also on III near margin; no gland spine on IV-VI; on each of abd VII and VIII a microduct is associated with a narrow, fimbriate and membranous process at the place where the presence of a gland spine is expected. Six small ducts occurring singly on margin on abd II-VII; larger ducts occurring submedially on dorsum of metathorax and abdomen and scattered marginally and submarginally on thorax and base of abdomen; among the dorsal macroducts, 4 pairs of submedian macroducts occurring on abd IV-VII and median macroducts (somewhat irregular in occurrence) are a little smaller than neighbouring macroducts and appear modified in structure, but their true nature is not clear. Microducts occurring submedially and submarginally on ventrum of abdomen. Anterior spiracle with 1 disc pore.

First instar female exuvial cast [Fig. 9]. Elongate, cuneiform, being flat on head margin, broadest across prothorax and then gradually tapering posteriorly; usually 0.37-0.41 mm long, about 1.7-1.8 times as long as wide. Posterior part of head produced medially to form a prominent tubercle; also thoracic segments and abd I-V each swollen medially to form a pair of tubercles. Five spinous processes marginally on abd IV-VIII, conical or irregularly shaped. A pair of enlarged ducts on head. A pair of gland spines occurring submedially on each of thoracic segments, and another pair laterally to anus; gland spines also occurring along margin dorsally on thorax and abdomen, 9 on each side. Antennae 5-segmented; segment V longer than I-IV combined, not annulate.

First instar male exuvial cast. Rather obovoid in shape; lacking enlarged ducts on head. Otherwise similar to female exuvial cast. Usually 0.46-0.48 mm long, about 1.5-1.8 times as long as wide.

Kyphosoma pinosukense, sp. nov.

Material. Collected on the Pinosuk Plateau, Kinabalu National Park, Sabah, alt. ca. 1,500 m, on *Lithocarpus* sp., Oct. 11, 1988 [88ML-126]. Occurring on the undersurface of the leaves. Tests [Figs. 38-41] similar to those of *K. kinabaluense*. Name-bearing specimen: adult female.

Adult female (based on 15 specimens, not all of them in good condition on slide) [Fig. 10]. Similar to adult female of *K. kinabaluense*, differing in gland spines and other features. Pygidium rounded marginally. Gland spines: 1-4 (usually 3) posteriorly to anterior spiracle, 1-2 (usually 1) anteriorly to posterior spiracle, 1-3 (usually 2) just laterally to posterior spiracle and another gland spine far laterally (thus situated nearer to margin), 1 on each of abd II-VI near margin, 1 on each of VII and VIII marginally. Median dorsal macroducts: 0-3 on abd I, 2-6 on II, and 3-6 on III-V each; submedian dorsal macroducts absent on prepygidial segments except for occasional presence of a few on V. Anterior spiracle with 0-2 (usually 1) disc pores.

Second instar female exuvial cast. Elongate, cuneiform, being flat on head margin, broadest in thorax and gradually tapering posteriorly in abdomen (not cleft laterally between metathorax and abd I), 0.48-0.54 mm long, 1.8-2.0 times as long as wide. Pectinae, ducts and gland spines similar to those in exuvial cast of *K. kinabaluense*.

Second instar male (some specimens, not all in good condition). As in *K. kinabaluense* in general characters, differing in some details. Median pair of pectinae often duplex. Gland spines: 1 or 2 posteriorly to anterior spiracle, 1 laterally to posterior spiracle, 1 or 2 on abd I and also on II submarginally; no gland spines on abd VII and VIII (on each of these segments a microduct is found at the place where the occurrence of a marginal gland spine is expected). Small marginal ducts as seen in *K. kinabaluense* absent; instead, microducts occurring along margin: 1 or 2 on abd III and 1 on VI and VII each.

First instar female exuvial cast [Fig. 11]. Similar to exuvial cast of *K. kinabaluense*, differing in lacking spinous processes marginally on abd IV-VIII, in gland spines occurring along margin much reduced in size, and in antennal segment V about as long as I-IV combined. Usually 0.36-0.40 mm long, 1.6-1.8 times as long as wide.

First instar male exuvial cast. With a pair of enlarged dorsal ducts on head as in female (thus differing from the 1st instar male of *K. kinabaluense*); 0.39-0.44 mm long.

Kyphosoma melayuense, sp. nov.

Material. Collected on Bukit Larut [Maxwell Hill], Perak, Malaya, alt. ca. 500 m, on *Lithocarpus wallichianus*, Oct. 7, 1986 [86ML-116]; on Bukit Perangin, Sik, Kedah, Malaya, on *Lithocarpus* sp., Nov. 9, 1991 [91ML-374]. Occurring on the undersurface of the leaves. Tests similar to those of *K. kinabaluense* and *K. pinosukense*; the female test [Figs. 34 & 35] is not smooth but rugged with transverse ribs, and in cross section with no particularly thickened part as in the other 2 species. Name-bearing specimen: adult female, mounted from 86ML-116.

Adult female (based on 15 specimens from 86ML-116 and 10 from 91ML-374, not all of them in good condition on slide) [Fig. 12]. Similar to *K. kinabaluense* and *K. pinosukense* in body shape, in general characters of pygidium, etc. Characterized by having 1-4 gland spines in front of anterior spiracle; 1-4 gland spines posteriorly to anterior spiracle, 1 or 2 (usually 1) anteriorly to posterior spiracle, 1-3 posterolaterally to posterior spiracle, 3-7 on abd I, 1 or 2 on II-V each, and 1 on VI-VIII each. Without median transverse rows of enlarged dorsal macroducts; often with macroducts on dorsum as anteriorly as abd II, but sometimes with none medially and submedially on prepygidial segments.

Second instar female (4 specimens and exuvial casts). Gland spines: 2 posteriorly to anterior spiracle, 1 laterally to posterior spiracle, 2 or 3 on abd I, 1 on II-VIII each. A macroduct often present laterally to anus on one or either side. Otherwise as in *K. kinabaluense*. Exuvial cast similar to that of *K. kinabaluense* in shape, 0.46-0.50 mm long, 1.7-2.0 times as long as wide.

Second instar male (a few specimens poor in condition). Similar to the 2nd instar male of *K. kinabaluense*. Median pair of pectinae single, lateral pair duplex or single. Gland spines: 2 posteriorly to anterior spiracle, 1 laterally to posterior spiracle, 1 or 2 on abd I, and 1 on II. Gland spines on abd VII and VIII represented each by a microduct (associated with a rudimentary process on VIII). There are small ducts on the abdominal margin as in *K. kinabaluense*, at least on abd III-VII.

First instar female exuvial cast. Six marginal spinous processes present on abd III-VIII (5 in *K. kinabaluense*, and none in *K. pinosukense*); antennal segment V as

long as I-IV combined as in *K. pinosukense* ; 0.31-0.34 mm long, 1.8-2.0 times as long as wide.

First instar male (some specimens) [Fig. 13]. Lacking enlarged dorsal ducts on head. Exuvial cast 0.32-0.37 mm long.

Kyphosoma, gen. nov.

Name-bearing species : *Kyphosoma kinabaluense*.

Adult female. Elongate, plump ; humpbacked at full growth, being abruptly swollen dorsally in thorax and then gradually decreasing in height posteriorly. Pygidium with 2 pairs of pectinae ; median pectinae widely separated from each other, lateral pair duplex. Gland spines occurring along margin in a segmentally interrupted row. Macroducts strewn dorsally on pygidium and laterally to the row of gland spines. Test highly convex dorsally, with secretory part compressed.

First instar female exuvial cast. Cuneiform. Head, thoracic segments and abd I-V produced medially to form tubercles. Three pairs of gland spines on thorax submedially ; a pair of similar gland spines laterally to anus.

Associated with fagaceous plants (*Lithocarpus* ; *Castanopsis*).

Pentacicola spinosus, sp. nov.

Material. Collected on Bukit Bauk, Daerah Dungun, Terengganu, Malaya, on *Pentace* sp., July 14, 1990 [90ML-202]. Occurring on the undersurface of the leaves. Female test [Figs. 42 & 43] subrhombic in outline and highly convex dorsally ; exuvial casts terminal, reddish gray ; secretory part occupying a small proportion of test, grayish, attenuating posteriorly, with a median ridge. Male test [Fig. 50] with secretory part white, elongate, and depressed dorsoventrally ; erect, attached to the leaf by its anterior end. Name-bearing specimen : adult female.

Adult female (based on 15 specimens) [Figs. 14, 25 & 26]. Subrhombic to subpyriform, broadest across meso- or metathorax, with pygidium produced. Segmentation indistinct ; at full growth head, thorax and abd I-III sclerotized throughout and dorsally convex, and anterior margin of head produced to form a broad and often undulate crest. Abd IV and V and base of pygidium remaining membranous. Pygidium reticulate dorsally toward apex ; marginally with a continuous series of processes as follows : at apex a pair of well-developed pectinae with a smaller pectina between, followed on each side by 1 gland spine, which is often accompanied by a few dentations basally, 2 well-developed pectinae, and 1 gland spine. Prepygidial gland spines swollen and sclerotized basally, with a membranous filiform extension, those on head and thorax with the extension especially long ; 1-5 in front of anterior spiracle ; a group of 2-6 gland spines posteriorly to anterior spiracle, laterally accompanied by another gland spine (or sometimes 2) and 2-5 microducts ; laterally to these microducts starts a row of about 20-35 gland spines, which extends transversely toward the margin for a short distance, then curves along the margin to run onto the base of the pygidium ; this row may be continuous throughout or, when with fewer gland spines, interrupted segmentally on the abdomen. Macroducts rather small but not slender, strewn dorsally on pygidium and abd V and also laterally to the row of gland spines. Antenna with a well-developed seta. Anterior spiracle with 1 disc pore. Anus and vulva situated near base of pygidium.

Second instar female exuvial cast [Fig. 15]. Nearly obovoid; broadly round along head margin, abruptly broadened on mesothorax, thereafter gradually tapering posteriorly, and round on pygidial margin; 0.36-0.41 mm long, 1.1-1.3 times as long as wide. Pectinae as in adult female on abd VII and VIII, 2 pectinae on VI usually rudimentary. Gland spines with a long apical extension as in adult female; a few gland spines in fused region of head and prothorax submarginally; some about mesothoracic region marginally to submarginally; metathorax and abd I-VIII each with 1 gland spine marginally. Small ducts arranged along margin singly on meso- and metathorax and abd I-VII.

Second instar male (a few specimens) [Fig. 16]. Pectinae absent. Gland spines with a long apical extension, 4-6 posteriorly to anterior spiracle, 2-4 laterally to posterior spiracle, and 2 or 3 submarginally on abd I; absent on abd II-VIII. Six macroducts along margin on abd II-VII (these macroducts appear to be somewhat modified in shape, but the true nature of the modification is not clear); other ducts slender, strewn both dorsally and ventrally on abdomen, a few on thorax. Setae occurring along margin of abdomen spinous. Anus close to apex of pygidium. Anterior spiracle with 1 disc pore.

First instar female exuvial cast [Fig. 17]. Obovoid, constricted about between head and prothorax, 0.29-0.32 mm long, 1.3-1.4 times as long as wide. Posterior part of head, thoracic segments and abd I-VI each swollen medially to form a tubercular prominence. Irregularly reticulate especially on head including median prominence and on thorax laterally and on median prominences. Enlarged ducts absent on head. Three pairs of sclerotized gland spines on thorax, the middle pair submarginal and the other pairs submedian; another pair laterally to anus. Three truncate gland spines (apical extension lost?) marginally on each side, probably belonging to thoracic segments. A pair of pectinae between caudal setae; another pair laterally to the setae. Setae mostly spinous, those occurring along margin on some anterior segments of abdomen especially strong. Antennae 6-segmented; segment VI not annulate, about as long as I-V combined.

First instar male exuvial cast. Similar to female exuvial cast, but not constricted between head and prothorax; 0.31-0.34 mm long.

Pentacicola fimbriatus, sp. nov.

Material. Collected in the grounds of the Forest Research Institute of Malaysia, Kepong, Selangor, Malaya, on *Pentace triptera*, Nov. 5, 1986 [86ML-413] and June 17, 1990 [90ML-23]. Tests [Figs. 44-48 & 51-53] similar to those of *P. spinosus*. Name-bearing specimen: adult female, mounted from 86ML-413.

Adult female (based on 30 specimens) [Figs. 18 & 27]. Similar to adult female of *P. spinosus* in body shape, differing in having an acute pygidium; at full growth head, thorax and abd I and II sclerotized, convex dorsally, with a crestlike projection on head as in *P. spinosus* (but the projection is not always well developed). Pectinae only in 1 pair at apex of pygidium; no marginal gland spines on pygidium (microducts present in place of gland spines). Prepygidial gland spines: 1-3 in front of anterior spiracle (sometimes undiscernible owing to overlapping mouthparts); 3-7 posteriorly to anterior spiracle, immediately followed laterally (or posterolaterally in full-grown specimens) by a row of about 27-37 gland spines, which runs as in *P. spinosus*. Macroducts strewn dorsally on abdomen except on basal 2 or 3 segments,

and laterally to the row of gland spines. Anterior spiracle with 1 disc pore (in 86ML-413) or none (90ML-23).

Second instar female exuvial cast. Similar to exuvial cast of *P. spinosus* in shape, but tending to be narrower; 0.42-0.46 mm (in 90ML-23) or 0.49-0.50 mm (86ML-413) long, about 1.2-1.5 times as long as wide. Pygidium with only a pair of pectinae at apex; no gland spine laterally to the pectinae. Other gland spines and ducts similar to those in *P. spinosus*.

Second instar male (15 specimens) [Fig. 19]. Similar to 2nd instar male of *P. spinosus*, having no trace of pygidial appendages. Head sometimes with a pair of tubercular prominences on margin. Gland spines as in *P. spinosus*, but it seems that they are not much elongate apically; 4-7 posteriorly to anterior spiracle, 2 or 3 lateroposteriorly to posterior spiracle, and 2 on abd I submarginally. Six macroducts along abdominal margin on each side, with a geminate structure at inner end. Other ducts more or less slender, abundant on both surfaces of abdomen and metathorax. Anterior spiracle with a long seta and often with a shorter and slenderer seta.

First instar female exuvial cast [Fig. 20]. Subrhombic, broadest in mesothorax; 0.30-0.34 mm (in 90ML-23) or 0.34-0.36 mm (86ML-413) long, 1.3-1.4 (90ML-23) or 1.5-2.0 times (86ML-413) as long as wide. Posterior part of head, thoracic segments and abd I-VI each swollen medially to form a tubercular prominence. Head irregularly reticulate within anterior margin and on median prominence; median prominences of thoracic segments also reticulate or tending to be so. Marginal setae on head and thorax thick, broadened and fimbriate apically; other setae also thick but smaller, tending to be fimbriate or blunt apically. Pectinae absent on apex of abdomen. Otherwise similar to exuvial cast of *P. spinosus*.

First instar male exuvial cast (90ML-23). Obovoid; 0.33-0.34 mm long, 1.6-1.8 times as long as wide. Otherwise similar to female exuvial cast.

Pentacicola echinatus, sp. nov.

Material. Collected in the Bako National Park, Sarawak, on *Pentace* sp., Oct. 12, 1991 [91ML-137]. Occurring on the undersurface of the leaves. Female test [Fig. 49] nearly as in *P. spinosus*, but with no distinct median ridge. Male test present, but only old ones, broken and incomplete, were observed. Name-bearing specimen: adult female.

Adult female (based on 15 specimens) [Figs. 21 & 28]. Elongate pyriform, broadest across metathorax; pygidium produced, round marginally; segmentation indistinct. At full growth head, thorax and abd I and II heavily sclerotized and convex dorsally; no crestlike process on head. Pygidium well sclerotized posteriorly to anus and vulva, which are situated near the base of the pygidium; reticulate dorsally, tuberculate ventrally especially toward base. Pectinae only in 1 pair at apex of pygidium; marginal gland spines indicated by microducts. Prepygidial gland spines sclerotized basally, with a long apical extension; 1-4 in front of anterior spiracle; 11-16 between anterior and posterior spiracles, forming an oblique row extending to margin, followed by a segmentally interrupted row running along margin onto base of pygidium: 2-4 (usually 3 or 4) laterally to posterior spiracle and on abd I, 2 or 3 (usually 2) on II, and 1 on III-VI each. Macroducts small, scattered dorsally on abdomen except on basal segments, and laterally to

gland spines. Antenna with a well-developed seta. Anterior spiracle with 1 disc pore.

Second instar female exuvial cast. Subpyriform to subrhombic, pygidium rather acute; 0.42-0.46 mm long, 1.3-1.9 times as long as wide. Pectinae in 1 pair at apex of pygidium. Gland spines: about 5-7 in fused region of head and prothorax submarginally; about 8-10 on mesothorax in an oblique row attaining margin; marginal gland spines on metathorax and abdomen, usually single but sometimes 2 or 3 on metathorax and 2 on abd I, the posteriormost occurring on VIII just laterally to pectina. Single small ducts occurring marginally on thorax and abdomen, 10 on each side, the posteriormost belonging to abd VII.

Second instar male (1 teneral specimen within skin of 1st instar). Almost as in *P. fimbriatus* so far as characters observable are concerned, differing in having less gland spines: 3 or 4 posteriorly to anterior spiracle, 1 laterally to posterior spiracle, and 1 on abd I submarginally. Six macroducts occurring along abdominal margin on each side, with a geminate structure at inner end, as in *P. fimbriatus*.

First instar female exuvial cast [Fig. 22]. Subpyriform; posterior end divided into a pair of robust processes (apical processes); there are 9 pairs of prominent cornuted processes on head, thorax and abdomen, followed by a similar but single process on abd VI (dorsal processes); head and a narrow median region of thorax irregularly reticulate; 0.33-0.36 mm long (from head margin to apices of apical processes), 1.5-1.8 times as long as wide. No enlarged dorsal ducts on head. Three pairs of sclerotized gland spines on thorax, the middle one submarginal and the others submedian; another pair laterally to anus. Three truncate gland spines marginally on each side (probably belonging to thoracic segments). Strong elongate setae around body, tending to be frayed toward apex especially on head and thorax, the posteriormost very strong, occurring on apices of apical processes; submedian setae also strong on supposed pro- and mesothorax. Other setae small but stiff. Antennae 6-segmented, segment VI shorter than I-V combined, annulate on apical half.

First instar male exuvial cast. Very similar to female exuvial cast, 0.34-0.36 mm long.

Pentacicola, gen. nov.

Name-bearing species: *Pentacicola spinosus*.

Adult female. Subrhombic to subpyriform, with pygidium produced; at full growth head, thorax and basal abdominal segments sclerotized, convex dorsally. Pygidium with pectinae. Prepygidial gland spines sclerotized, with a long apical extension; arranged in a continuous or interrupeted row, which starts between the anterior and posterior spiracles, extends toward the margin, then curves along the margin to run onto the base of the pygidium. Macroducts strewn dorsally on pygidium and some prepygidial segments, and laterally to the row of gland spines. Anus and vulva near base of pygidium. Test subrhombic in outline, convex dorsally.

First instar exuvial cast. Obovoid, subrhombic or subpyriform, medially swollen to form tubercular prominences or cornuted processes on head and thoracic and abdominal segments. Setae, especially those occurring along margin, spinous, fimbriate or frayed. Three pairs of sclerotized gland spines on thorax, the middle

pair submedian and the other pairs submarginal; another pair laterally to anus. Antennae 6-segmented.

Associated with *Pentace* [Tiliaceae].

Thoa lophopetali, sp. nov.

Material. Collected at the Mencali Forest Reserve, near Kuala Rompin, Pahang, Malaya, on *Lophopetalum floribundum*, Aug. 17, 1990 [90ML-533]. Occurring on the undersurface of the leaves. Female test [Figs. 54-56] highly convex dorsally; secretory part dark brown, with transverse ribs; exuvial casts terminal, pale yellow, reddish at posterior apex. Male test [Figs. 57-60], even when completed, largely composed of 1st instar exuvial cast, with a small amount of waxy material behind. Name-bearing specimen: adult female.

Adult female (based on 15 specimens all full-grown and more or less distorted on slide owing to swollen body) [Fig. 23]. Robust, much swollen dorsally; segmentation indistinct. Derm remaining membranous, wrinkled in an elaborate network in a broad marginal region of metathorax and abdomen. Pygidium broadly round marginally, with a continuous series of pectinae and gland spines; on apex of pygidium (abd VIII) 2 pairs of pectinae accompanied laterally by a pair of gland spines, the outer pair being often sclerotized and little fimbriate, thus appearing like lobes; on each of 3 preceding segments (V-VII) 3 pectinae followed by 1 gland spine, on VII one or two of the pectinae being sometimes lobelike. On each of abd III and IV 1 marginal gland spine. About 3-7 tubercular gland spines submarginally on base of abdomen (about abd I and II); 1 or 2 small gland spines sometimes present just laterally to posterior spiracle. Macroducts strewn dorsally on pygidium and also laterally on prepygidial segments as anteriorly as mesothoracic region. Microducts scattered on prepygidial ventrum. Anterior spiracle with 1 or 2 (usually 1) disc pores. Antenna with a thick seta.

Second instar female exuvial cast. Broadly pyriform, with head somewhat produced and abdomen round marginally; deeply cleft laterally between metathorax and abd I; 0.51-0.55 mm long. Pectinae fewer than in adult female. Gland spines single on abdominal segments marginally; a few on each of meso- and metathorax submarginally. Ducts small, occurring along margin.

First instar female exuvial cast [Fig. 24]. Elongate circular, 0.34-0.39 mm long, about 1.3-1.4 times as long as wide. Margin undulate posteriorly to mesothorax, being gently concave on each of metathorax and abd I-VI. Posterior part of head produced medially to form a tubercle; thoracic segments produced to form remarkable tubercles in a broad median region; abd I-VI slightly swollen medially, forming a pair of tubercles on each segment (tubercles coalescent or almost so on V and VI). Small conical spines scattered over thoracic segments and abd I-VI. A pair of small sharp processes between caudal setae; another pair laterally to the setae. No enlarged ducts on head. Three pairs of sclerotized gland spines on thorax submedially; gland spines also along margin on thorax and abdomen, 9 on each side. A pair of minute ducts laterally to anus. Antennae 5-segmented, segment V as long as I-IV combined, annulate.

First instar male exuvial cast. Similar to female exuvial cast, but little or only slightly undulate marginally; 0.40-0.50 mm long.

Thoa, gen. nov.

Name-bearing species: *Thoa lophopetali*, sp. nov.

This genus is represented only by the species above, of which the description substantially stands for a generic description. Above all, it is characterized in the 1st instar by having a number of small spines scattered over the thorax and abdomen.

INSTARS REVISED

Adult females

As stated at the beginning of New taxa the genera described above agree with *Megacanthaspis* in some general characters. In my revision (Takagi 1981) of *Megacanthaspis* I concluded that *M. leucaspis* is the most primitive in the genus. (The other 4 species are peculiar in having thickened multiglandular spines on the abdomen, but otherwise are similar to *M. leucaspis*.) As compared with *M. leucaspis* the genera from Malaysia are considerably modified. The body is plump and swollen, with segmentation obscured, and assumes a genus-characteristic shape. The pygidial appendages are reductive except in *Thoa*, in which, however, no gland spines occur in the region anterior to the metathorax. In accord with the obscured segmentation the prepygidial gland spines form a more or less continuous longitudinal row along the margin through the prepygidial segments in *Dungunia, Kyphosoma* and *Pentacicola*. The macroducts are scattered except for the segmental rows of median macroducts occurring in *Kyphosoma kinabaluense* and *K. pinosukense*. These median macroducts are responsible for the peculiarly thickened tests. After all, the Malaysian genera as compared with *M. leucaspis* are derivative. *Dungunia, Kyphosoma* and *Pentacicola* are similar in the arrangement of gland spines, but this similarity is, as stated above, due to the obscured segmentation. *Thoa* is quite different from them. I have failed to find any immediate phylogenetic relationship (for example, ancestral-descendant relationship) among the Asian genera, which are apparently divergent.

While the reduction of pygidial appendages seems to be a trend in this group of genera, *Thoa* clearly retains them. Pectinae at certain positions even appear somewhat like lobes, thus exhibiting a slight tendency toward a complicated organization of appendages, but this state is not stable.

The completed female tests of *Kyphosoma, Pentacicola* and *Thoa* are highly convex, while the test of *Dungunia* is completed with an unusually small amount of waxy material behind the 2nd instar exuvial cast. *Megacanthaspis langtangana* makes no oscillatory movements when forming its test (Takagi 1990a). SEM-observed tests show no unmistakable trace of movements also in *Kyphosoma, Pentacicola* and *Thoa*. In fact, their tests are formed in accord with the immovable swollen body.

Second instar females

In diaspidid taxonomy in general the 2nd instar female attracts little attention except for pupillarial forms. This stage is a simplified copy of the adult female. This is true with the Malaysian genera, too, yet their 2nd instar females are noteworthy. *Dungunia cnestis* has no ducts on either surface (except for gland

spines). In *Kyphosoma, Pentacicola* and *Thoa* the exuvial casts show traces of middorsal growth corresponding to the middorsal prominences in the 1st instar ; in 3 species (*Kyphosoma kinabaluense, K. melayuense* and *Thoa lophopetali*) they are deeply cleft laterally, the part posterior to the clefts being pushed up in accord with the upheaved test.

Second instar males

In *Megacanthaspis* the second instar male is very similar to the 2nd instar female, differing mainly in having more ducts (Takagi 1981). In *Dungunia* and *Kyphosoma*, too, the sexual dimorphism is remarkable mainly in the occurrence of ducts, the pygidial appendages being represented nearly as in the female. *Dungunia*, however, has modified marginal ducts, which are probably 'frame ducts'. *Kyphosoma*, too, has some seemingly modified macroducts medially and submedially and also very small ducts marginally (replaced by microducts in *K. pinosukense*) on the abdomen. On the other hand, the 2nd instar males of *Pentacicola* are different from the 2nd instar females not only in having many ducts but also in having no trace of pygidial appendages ; in 2 species (*P. fimbriatus* and *P. echinatus*) the macroducts occurring along the abdominal margin are all modified into the geminate type. It seems that the male tests of *Pentacicola* are wholly composed of solid cylindrical wax filaments, which may be secreted not only by the geminate-type marginal ducts but also by other ducts. The male test of *Thoa lophopetali* is completed with an unusually small amount of secreted wax. In this respect some unusual type of the 2nd instar male may be expected, but no specimen of this stage was available in the material.

First instar larvae

Quite unusually for diaspidids, the 1st instar larvae are elaborately decorated in *Kyphosoma, Pentacicola* and *Thoa*. They are commonly characterized by having middorsal prominences. These are especially remarkable in *Pentacicola echinatus* : the dorsal prominences are produced into hornlike processes (dorsal processes) and the posteriormost segment also forms a pair of prominent processes (apical processes), which are very like the anal lobes of eriococcids. However, the apical processes differ from the anal lobes in having the caudal setae not at the apices but on the ventral bases. They may correspond to the dorsal processes. Most body setae are strongly developed in *Pentacicola*, and in 2 species they are even frayed or fimbriate. *Thoa lophopetali* is equipped with a number of small spines over the dorsum.

Megacanthaspis, Dungunia and *Thoa* have a pair of small ducts laterally to the anus, while in *Kyphosoma* and *Pentacicola* there is, at this position, a pair of well-developed sclerotized gland spines. In *Megacanthaspis* each duct opens at the apex of a small tubercle or spine. Thus it seems that the ducts and the gland spines are homologous. (In other diaspidids, too, microducts and gland spines are interchangeable.)

Discussions

Taxonomic position

The agreement in the characters mentioned at the beginning of New taxa strongly suggests that the 4 Malaysian genera and *Megacanthaspis* are related to

each other. I (Takagi 1981) once suggested a relationship between *Megacanthaspis* and the American *Protodiaspis*. Howell and Tippins (1981) studied immature stages of 2 species of *Protodiaspis*. As will be discussed later, their study supports the supposed relationship. I feel, however, some hesitation in connecting *Protodiaspis* with the Asian genera because of 'the morphological vagaries of the adult females' (Ferris 1937). Above all, *Protodiaspis parvula*, the name-bearing species, is described as having 'three pairs of weakly sclerotized lobes' (Ferris 1937) ; some other species of the genus also 'have lobes of some sort in the adult' (Brown and McKenzie 1962). Moreover, I have examined no species of the genus. *Protodiaspis* should, therefore, only tentatively be united with the Asian genera on the supposition that the lobes described as such are not true lobes but modified pectinae. In this connection it should be mentioned that in *Thoa lophopetali* certain pectinae are sometimes lobelike in appearance.

Some species of *Protodiaspis* have no pygidial appendages, and *P. parvula* and others have no gland spines. This can be secondary. The species of *Pentacicola* afford another example of reducing appendages on the pygidium.

It is the opinion here adopted that all these genera, while having no lobes, primarily have pectinae and gland spines. The spiracular disc pores are 3-locular in the Asian genera and, according to Howell and Tippins (1981), in at least part of *Protodiaspis*. By the presence of gland spines and by the 3-locular spiracular disc pores they are referable to the subfamily Diaspidinae (sensu Takagi 1992), and by the absence of lobes they should represent a primitive stage. The occurrence of pectinae, which is exceptional in the subfamily, should also be a primitive character. These pectinae are nonglandular (that is, with no microduct associated). Also in the subfamily Aspidiotinae (sensu Takagi 1992), in which pectinae are universal, the occurrence of nonglandular pectinae is limited to forms supposed to be primitive (*Thysanaspis* ; Leucaspidini).

However, in spite of the apparent primitive state of the adult female, the perivulvar disc pores and certain larval features suggest a connection with advanced forms of the Diaspidinae. SEM observations of the disc pores of *Megacanthaspis langtangana* show structures common to other Diaspidinae and nothing particular (Takagi 1990b). Howell and Tippins (1981) found 'frame ducts' in the 2nd instar males of *Protodiaspis varus* and *P. didymus*. According to them, this discovery is 'surprising because this particular type of duct has previously been known to occur only in genera centering around *Chionaspis*'. In the 2nd instar male of *Dungunia cnestis* there are on the margin of the abdomen some modified macroducts, which appear to be 'frame ducts'. The 2nd instar males of *Dungunia, Kyphosoma* and *Pentacicola* are similar to certain types (including undescribed ones) in *Chionaspis* and related genera (subtribe Chionaspidina).

Howell and Tippins also examined the 1st instar larvae of the 2 species of *Protodiaspis* and ascertained the occurrence of a pair of enlarged ducts in the anal region. These ducts, occurring laterally to the anus, are 'suranal' according to their term, and suranal ducts have also been found in chionaspidines. The Asian genera, too, are characterized by having ducts at this position, which are small as usual in chionaspidines or associated with strong spines. Thus the suranal ducts are variable, yet they persist. According to Howell (1980) these ducts are displaced marginal ducts on the 8th abdominal segment. However, for example, in

Pentacicola there are no marginal ducts on segments anterior to the 8th and yet the supposed suranal ducts are present in the form of strong gland spines. It seems that these ducts are stable in their occurrence irrespective of marginal ducts, and then may have considerable significance in phylogeny.*

The apparent connection with advanced Diaspidinae suggested above requires reevaluation of adult female characters. The organization of pygidial appendages is indeed simple and may rightly be regarded as primitive, but there are no other features or characters peculiar to the genera. Nonglandular pectinae also occur in *Kuwanaspis* and other genera (*Nikkoaspis* and undescribed forms), which have well-formed lobes, thus mediating between the primitive genera and advanced forms of the Diaspidinae (so far as the pygidial appendages are concerned).

The subfamily Diaspidinae comprises the tribes Diaspidini and Lepidosaphedini. Distinction between these tribes is not always clear in adult female characters. However, so far as known, sexual dimorphism in the 2nd instar is very remarkable in part (or most ?) of the Diaspidini, while this is not true of the Lepidosaphedini ; in the 1st instar there is a strong seta on the tarsus toward the apex on the ventral side in the Lepidosaphedini, but such a seta is lacking in the Diaspidini.

The genera in question do not belong to the Lepidosaphedini. They may be referable to the Diaspidini or represent another tribe of the Diaspidinae. I am inclined to refer them to the Diaspidini and, thus, to regard them as primitive Diaspidini.

Varshney (1985) in his catalogue of Indian coccoids erected the subfamily Protodiaspidinae, referring *Megacanthaspis* to it. Therefore, when all these genera are supposed to constitute their own higher taxon, the name of this taxon should be based on *Protodiaspis* irrespective of category — the subtribe Protodiaspidina according to the view adopted here. Unfortunately, *Protodiaspis* is connected with the Asian genera only tentatively. However, the name has its merit. It will evoke interest in the supposed connection between the American and Asian genera, and then in their biogeography and in diaspidid evolution.

I would like to conclude this section with a comment on the tribe Rugaspidiotini, because *Protodiaspis* was placed in this tribe by Borchsenius (1966). In my view this tribe as composed by him and other authors is much confused, being an aggregate of unrelated forms gleaned from the Diaspidinae and Aspidiotinae. I myself once contributed to this confusion, adding *Smilacicola* to the tribe. *Protodiaspis* has nothing to do with *Rugaspidiotus arizonicus*, which may be the only representative of the tribe.

Incidentally induced phenotypes : atavistic manifestation

The subtribe Protodiaspidina has proved to be considerably polymorphic in the 2nd instar male, and further types of this stage (e.g., the *xerospermi*-type discussed by Takagi, Tho and Khoo 1989) are expected to be found. So far as represented by the

* Prof. J.O. Howell has revised the manuscript and enumerated chionaspidine characters in the *Dungunia* 1st instar based on the description and figure: '1) suranal ducts; 2) 5-segmented antennae ; 3) apical [antennal] segment not annulate (usually non-annulate in Chionaspidini — few exceptions) ; 4) abdominal gland spines present but may be severely reduced, and absent posterior to lobes 2 ; 5) row of submedian setae not present on abdominal venter'.

known types (excepting the 2nd instar males of *Megacanthaspis*) it comes more closely to the Chionaspidina than to any other groups of the Diaspidini. On the other hand, the 2nd instar males of *Pentacicola fimbriatus* and *P. echinatus* are also very similar to the adult female and the 2nd instar female and male of *Ulucoccus*, a very primitive diaspidid. Further, as already stated, their tests are composed of cylindrical wax filaments as in *Ulucoccus*. They are, however, formed in a definite shape, thus differing from the test of *Ulucoccus*, which is a fluffy mass of filaments (as to *Ulucoccus*, see Takagi, Tho and Khoo, 1990).

For years I have beeen arguing that the 2nd instar polymorphism of the Diaspididae is, at least largely, caused by the appearance of atavistic patterns of characters and that these patterns are manifested incidentally to the evolving adult females (Takagi 1980; Takagi, Tho and Khoo 1989; Takagi 1990c). The 2nd instar males examined of the Asian Protodiaspidina form a roughly graded series in their divergence from the 2nd instar females, and the gradation is somewhat parallel to the evolutionary states of the adult females:

1) In *Megacanthaspis* the female and male of the 2nd instar are considerably similar to each other and also to the adult female. This state of sexual dimorphism should be primitive, because the genus represents the most primitive pattern of adult female characters in the subtribe (except for the enlarged multiglandular spines occurring in 4 of the 5 known species).

2) The 2nd instar males of *Dungunia* and *Kyphosoma* still retain pygidial appendages, yet some ducts are modified in shape. The adult females compared with *Megacanthaspis* are apparently derivative.

3) The 3 species of *Pentacicola* are also derivative in the adult females, and *P. fimbriatus* and *P. echinatus* are more so than *P. spinosus* (and than *Dungunia* and *Kyphosoma*) in the state of the pygidial appendages. The 2nd instar males have no appendages on the pygidium, somewhat differing in other features between *P. spinosus* and the others. They are remarkably different from the 2nd instar females. As already stated, the 2nd instar males of *P. fimbriatus* and *P. echinatus* are noteworthy for their resemblance to *Ulucoccus*, a very primitive diaspidid.

I feel, therefore, no need to change my view as to the atavistic element in the 2nd instar male polymorphism of the Diaspididae. However, not every odd feature of the 2nd instar males may be atavistic (Takagi, Tho and Khoo 1989). On the other hand, the occurrence of 2nd instar males similar to the adult and 2nd instar females also can be derivative and atavistic, provided the adult females are considerably derivative, because in the primitive state the 2nd instar male and female and the adult female are all similar. This is the case with some *Rhododendron*-associated species of *Fiorinia*, in which the 2nd instar males are copies of the derivative females in discord with many other species of the genus (Takagi 1975; 1979).

Incidentally induced phenotypes : new structures ?

The decorated 1st instar larvae of *Kyphosoma, Pentacicola* and *Thoa* are quite extraordinary in the family. Questions naturally arise:

1) Is the decoration an indication of a close phylogenetic relationship? The 3 genera agree in having middorsal prominences, but differ in the details of the decoration; in *Pentacicola* most body setae are strong and, in 2 species, even fimbriate or frayed, but in the other genera no modification of setae occurs; in *Thoa*

the dorsum is strewn over with numerous small spines, but this is not the case with the other genera. The exuvial casts are shaped characteristically in each genus. So far as the adult females are concerned, *Kyphosoma* and *Pentacicola* may be closely related, but there is no reason to believe that *Thoa* is more closely related to them than to *Dungunia* or to *Megacanthaspis*.

2) Is the decoration functional in any way? The larvae of *Pentacicola* and *Thoa* in particular appear to be armed. Then against what? If this type of armament is functional and advantageous, why is it not universal in the Diaspididae? I have found no functional as well as phylogenetic explanation plausible. Then another question:

3) Is the appearance of decorative features incidental to any other development? The 3 genera are commonly characterized in the adult female by the body remarkably expanded dorsally (but in different ways among the genera). The decoration would be another manifestation of the unusual dorsal growth ('dorsal overgrowth' hereinafter), sharing the same genetic basis. There seems to be no positive reason for adopting this supposition, either. The only apparent fact is that both the elaborate decoration and the dorsal overgrowth are quite rare in diaspidids. I do not know other cases of the 1st instar decoration. Adult females may be somewhat plump in a few other species. In the great majority of the Diaspididae, however, the adult females are flat and make horizontal movements in forming the test; thus they create an open space under the test.

The space-making, probably for accommodating eggs or crawlers, may have an essential adaptive significance (otherwise it would have never developed universally in the family). For diaspidids that make no movements, the formation of an upheaved test is the only way to increase the space under the test (after the shrinkage of the mother's body). An understanding of the dorsal overgrowth, or enhanced cell division on the dorsal side, in the protodiaspidine adult females clearly shows it to be adaptive. It may not be unreasonable to postulate another effect of the enhanced cell division on another stage. The result would be the appearance of decoration on the 1st instar dorsum, different in detail in accord with the different ways of dorsal overgrowth in the adult females or with the more or less different genetic milieus among the genera and species.

There is no evidence to show that a complicated decoration such as found in *Pentacicola echinatus* is an ancestral pattern now lost or suppressed in other diaspidids. The apical processes are similar to the anal lobes of eriococcids, but the resemblance is superficial as already discussed. I am inclined to the view that the 1st instar decoration has appeared newly in the subtribe Protodiaspidina.

Conclusion

My study on the Protodiaspidina is far from complete. Yet the results are interesting enough to show that further study of the subtribe will be helpful especially for approaching the evolution and systematics of the Diaspidini. It should be emphasized that the subtribe connects the Chionaspidina with *Ulucoccus* in the 2nd instar male, favouring the view presented by Takagi, Tho and Khoo (1990) as to the phylogenetic significance of *Ulucoccus*. This in turn supports the view that the Protodiaspidina are primitive Diaspidini.

The 4 genera erected in this study are, when compared with *Megacanthaspis*, considerably derivative in adult female characters. Larval traits occurring in them but not in *Megacanthaspis* are, therefore, seemingly associated with the derivative states of the adult females.

The 2nd instar males of the subtribe I have observed compose a roughly graded series toward augmented sexual dimorphism. The 2nd instar males that are most closely similar to the 2nd instar females occur in *Megacanthaspis*, which is the most primitive in the subtribe so far as based on adult female characters. *Pentacicola fimbriatus* and *P. echinatus* are most derivative among the Asian genera in the state of the pygidial appendages; their 2nd instar males are remarkably different from the 2nd instar females and most closely similar to *Ulucoccus*. All this affords another example of the appearance of atavistic 2nd instar males in association with derivative adult females.

The 1st instar larvae are extraordinarily decorated dorsally in *Kyphosoma, Pentacicola* and *Thoa*. This state is assumed to have been brought about in association with the unusual dorsal growth of the adult females. The decoration is especially complicated in *P. echinatus*. It is surprising to see how complicated structures can be manifested by the 1st instar larva, which is generally simple-featured.

'Anomalous' larvae in the Diaspididae, while they may be helpful for taxonomic arguments, are sometimes difficult to interpret. But the appearance of these larvae is connected at its depth with general, still unsettled problems in biology. It is my conviction, based on the larval polymorphism of diaspidids and some documented cases in other organisms, that a phenotype, as we define it, is only an embodied part of a huge potential held in the genetic-epigenetic system of the concerned organism. Anomalies are other possible manifested phenotypes. When they are atavistic, they are of particular value — living fossils of another kind. They must also involve new structures. The elaborately decorated 1st instar may be worthy of study from this viewpoint. I hope to come across other cases helpful for approaching the problem.

I (Takagi 1981) once thought that *Megacanthaspis* and *Protodiaspis* fit the 'Asio-American bicontinental pattern of distribution', which is well documented for some plant and animal taxa occurring in the temperate regions of the continents. Among the 4 genera erected in this paper, *Kyphosoma* seems to belong to the montane oak forest and may be interpreted as an extension from the temperate region. The other 3 genera, however, inhabit lowland tropical forests. If further forms of the Protodiaspidina occur in tropical Africa and South America or if the Australian '*Fiorinia*' *syncarpiae* (see Appendix I, NB 3) is really a protodiaspidine, we have to start our biogeography over again.

Acknowledgements

The material studied was collected in Malaysia under the project 'Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia'. In this country the project was started with preliminary trips to some study areas in 1985, followed by surveys 1986 (Malaya), 1988 (Sabah), and 1990 (Malaya), and ended with surveys carried out in 1991 (Sarawak and Malaya). On this occasion I express my hearty thanks to the involved Authorities of Malaysia and all persons who

cooperated with us. Shortly after the surveys ended in Malaysia, Dr Tho Yow Pong, our coordinator, suddenly passed away. I dedicate to him one of the new genera in his honour.

The host plants of the species studied were identified by Mr. K.M. Kochummen, ex-Botanist at the Forest Research Institute of Malaysia [FRIM], and by botanists at the Forest Research Centre, Sandakan. The name-bearing specimens [holotypes], together with half of the specimens examined of each species, are deposited in the collection of Entomology Division, FRIM.

Prof. J.O. Howell, University of Georgia, has kindly read the manuscript and made a number of suggestions throughout the text.

LITERATURE

Borchsenius, N.S. 1966. A catalogue of the armoured scale insects (Diaspidoidea) of the world. Nauk, 449 pp.

Brown, S.W. and McKenzie, H.L. 1962. Evolutionary patterns in the armored scale insects and their allies (Homoptera : Coccoidea : Diaspididae, Phoenicococcidae, and Asterolecaniidae). Hilgardia 33 : 141-169.

Ferris, G.F. 1937. Atlas of the Scale Insects of North America I. Stanford University Press.

Ferris, G.F. 1941. Atlas of the Scale Insects of North America III. Stanford University Press.

Ferris, G.F. 1942. Atlas of the Scale Insects of North America IV. Stanford University Press.

Howell, J.O. 1980. The value of second-stage males in armoured scale insects (Diaspididae) phyletics. Israel Journal of Entomology 14 : 87-96.

Howell, J.O. and Tippins, H.H. 1981. Some immature stages of two species of *Protodiaspis*. J. Georgia Entomol. Soc. 16(4) : 412-420.

Takagi, S. 1975. The *horii*-group of *Fiorinia* associated with rhododendrons in East Asia (Homoptera : Coccoidea : Diaspididae). Insecta Matsumurana New Series 6 : 35-61.

Takagi, S. 1979. A further study on the *horii*-group of *Fiorinia* (Homoptera : Coccoidea : Diaspididae). Insecta Matsumurana New Series 16, 32 pp.

Takagi, S. 1980. An interpretation of second instar male characters in the systematics of the Diaspididae. Israel Journal of Entomology 14 : 99-104.

Takagi, S. 1981. The genus *Megacanthaspis*, a possible relic of an earlier stock of the Diaspididae (Homoptera : Coccoidea). Insecta Matsumurana New Series 25, 43 pp.

Takagi, S. 1983. Addendum and corrigenda to "The scale insect genus *Megacanthaspis*, a possible relic of an earlier stock of the Diaspididae (Homoptera : Coccoidea)", Insecta Matsumurana New Series 25, 1981. Insecta Matsumurana New Series 27 : 107.

Takagi, S. 1990a. SEM observations on the tests of some Diaspididae (Homoptera : Coccoidea). Insecta Matsumurana New Series 44 : 17-80.

Takagi, S. 1990b. Disc pores of Diaspididae : Microstructure and taxonomic value (Homoptera : Coccoidea). Insecta Matsumurana New Series 44 : 81-112.

Takagi, S. 1990c. Polymorphism. In : Rosen, D. (ed.), Armoured Scale Insects, Their Biology, Natural Enemies and Control [World Crop Pest 4A], Elsevier, pp. 59-64.

Takagi, S. 1992. *Mitulaspis* and *Sclopetaspis* : their distributions and taxonomic positions (Homoptera : Coccoidea : Diaspididae). Insecta Matsumurana New Series 47 : 33-90.

Takagi, S., Tho Y.P. and Khoo S.G. 1989. Beginning with *Diaulacaspis* (Homoptera : Coccoidea : Diaspididae) : Convergence or effect? Insecta Matsumurana New Series 42 : 143-199.

Takagi, S., Tho Y.P. and Khoo S.G. 1990. Genus *Ulucoccus* novum : A key form to diaspidid evolution (Homoptera : Coccoidea). Insecta Matsumurana New Series 44 : 1-15.

Varshney, R.K. 1985. A review of Indian coccids (Homoptera : Coccoidea). Oriental Insects 19 : 1-101.

APPENDIX I: A TENTATIVE LIST OF THE PROTODIASPIDINA

Protodiaspidina Varshney (1985)
[Originally Protodiaspidinae]

Genus *Megacanthaspis* Takagi (1961)
Name-bearing species: *Megacanthaspis actinodaphnes*.
Syn.: *Nanmuaspis* Tang (1977) [name-bearing species: *Nanmuaspis phoebia*].

Megacanthaspis leucaspis Takagi (1981)
Japan: Kii Peninsula, Honsyû; Sikoku; southern Kyûsyû.
On *Actinodaphne longifolia*.

Megacanthaspis phoebia (Tang 1977)
China: Hangchow, Chekiang.
On *Phoebe sheareri*.

Megacanthaspis litseae Takagi (1970)
China: Fen-chi-hu, Taiwan.
On *Litsea akoensis*.

Megacanthaspis langtangana Takagi (1981)
Nepal: Langtang Valley [1,820 m]; Nagarjun [1,470 m], near Kathmandu.
On *Machilus duthiei* and *Dodecadenia grandiflora*.

Megacanthaspis actinodaphnes Takagi (1961)
Japan: Sikoku; southern Kyûsyû.
On *Actinodaphne longifolia*.

Dungunia Takagi, gen. nov.
Name-bearing species: *Dungunia cnestis*.

Dungunia cnestis Takagi, sp. nov.
Malaysia: Kuala Dungun, Terengganu, Malaya.
On *Cnestis palala*.

Kyphosoma Takagi, gen. nov.
Name-bearing species: *Kyphosoma kinabaluense*.

Kyphosoma kinabaluense Takagi, sp. nov.
Malaysia: Kinabalu National Park [1,500-1,600 m], Sabah.
On *Lithocarpus* spp. and *Castanopsis* sp.

Kyphosoma pinosukense Takagi, sp. nov.
Malaysia: Kinabalu National Park [1,500 m], Sabah.
On *Lithocarpus* sp.

Kyphosoma melayuense Takagi, sp. nov.
Malaysia: Bukit Larut [500 m], Perak, Malaya; Bukit Perangin, Sik, Kedah, Malaya.
On *Lithocarpus wallichianus* and *L.* sp.

Pentacicola Takagi, gen. nov.
Name-bearing species: *Pentacicola spinosus*.

Pentacicola spinosus Takagi, sp. nov.
Malaysia: Bukit Bauk, Terengganu, Malaya.
On *Pentace* sp.

Pentacicola fimbriatus Takagi, sp. nov.
Malaysia: Kepong [Forest Research Institute of Malaysia], Selangor, Malaya.
On *Pentace triptera*.

Pentacicola echinatus Takagi, sp. nov.
Malaysia: Bako National Park, Sarawak.
On *Pentace* sp.

Thoa Takagi, gen. nov.
Name-bearing species: *Thoa lophopetali.*

Thoa lophopetali Takagi, sp. nov.
Malaysia: southern Pahang [Mencali Forest Reserve], Malaysia.
On *Lophopetalum floribundum.*

Protodiaspis Cockerell (1898)
Name-bearing species: *Protodiaspis parvula.*
Syn.: *Essigaspis* MacGillivray (1921) [name-bearing species: *Protodiaspis agrifoliae*]; *Obluctaspis* MacGillivray (1921) [name-bearing species: *Protodiaspis lobata*]; *Variaspis* Lindinger (1932) [name-bearing species: *Protodiaspis lagunae*].

Protodiaspis infidelis Ferris (1942)
Mexico: La Providencia, Guerrero.
Panama: Boquete, Chiriqui.
On oak and *Byrsonima crassifolia.*

Protodiaspis chichi McKenzie and Nelson-Rees (1962)
Guatemala: Sololá.
On *Quercus crassifolia.*

Protodiaspis varus Hoke (1928)
U.S.A.: Jaspar Co., Arkansas: Meridian, Mississippi; Chisos Mountains and Davis Mountains, Texas.
Mexico: Amecameca.
On *Quercus hypoleuca, Q. laurifolia, Q. texana* and *Q.* spp.

Protodiaspis lagunae Ferris (1921)
Mexico: El Triunfo, Santiago and Laguna, Cape Region, Baja California.
On *Quercus brandegeei.*

Protodiaspis lobata Ferris (1920)
U.S.A.: Raton Pass, Colorado; Santa Fe, New Mexico; Chisos Mountains and Davis Mountains, Texas.
On *Quercus gambelii, Q. grisea* and *Q.* spp.

Protodiaspis pulchra Ferris (1920)
U.S.A.: Chiricahua Mountains, Arizona.
On *Quercus toumeyi.*

Protodiaspis praetexta Ferris (1941)
Mexico: Chivela, Oaxaca.
On oak.

Protodiaspis signata Ferris (1941)
Panama: Volcano Chiriqui [8,000 feet].
On oak.

Protodiaspis parvula Cockerell (1898)
Mexico: Amecameca.
On oak.

Protodiaspis agrifoliae Essig (1914)
U.S.A.: San Diego Co. and Claremont, California.
On *Quercus agrifolia.*

Protodiaspis didymus McKenzie and Nelson-Rees (1962)
U.S.A.: Greenlee Co. and Grand Canyon, Arizona.

On *Quercus grisea* × *Q. turbinella* and *Q.* sp.

Protodiaspis colimae Ferris (1937)
Mexico: Volcano Colima [5,000 feet] and Michoacan.
Panama: Volcano Chiriqui [7,000 feet].
On *Quercus* spp.

Protodiaspis emoryi Ferris (1937)
U.S.A.: Fort Davis, Texas.
On *Quercus emoryi*.

Protodiaspis sulcata Ferris (1942)
Mexico: La Providencia, Guerrero.
On oak.

NB 1. *Megacanthaspis langtangana* is newly recorded from Nagarjun and from *Dodecadenia grandiflora*; collection date: Oct. 12, 1983.
NB 2. *Protodiaspis cinchonae* McKenzie is excluded from the list. It is, in my view, a species of the *Pseudoparlatoria* group.
NB 3. Borchsenius (1966) in his catalogue referred another species to *Protodiaspis*: *Fiorinia syncarpiae* Maskell, described from Australia as occurring on *Syncarpia laurifolia*.
NB 4. The 14 species of *Protodiaspis* listed above are arranged roughly in accord with the states of the adult females (though they do not exactly fit a linear arrangement). The 1st 3 species have well-developed pectinae as well as gland spines, followed by *P. lagunae* and *P. lobata*, which are described as having distinct (*P. lagunae*) or weakly developed (*P. lobata*) 'lobes'. In some succeeding species the 'lobes' are weakly developed or suggested by marginal prominences. *P. parvula*, the name-bearing species, is described as having weakly sclerotized 'lobes' and no gland spines. *P. agrifoliae* and *P. didymus* have no lobelike appendages nor gland spines. The last 3 species are peculiar and, according to Ferris (1942), especially problematical as to their generic assignment.

Appendix II: A tentative key to the genera of the subtribe Protodiaspidina

Adult female primarily with nonglandular pectinae and gland spines (without true lobes). Spiracular disc pores 3-locular. First instar with a pair of ducts or gland spines laterally to anus.

1. Adult female with dorsal ducts rather large to small, but not slender; with at least 1 pair of pectinae on pygidial margin; gland spines present at least in prepygidial region. First instar with a pair of small ducts or sclerotized gland spines laterally to anus; antennae 5- or 6-segmented. 2
— Adult female with dorsal ducts all small and slender; pectinae may be modified into lobelike processes or lost; gland spines may be lost. First instar with a pair of enlarged ducts laterally to anus; antennae 6-segmented. Associated primarily with Fagaceae. ..... *Protodiaspis*
2. Adult female elongate, not particularly swollen dorsally even at full growth; macroducts thickly rimmed around orifice; gland spines in well-defined segmental groups, [in 4 of the 5 known species] abd II (or III)–VIII each marginally with a thickened spine bearing 1 or more microducts. First instar with a pair of small ducts laterally to anus, each of these ducts being opened at apex of a small tubercle or spine; antennae 5-segmented. Associated with Lauraceae. ..... *Megacanthaspis*
— Adult female plump or eminently swollen dorsally at full growth, and, when flattened dorsoventrally on slide, with marginal gland spines retracted within (especially in prepygidial region); macroducts at most only thinly rimmed around orifice. 3
3. Adult female without gland spines in region anterior to metathorax; body robust, eminently swollen dorsally; pygidium broadly round along margin, with a series of pectinae and gland spines. First instar with eminent tubercular prominences middorsally, and with a number of small spines over dorsum; a pair of small ducts laterally to anus; antennae 5-segmented, terminal segment annulate. ..... *Thoa*

— Adult female with gland spines in region anterior to metathorax. ····· 4

4. Adult female on slide nearly ovoid ; gland spines forming a row along margin in prepygidial region, the row running laterally to spiracles. First instar with a pair of small ducts laterally to anus ; antennae 5-segmented ; without eminent prominences middorsally. ····· *Dungunia*

— Adult female with gland spines posteriorly to anterior spiracle. First instar with a pair of sclerotized gland spines laterally to anus ; exuvial cast with eminent prominences middorsally. ····· 5

5. Adult female elongate, at full growth abruptly swollen dorsally in thorax, then gradually decreasing in height posteriorly. First instar with setae not particularly developed ; antennae 5-segmented. Associated with Fagaceae. ····· *Kyphosoma*

— Adult female subrhombic to subpyriform ; head, thorax and basal abdominal segments swollen dorsally and sclerotized at full growth. First instar with dorsal setae thickened, spinelike or fimbriate or frayed ; antennae 6-segmented. Associated with *Pentace*. ····· *Pentacicola*

PLATES

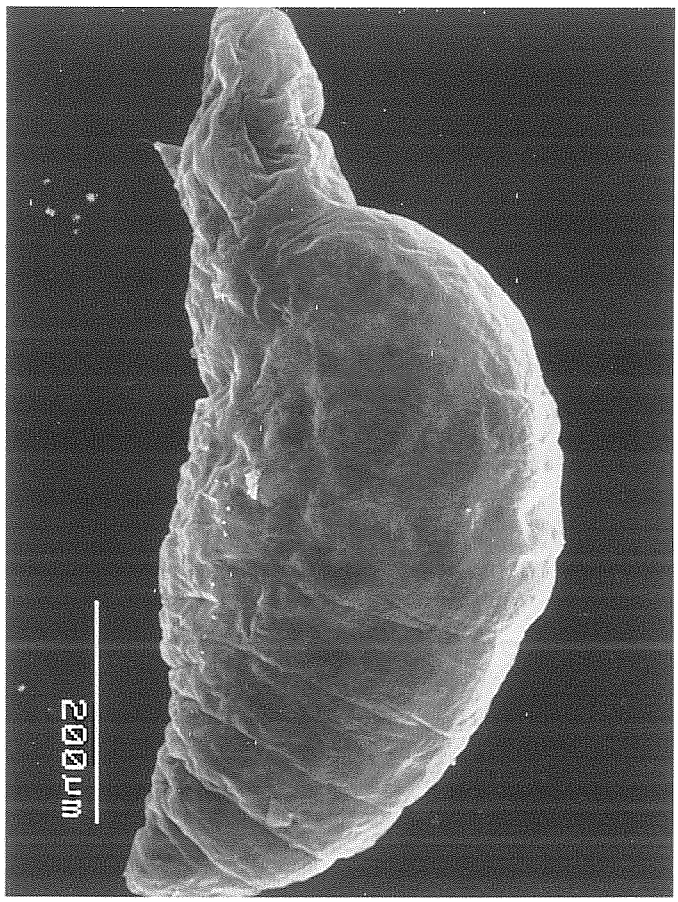

Fig. 1. *Kyphosoma kinabaluense*, adult female in lateral view [88ML-63].

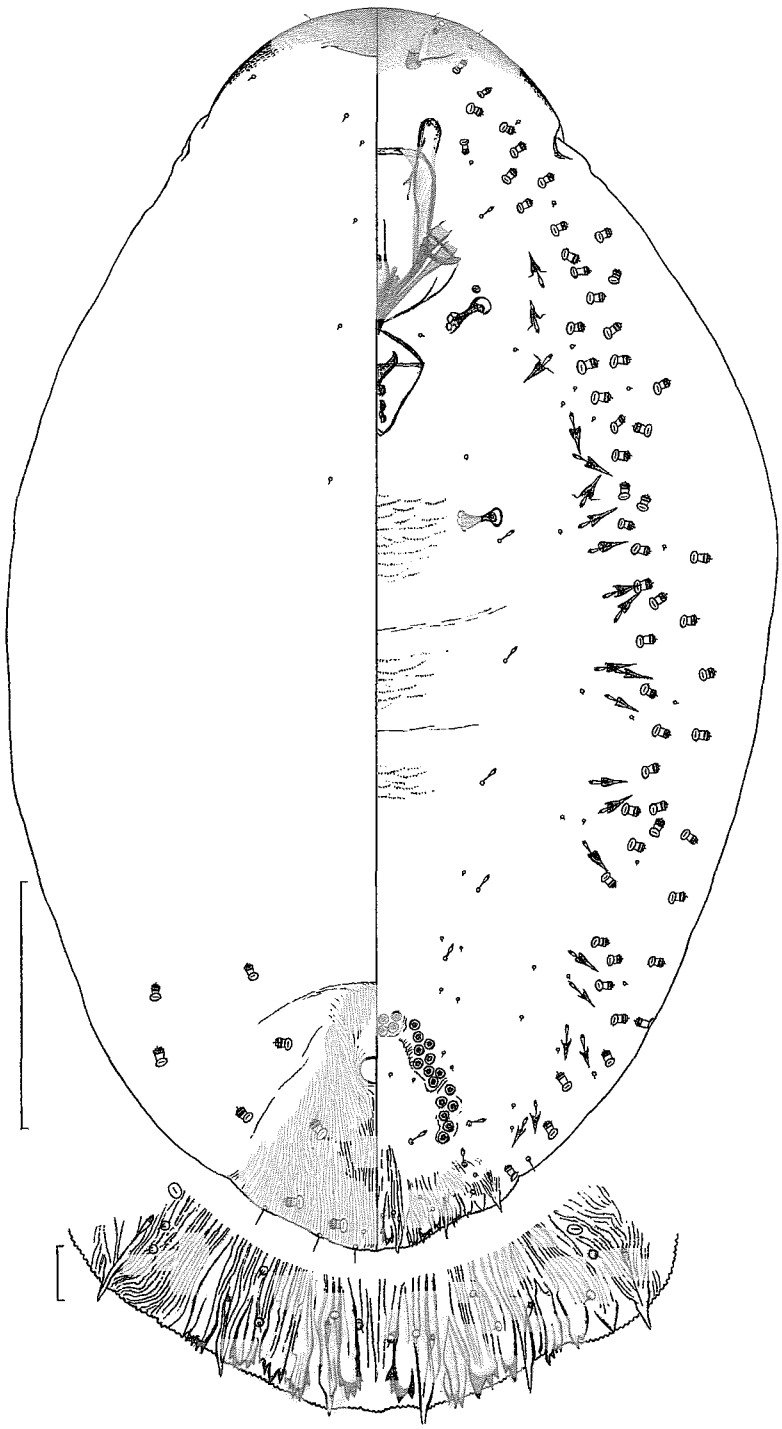

Fig. 2. *Dungunia cnestis*, adult female, body and pygidial margin in ventral view (scale : 0.1 mm for body ; 0.01 mm for pygidial margin).

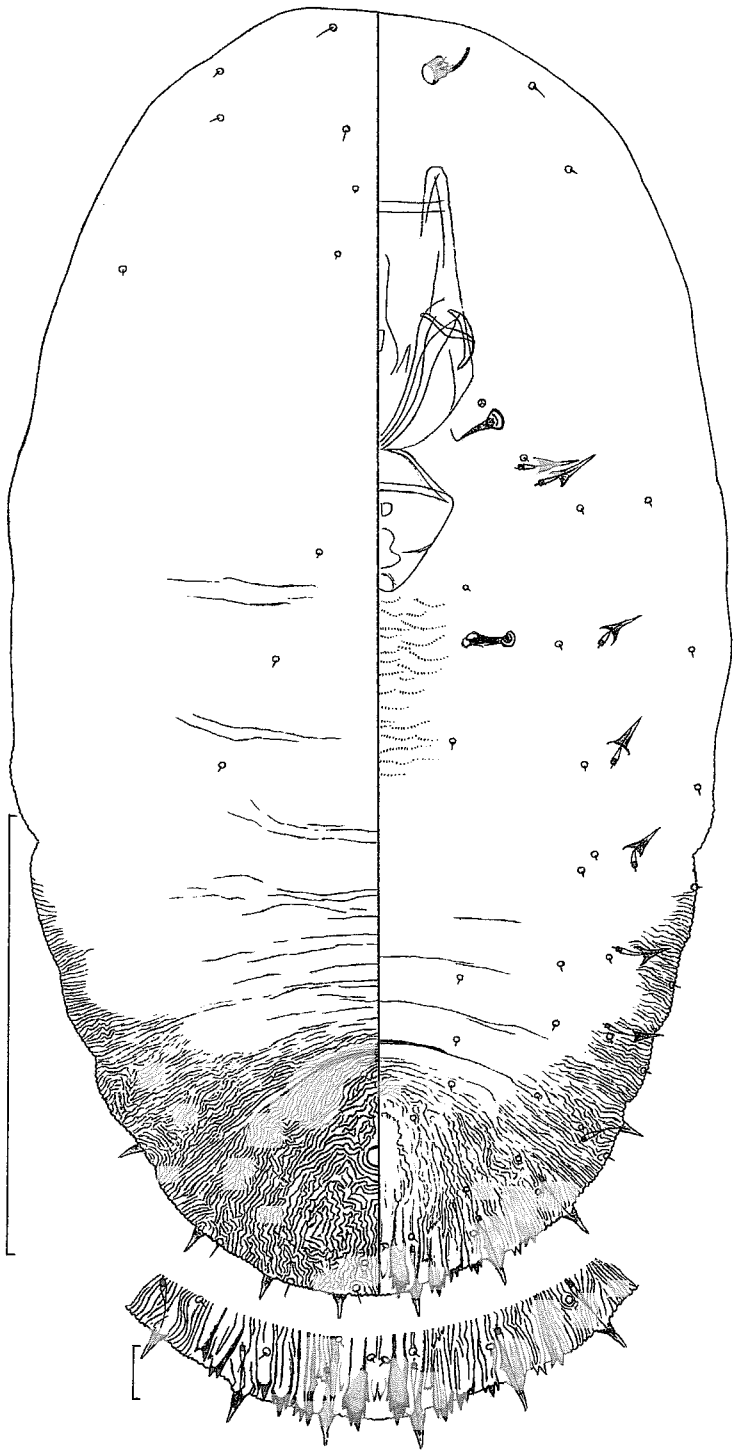

Fig. 3. *Dungunia cnestis*, 2nd instar female, body and pygidial margin in ventral view (scale : 0.1 mm for body : 0.01 mm for pygidial margin).

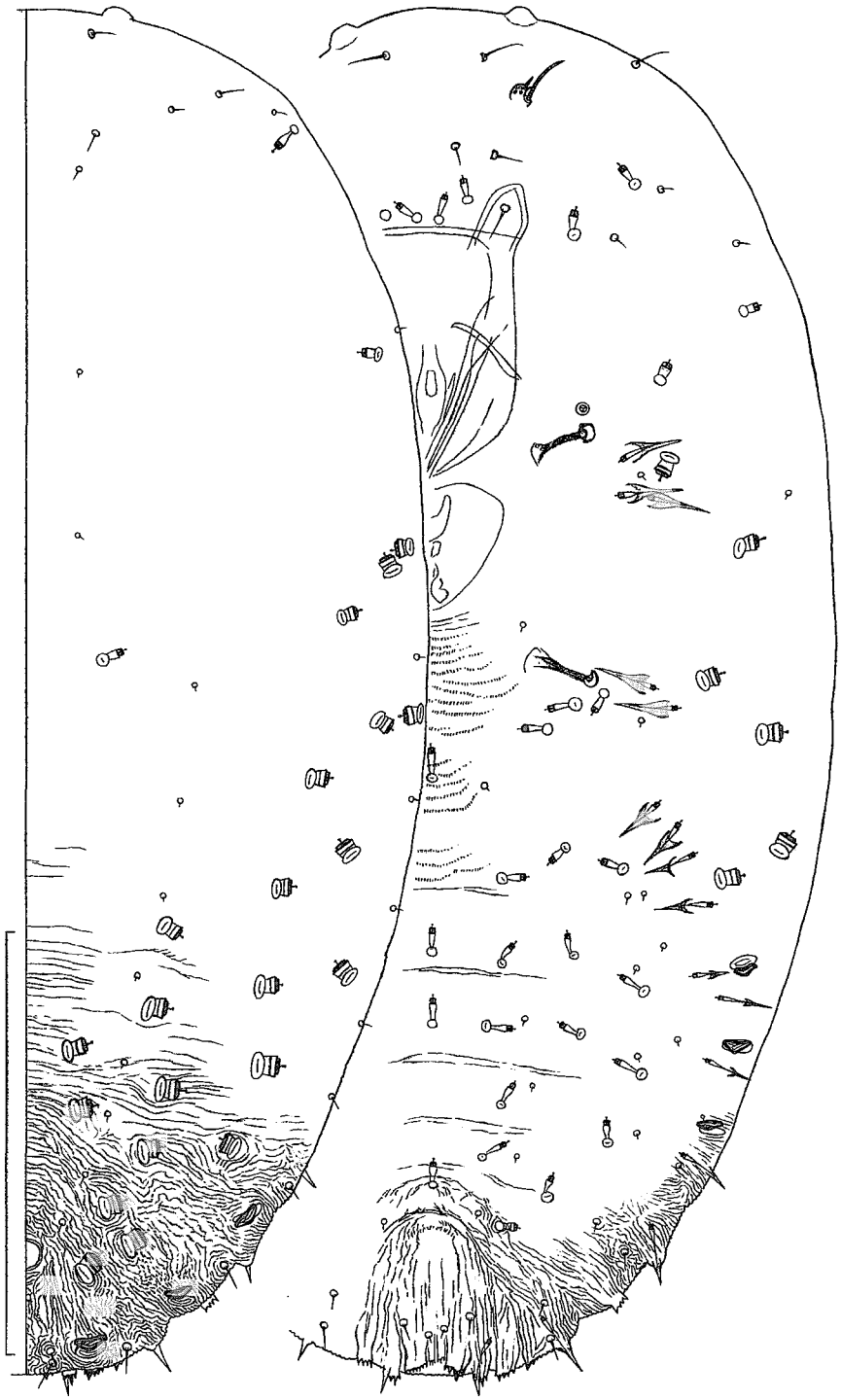

Fig. 4. *Dungunia cnestis*, 2nd instar male, body in dorsal and ventral views (scale: 0.1 mm). (Drawn from a distorted specimen, so that some parts, especially setae on the head, may not be exact.)

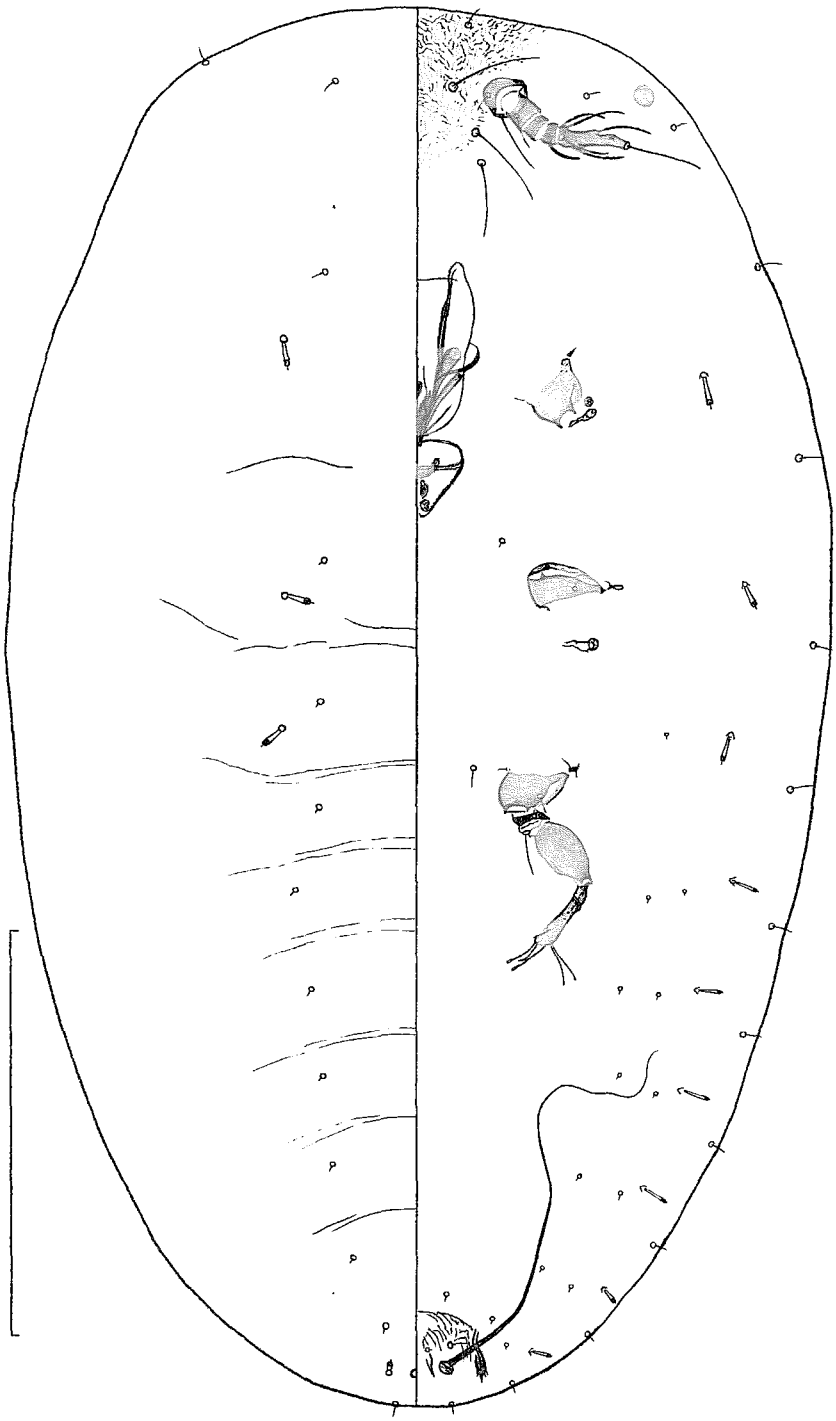

Fig. 5. *Dungunia cnestis*, 1st instar larva (scale : 0.1 mm).

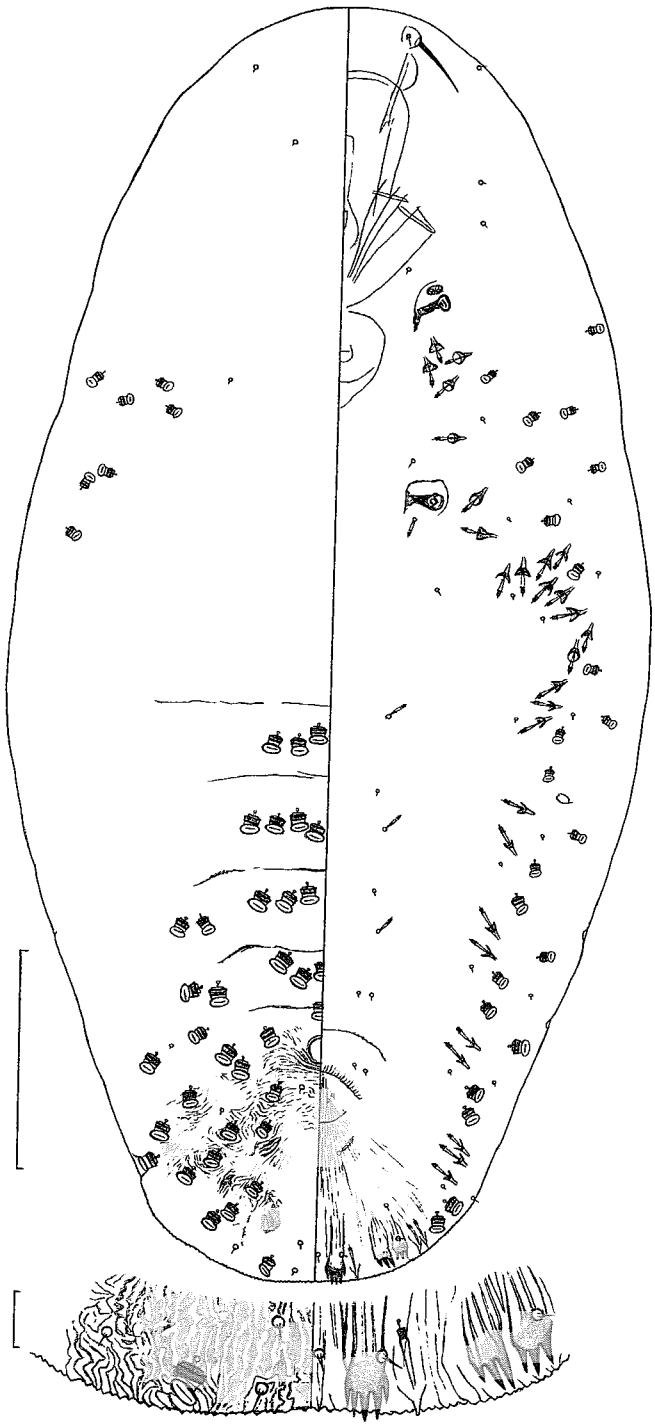

Fig. 6. *Kyphosoma kinabaluense*, adult female, body and pygidial margin (scale : 0.1 mm for body ; 0.01 mm for pygidial margin) [88ML-43]. (Drawn from an immature adult female, which is not much swollen dorsally.)

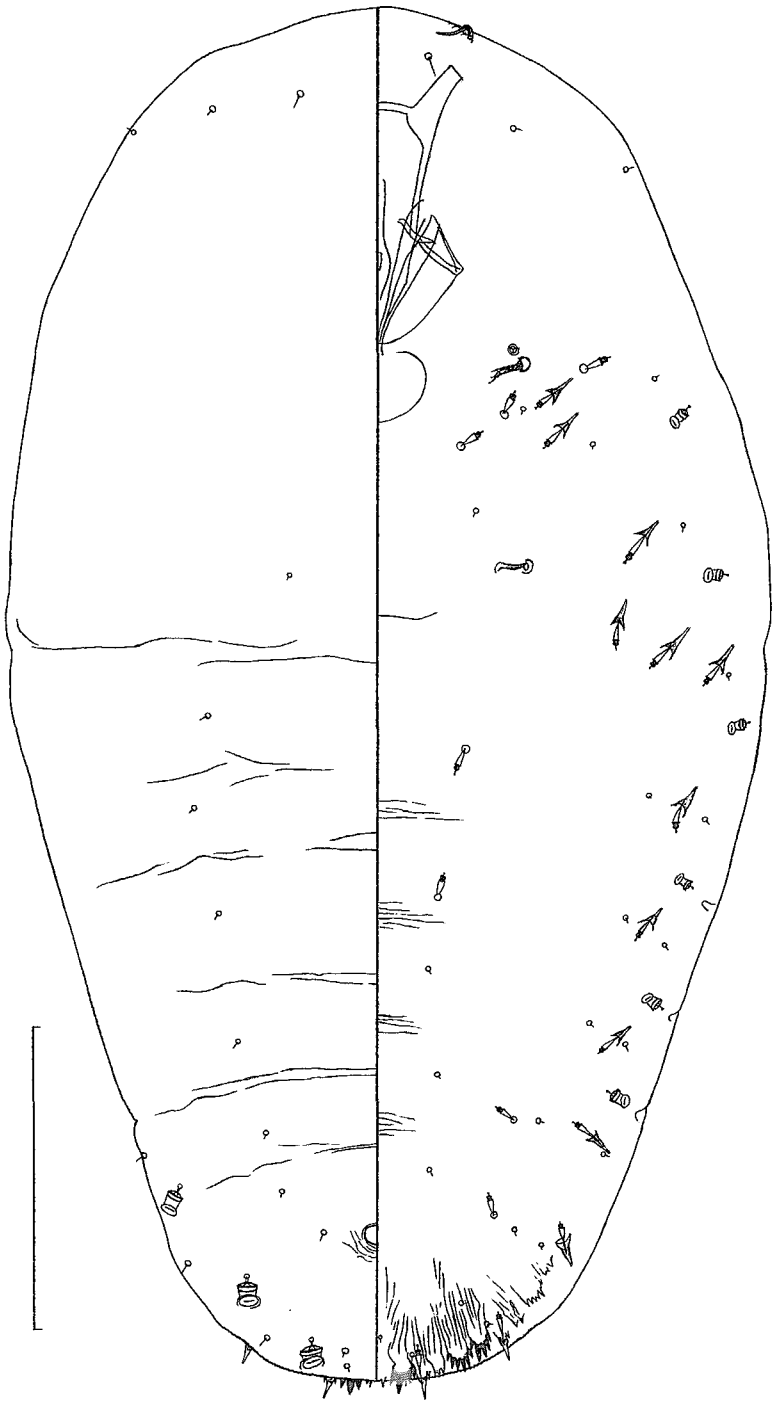

Fig. 7. *Kyphosoma kinabaluense*, 2nd instar female (scale: 0.1 mm) [88ML-43].

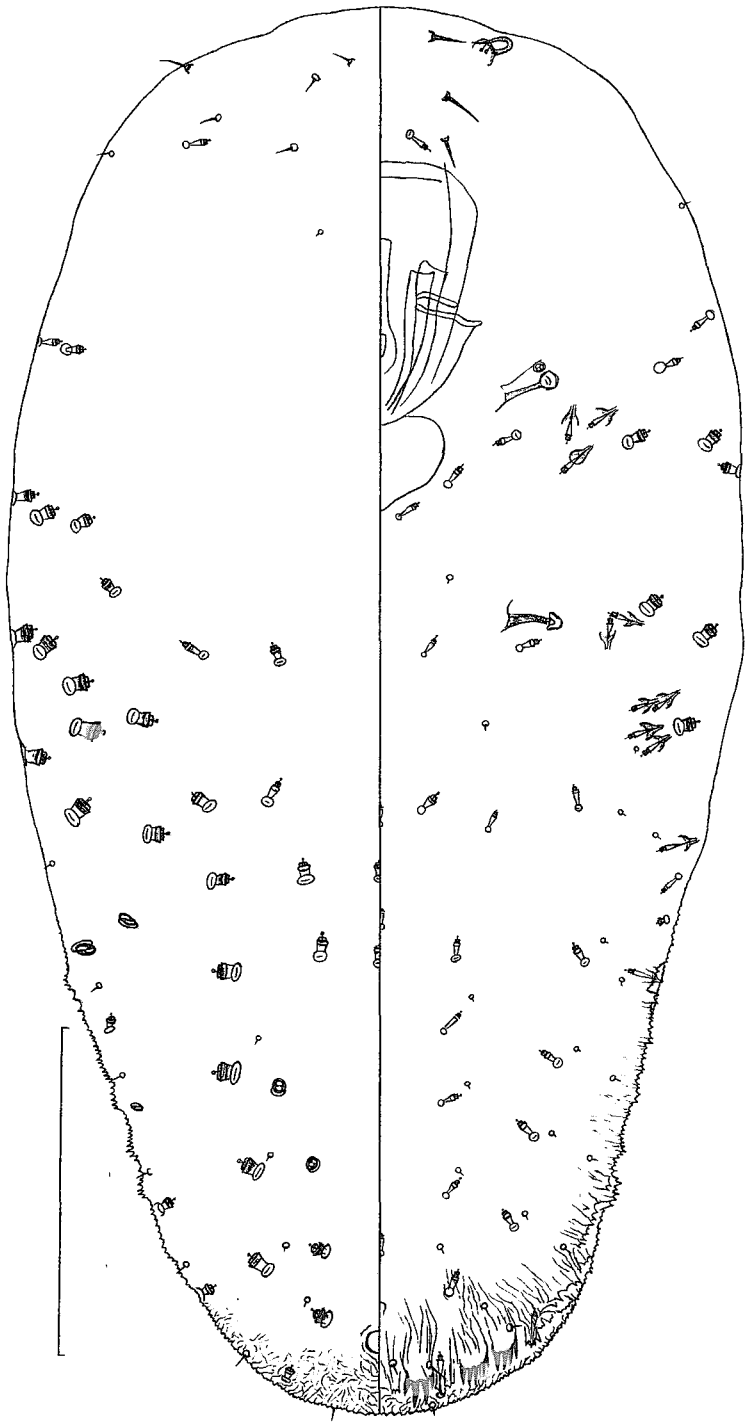

Fig. 8. *Kyphosoma kinabaluense*, 2nd instar male (scale: 0.1 mm) [88ML-43].

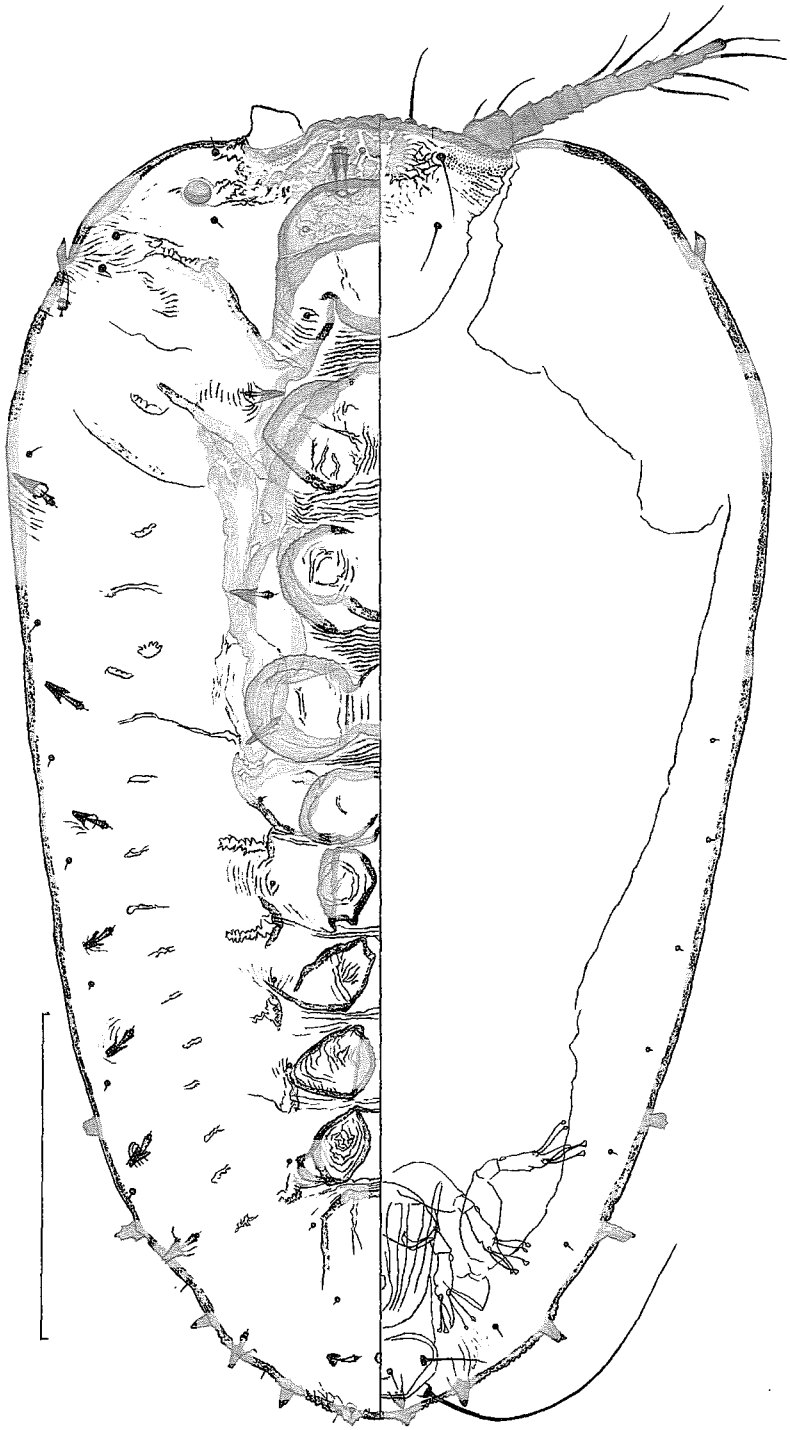

Fig. 9. *Kyphosoma kinabaluense*, 1st instar female exuvial cast (scale: 0.1 mm) [88ML-43].

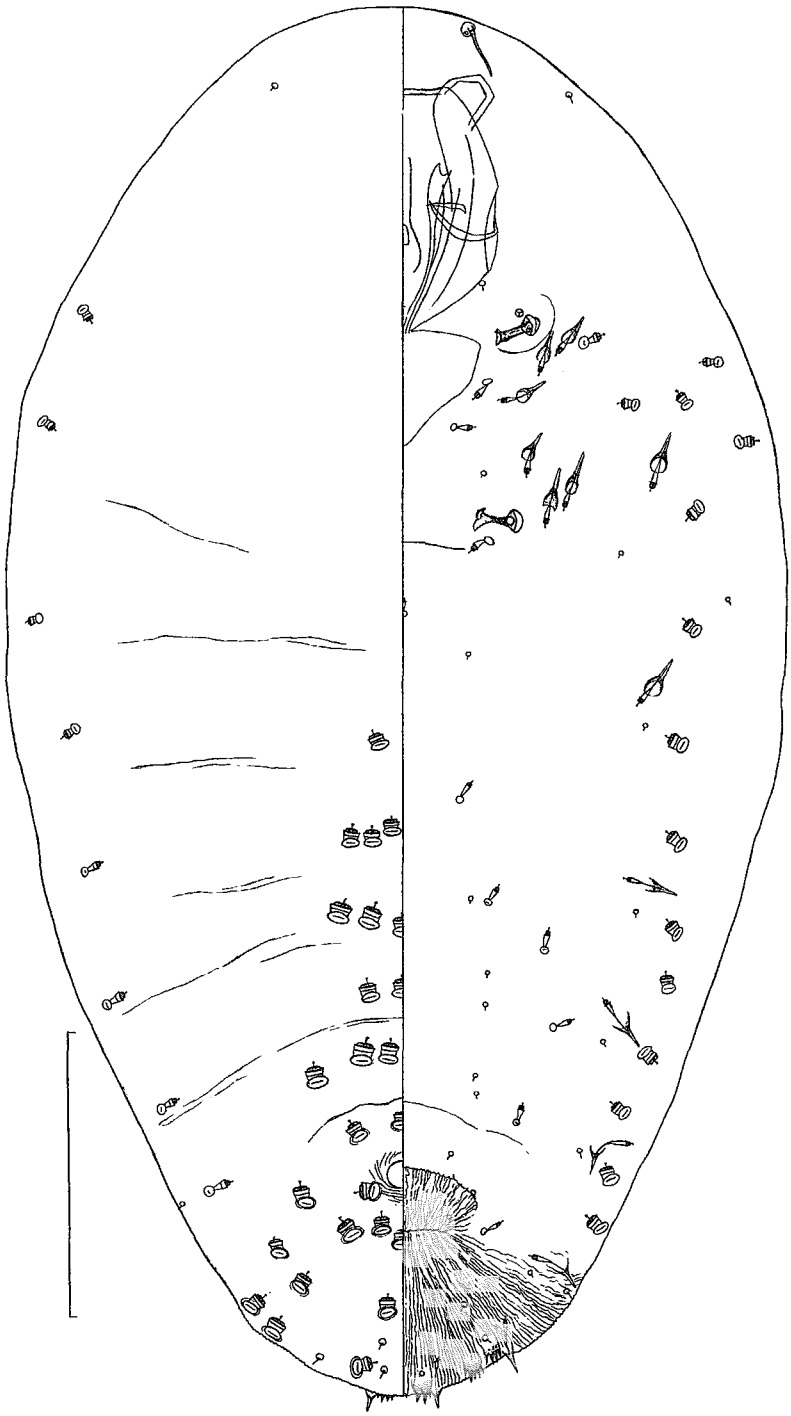

Fig. 10. *Kyphosoma pinosukense*, adult female (scale: 0.1 mm). (Drawn from an immature adult female, which is not much swollen dorsally.)

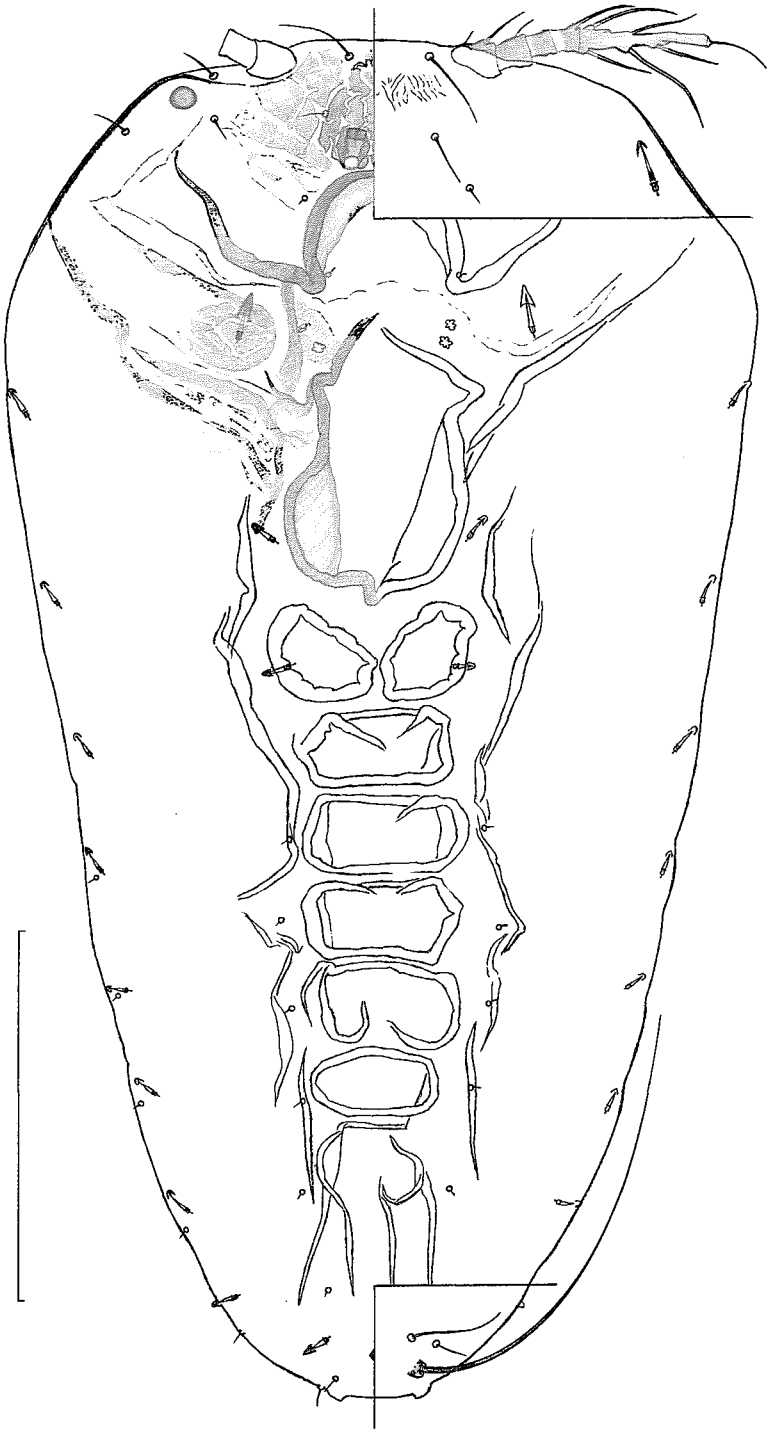

Fig. 11. *Kyphosoma pinosukense*, 1st instar female exuvial cast (scale : 0.1 mm).

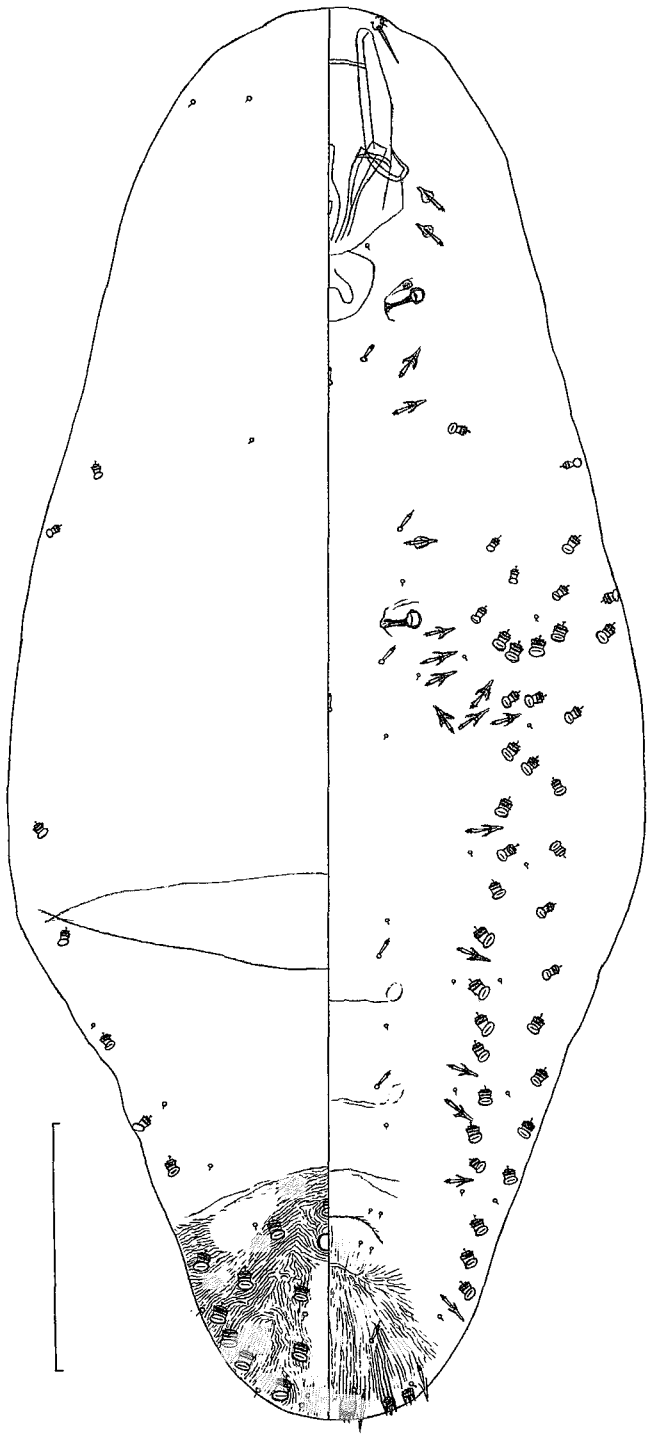

Fig. 12. *Kyphosoma melayuense*, adult female (scale : 0.1 mm) [86ML-116]. (Drawn from an immature adult female, which is not much swollen dorsally.)

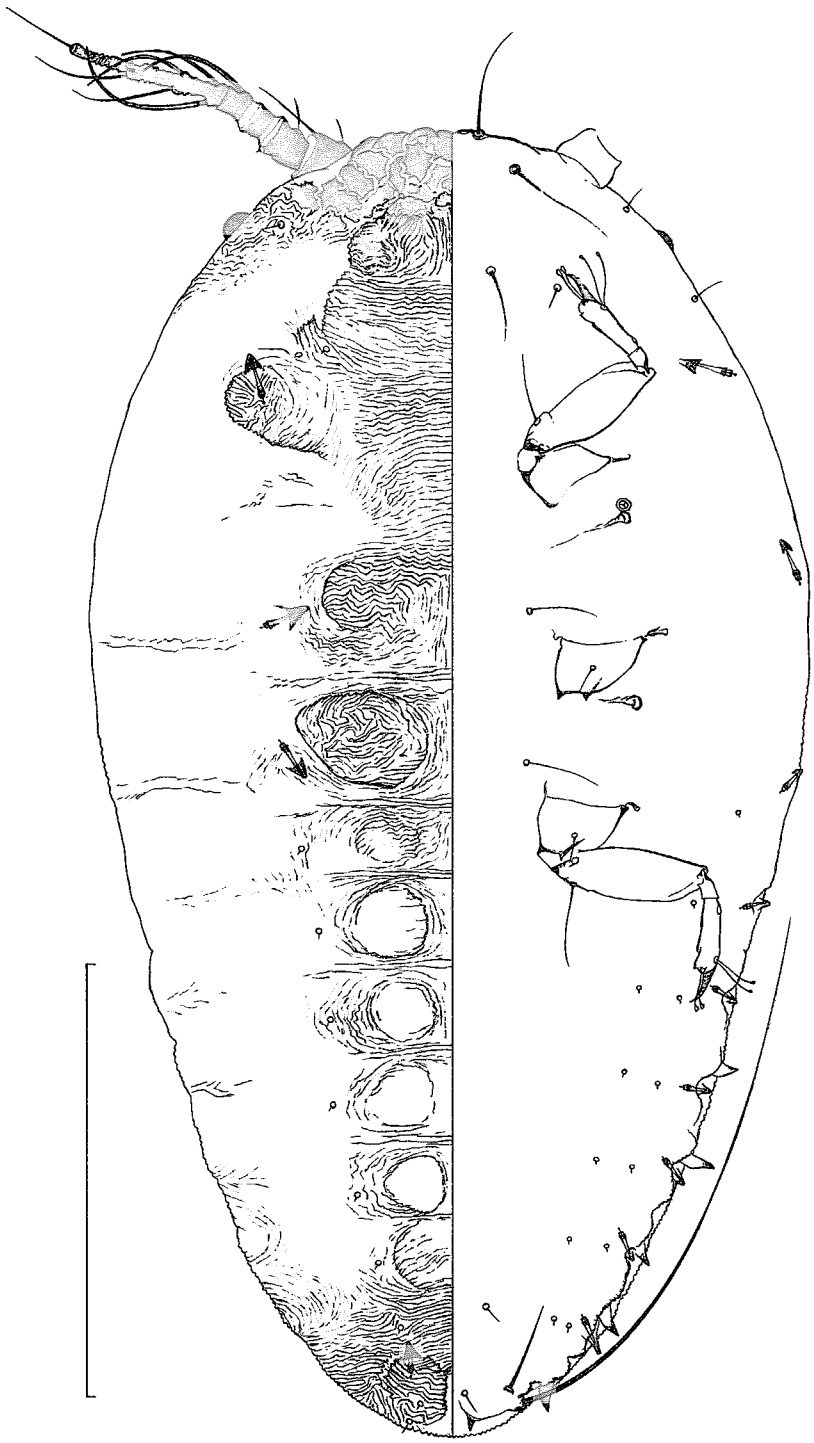

Fig. 13. *Kyphosoma melayuense*, 1st instar male (scale : 0.1 mm) [91ML-374].

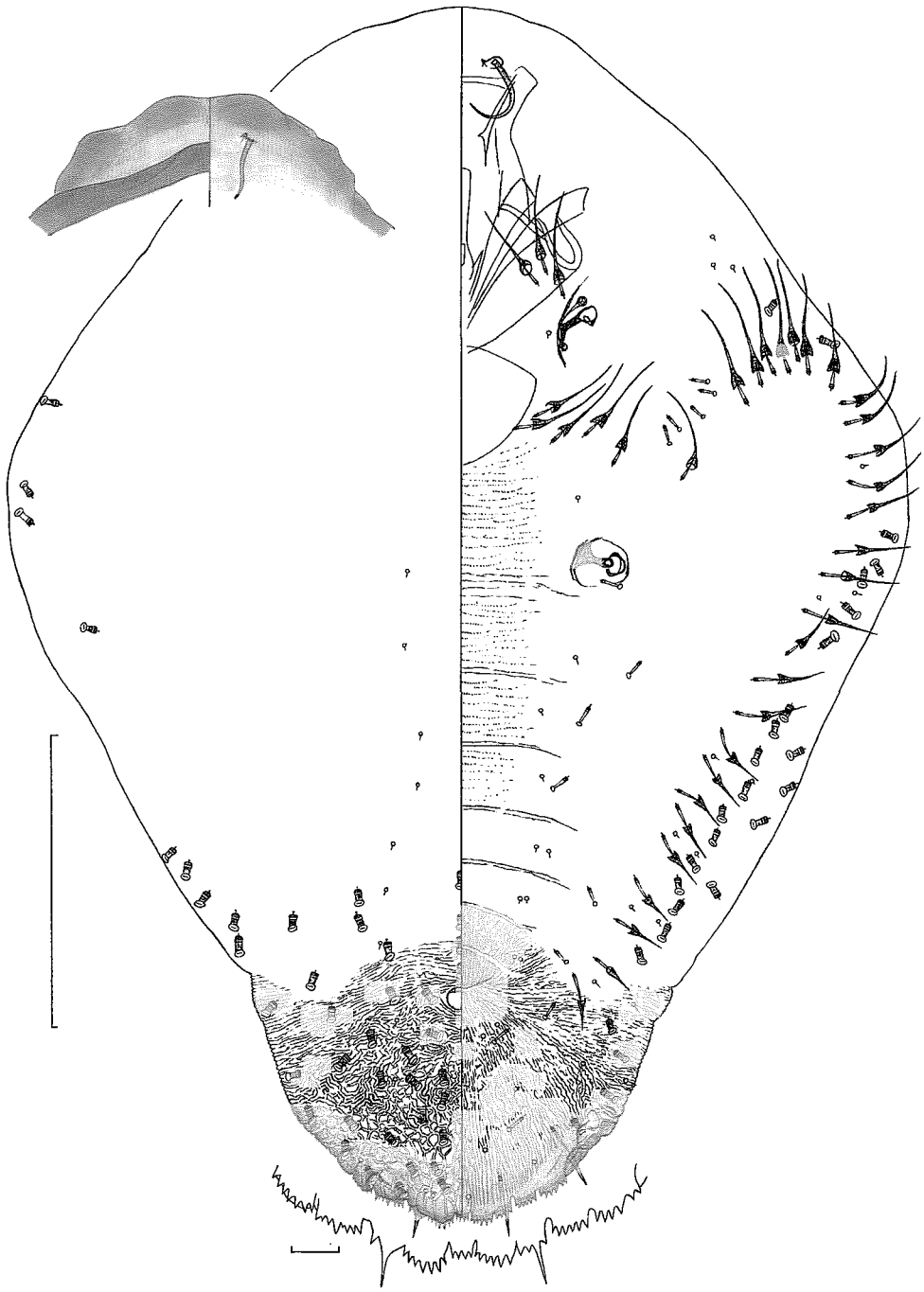

Fig. 14. *Pentacicola spinosus*, adult female, body, head and pygidial margin (scale: 0.1 mm for body; 0.01 mm for pygidial margin). (Body and pygidial margin are drawn from an immature adult female; head from a full-grown specimen.)

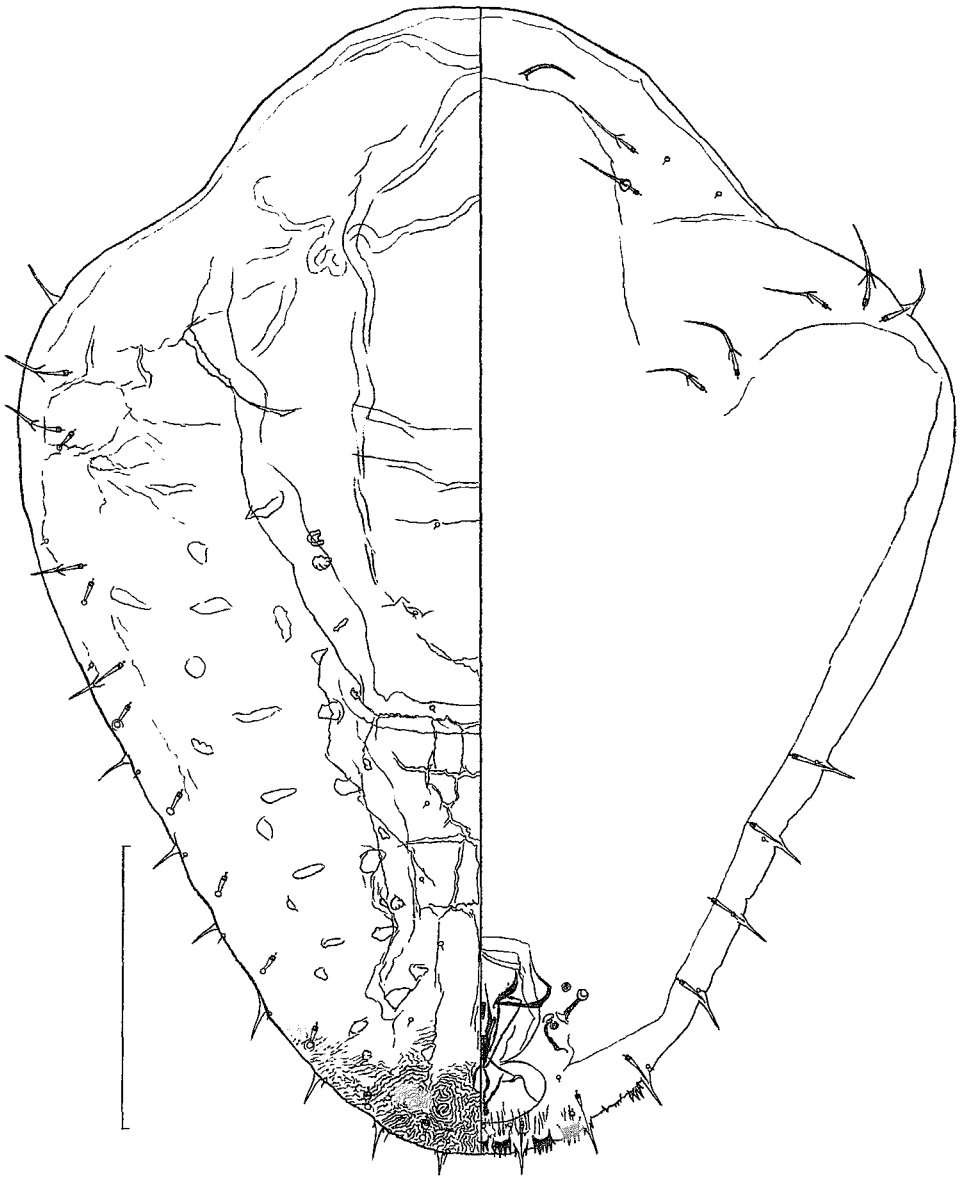

Fig. 15. *Pentacicola spinosus*, 2nd instar female exuvial cast (scale : 0.1 mm).

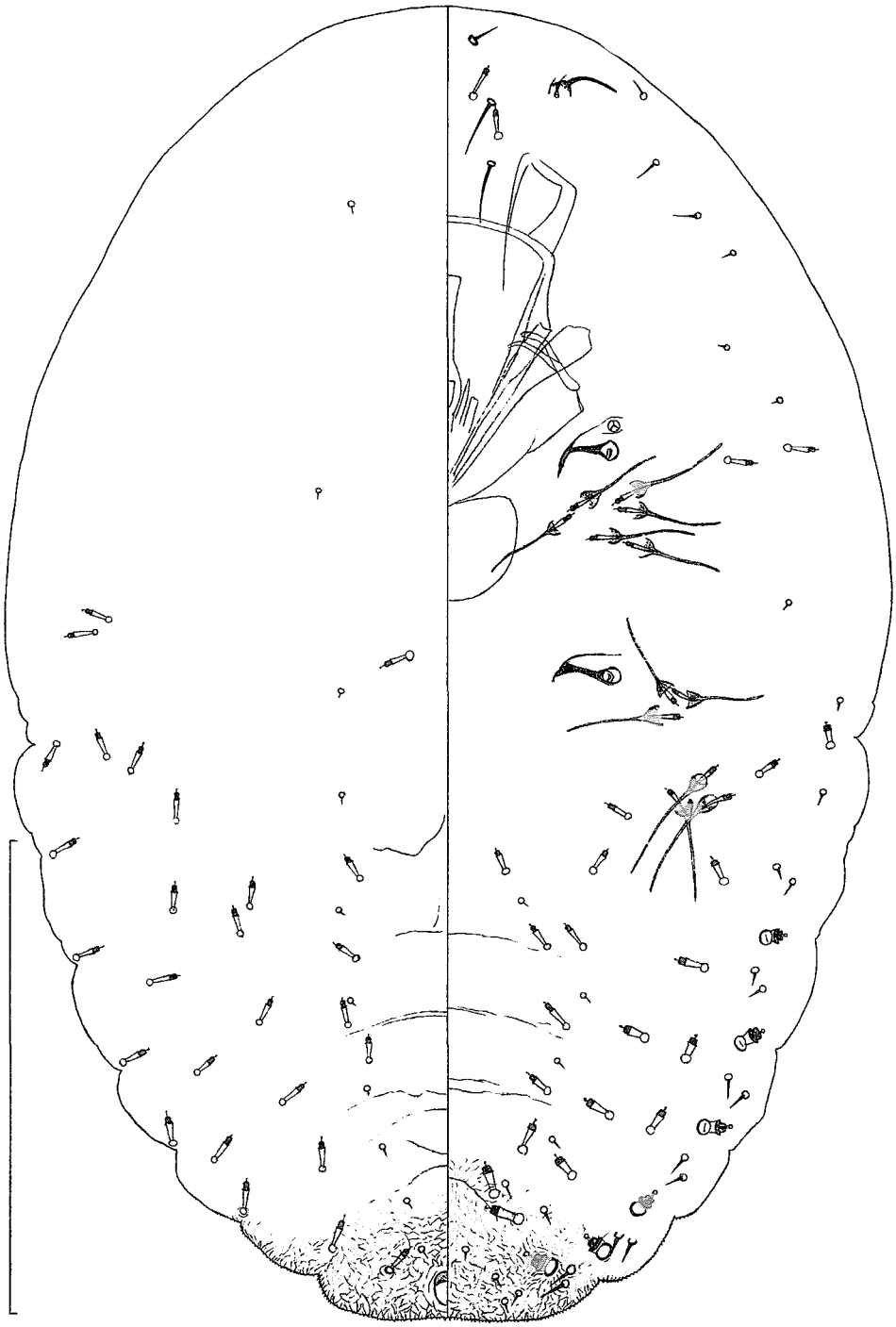

Fig. 16. *Pentacicola spinosus*, 2nd instar male (scale : 0.1 mm).

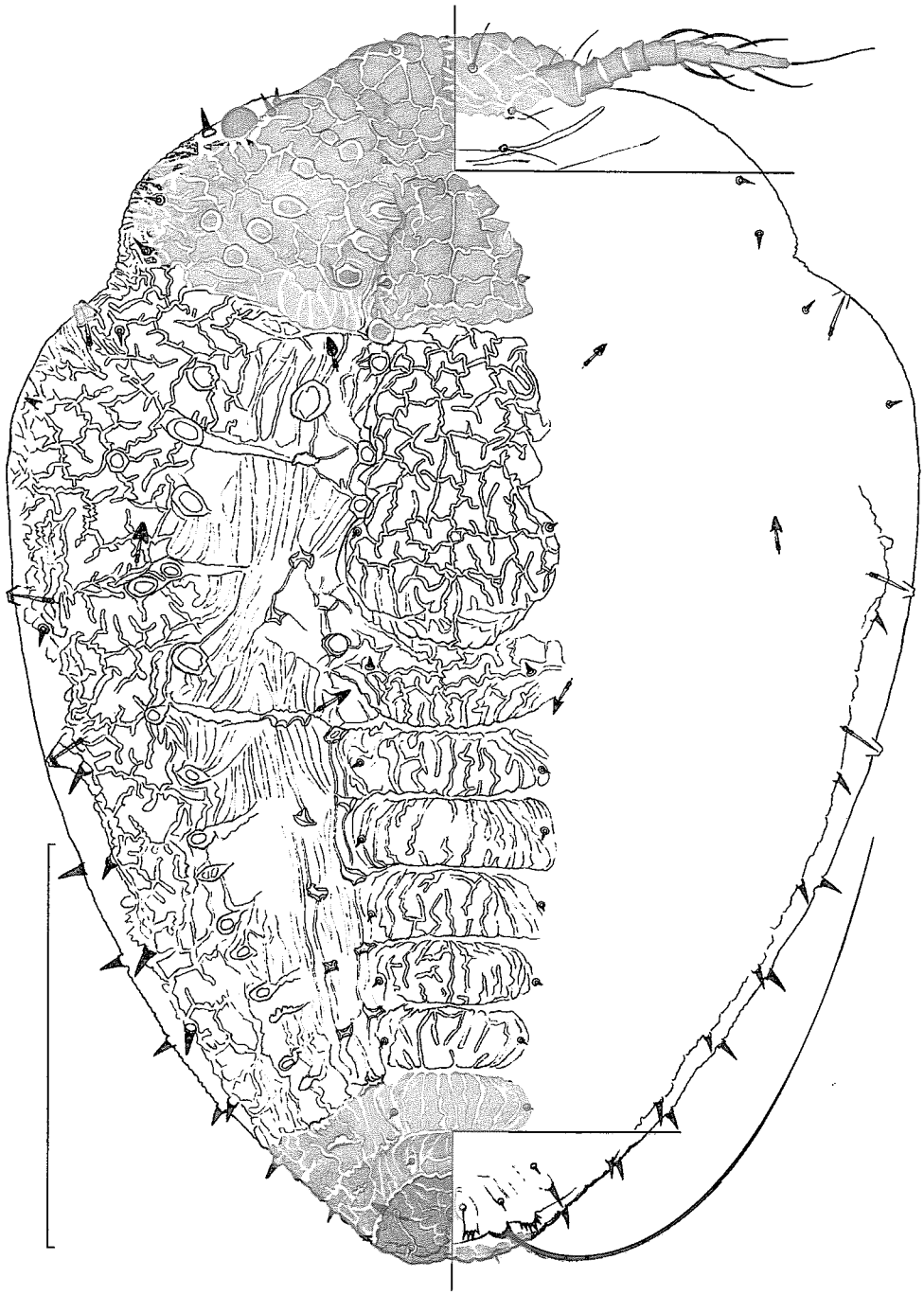

Fig. 17. *Pentacicola spinosus*, 1st instar female exuvial cast (scale : 0.1 mm).

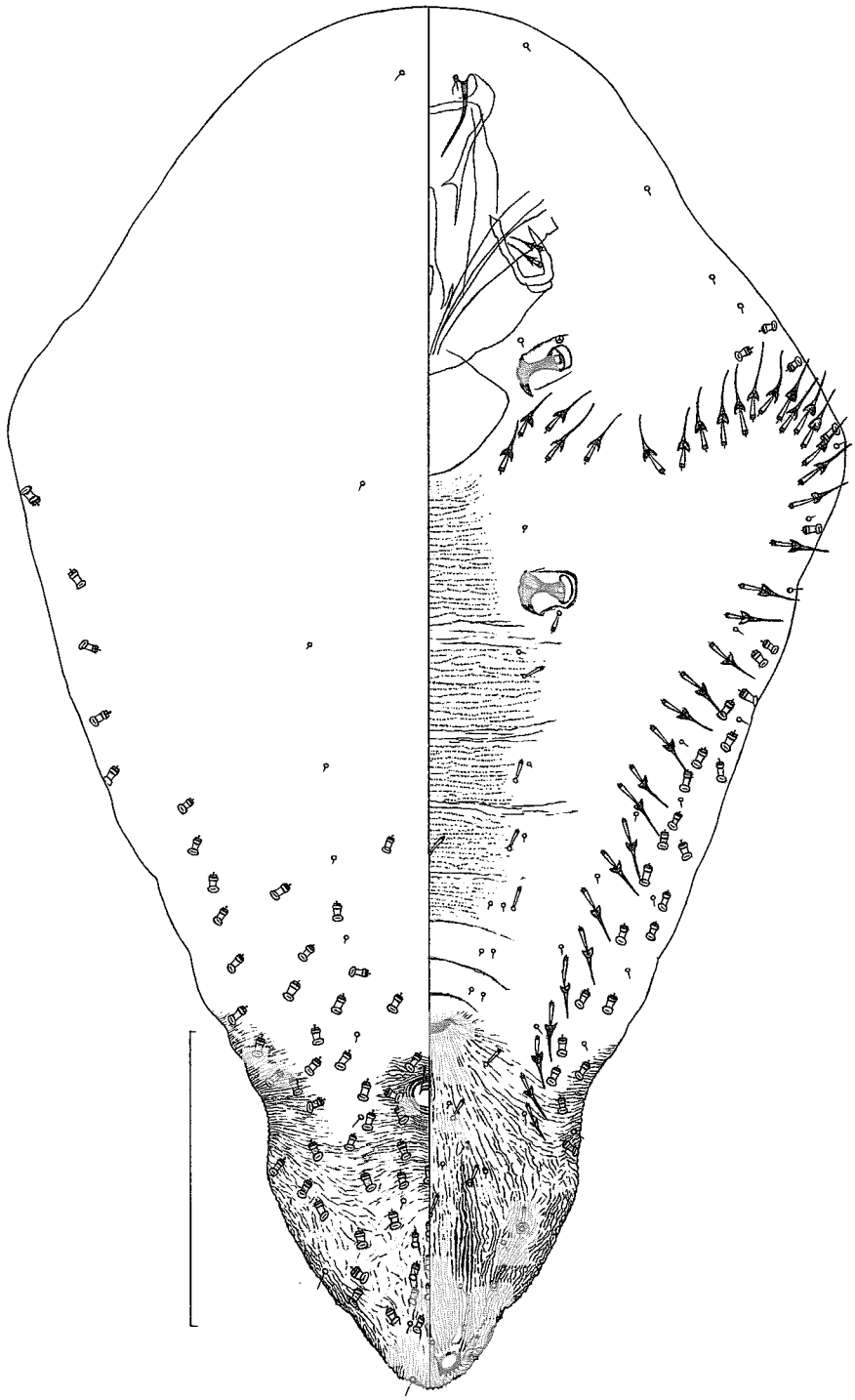

Fig. 18. *Pentacicola fimbriatus*, adult female (scale: 0.1 mm) [86ML-413]. (Drawn from an immature adult female.)

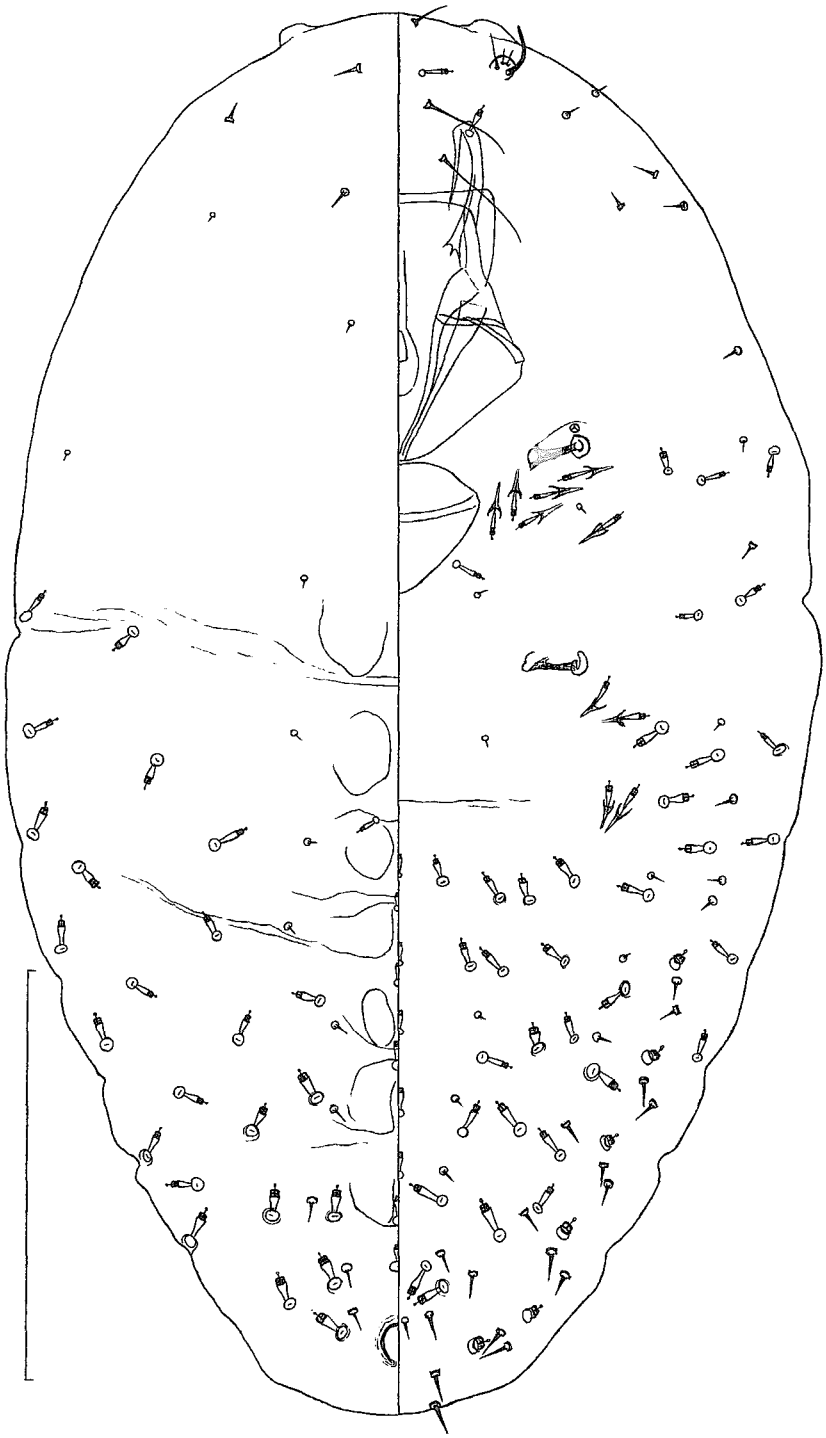

Fig. 19. *Pentacicola fimbriatus*, 2nd instar male (scale : 0.1 mm) [86ML-413].

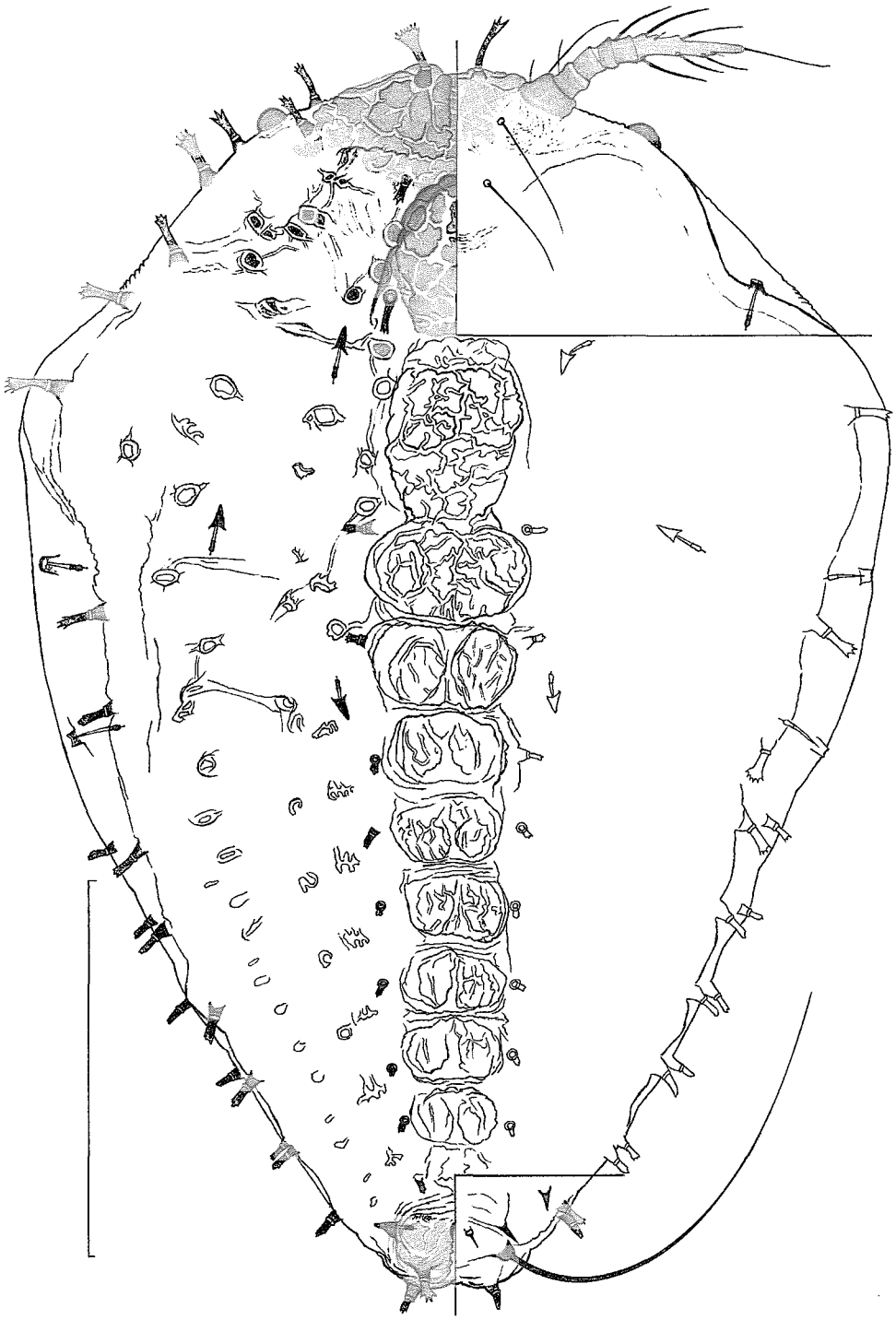

Fig. 20. *Pentacicola fimbriatus*, 1st instar female exuvial cast (scale : 0.1 mm) [90ML-23].

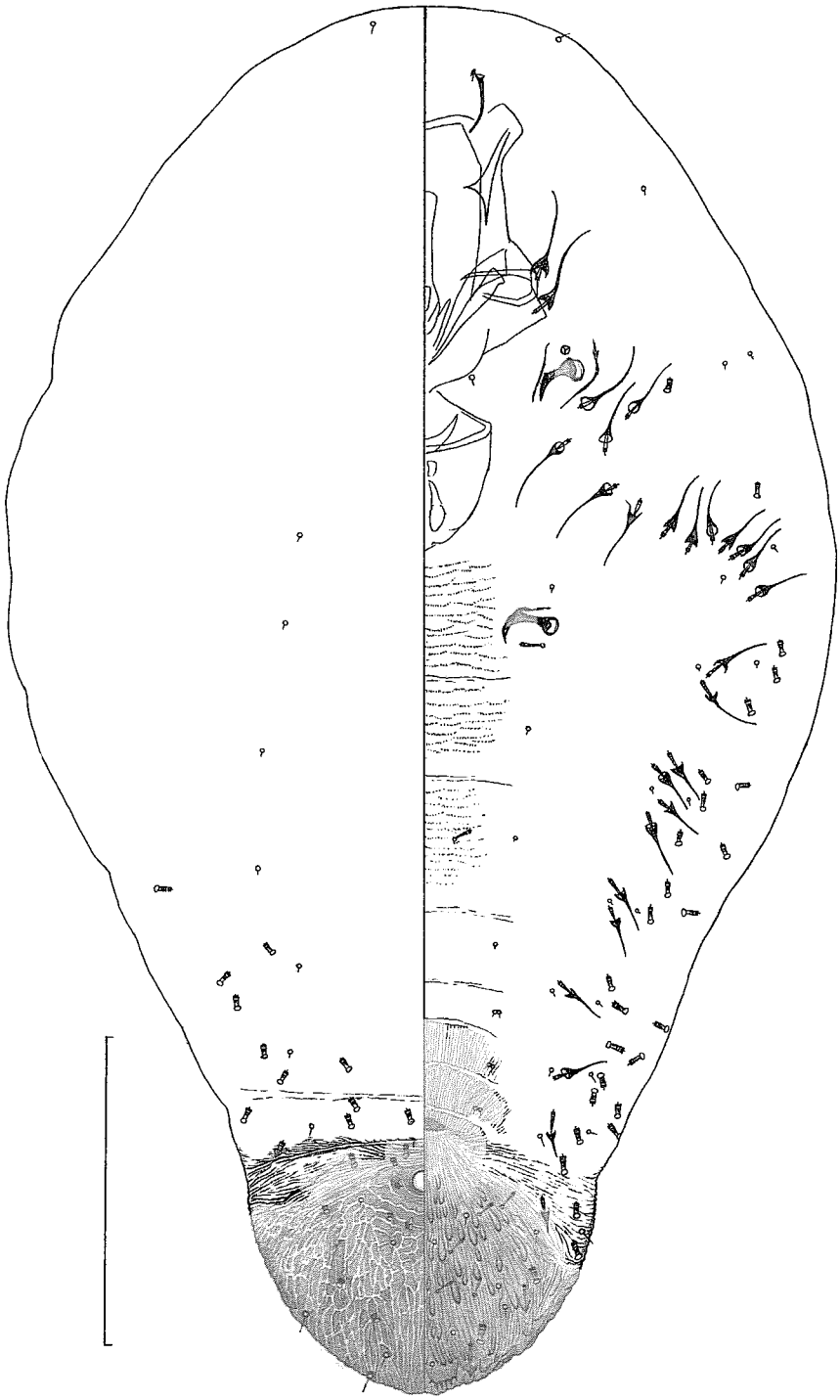

Fig. 21. *Pentacicola echinatus*, adult female (scale : 0.1 mm). (Drawn from an immature adult female.)

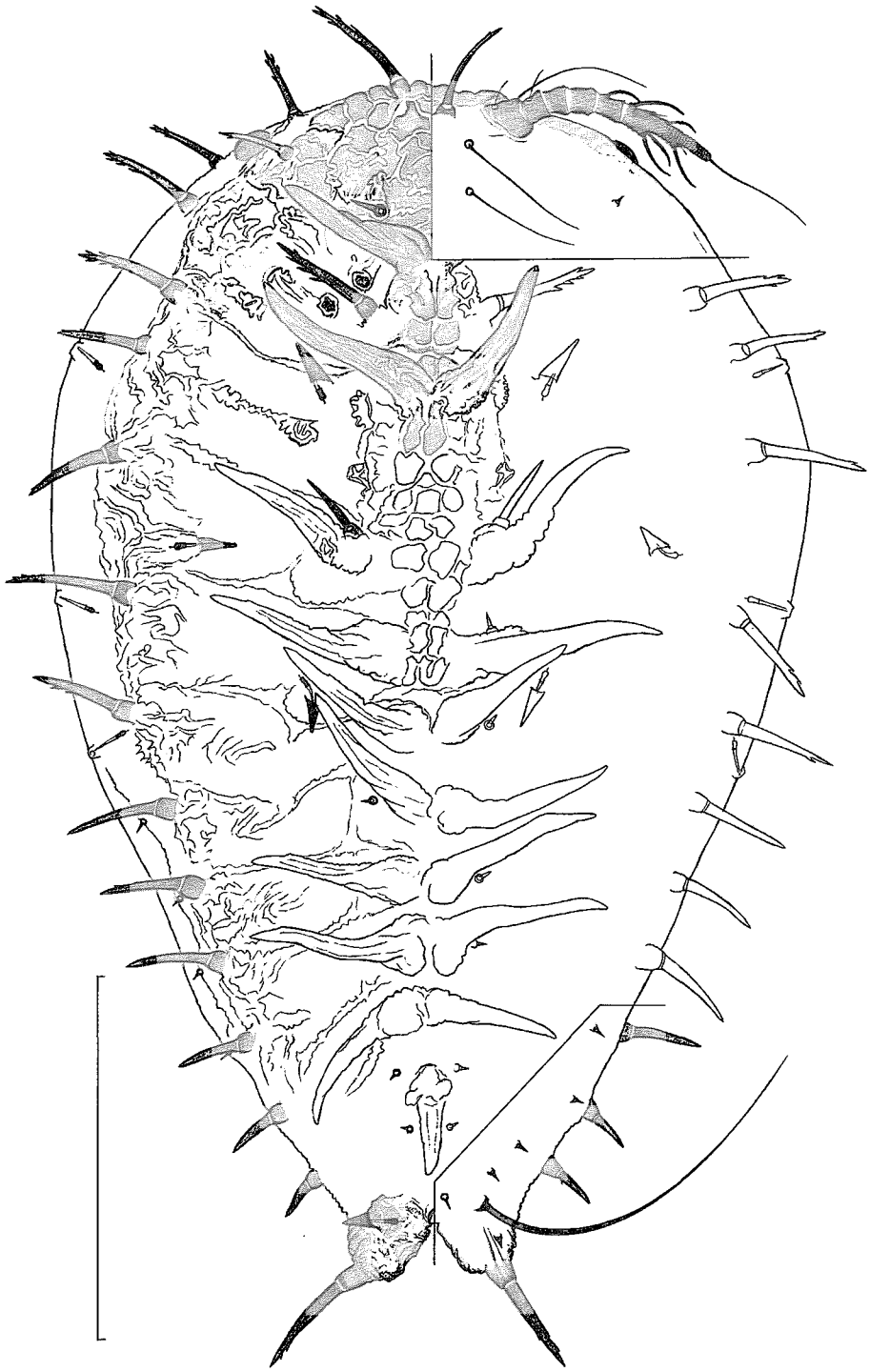

Fig. 22. *Pentacicola echinatus*, 1st instar female exuvial cast (scale : 0.1 mm).

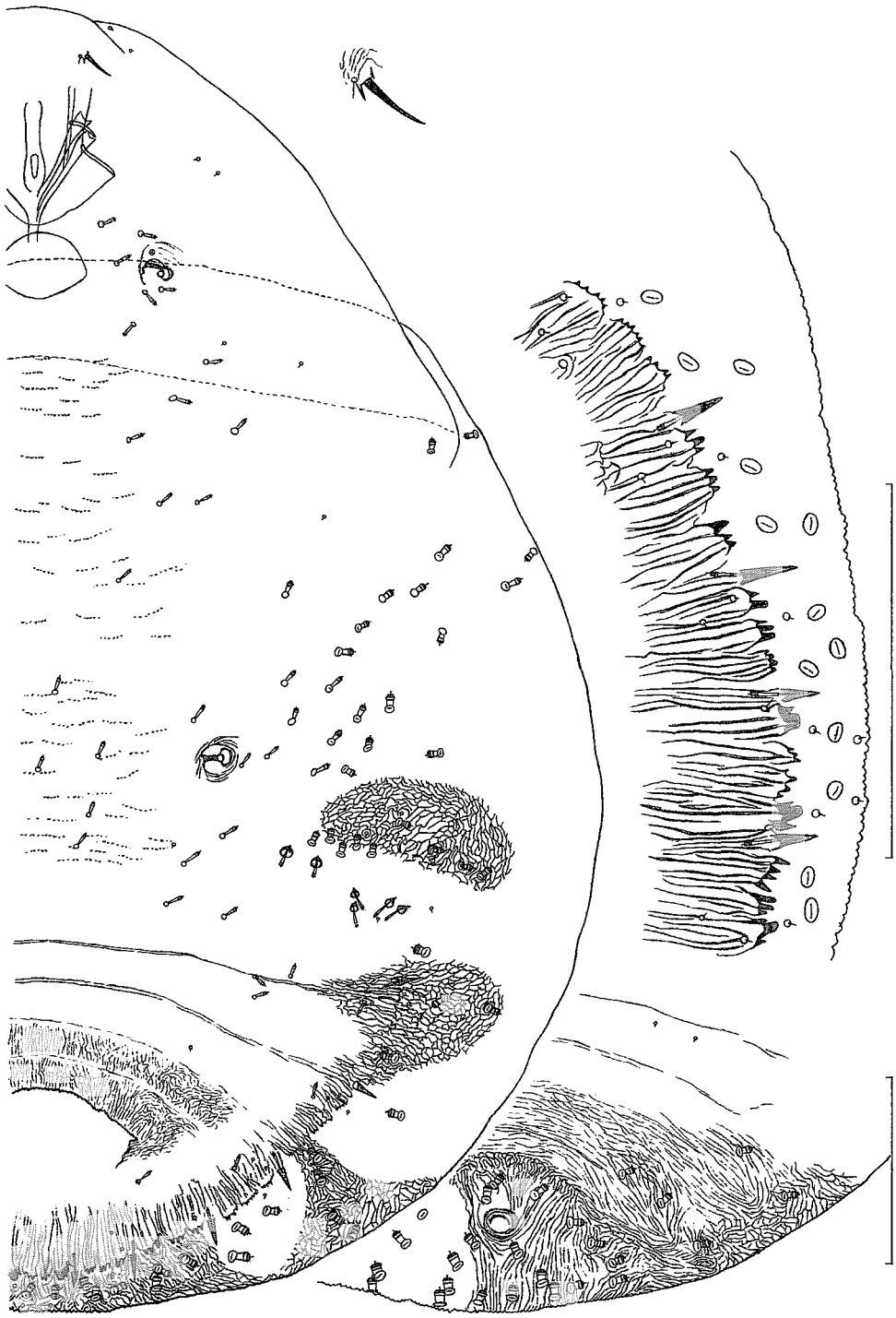

Fig. 23. *Thoa lophopetali*, adult female, body in ventral view, pygidium in dorsal view, pygidial margin in ventral view and antenna (scales: 0.1 mm).

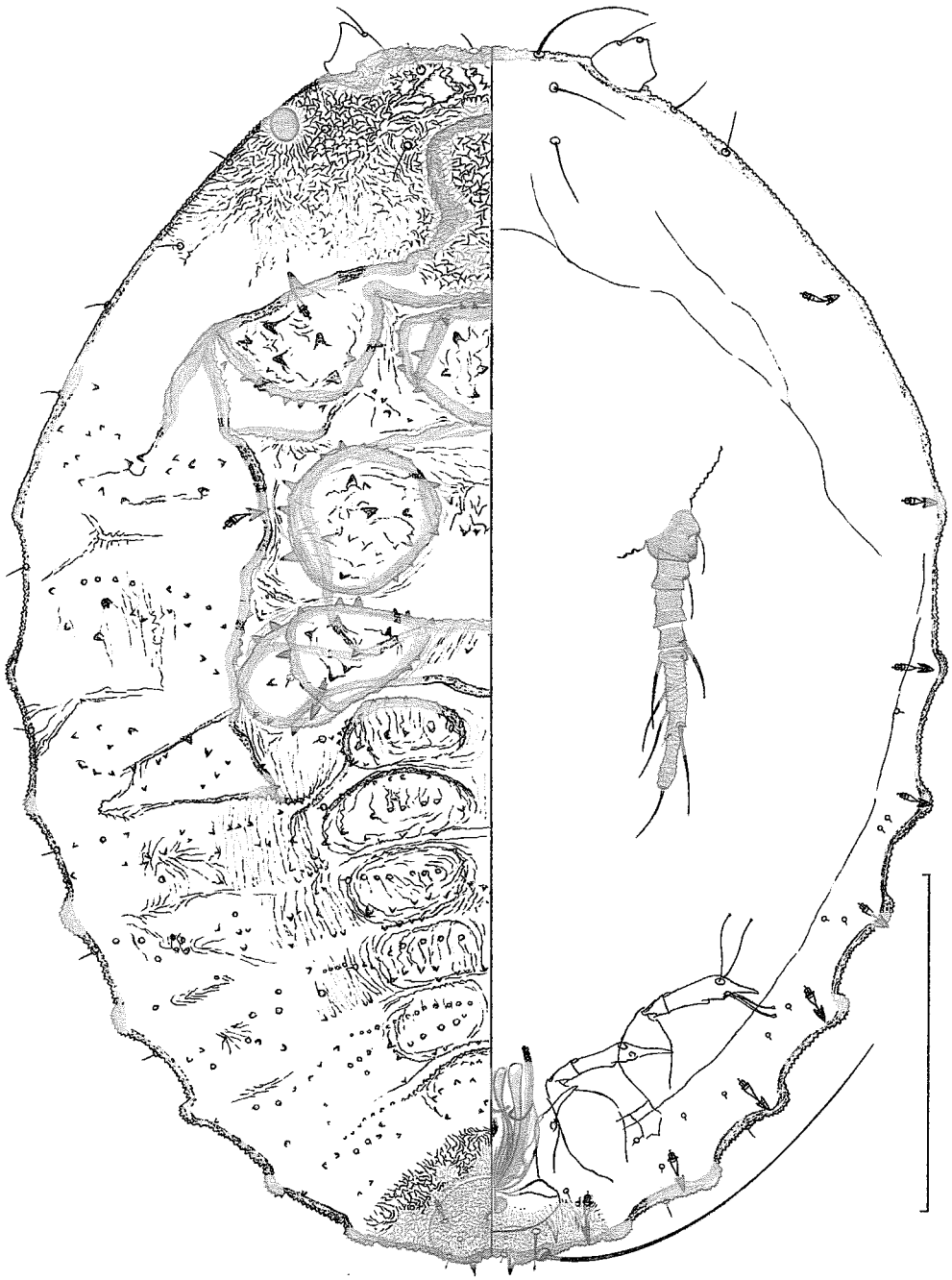

Fig. 24. *Thoa lophopetali*, 1st instar female exuvial cast (scale: 0.1 mm). (Antenna drawn from another specimen.)

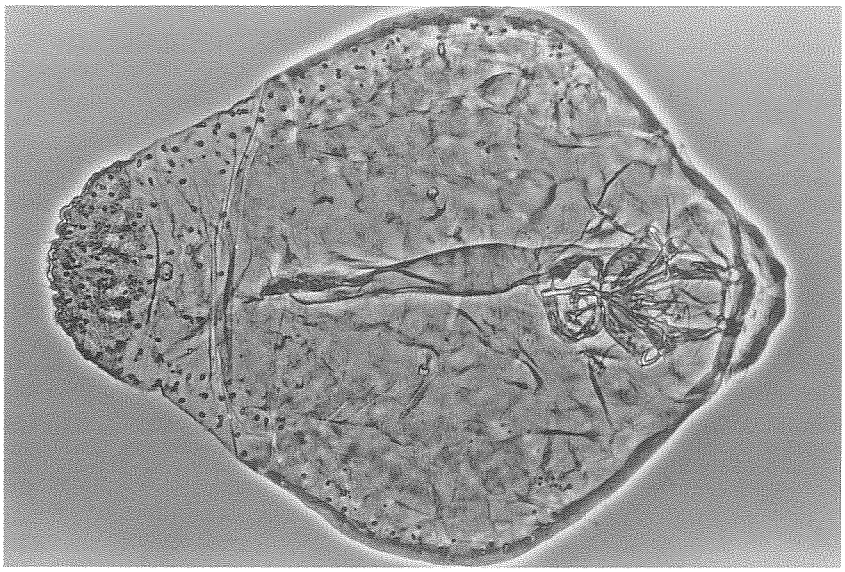

Fig. 25. *Pentacicola spinosus*, adult female, a full-grown specimen.

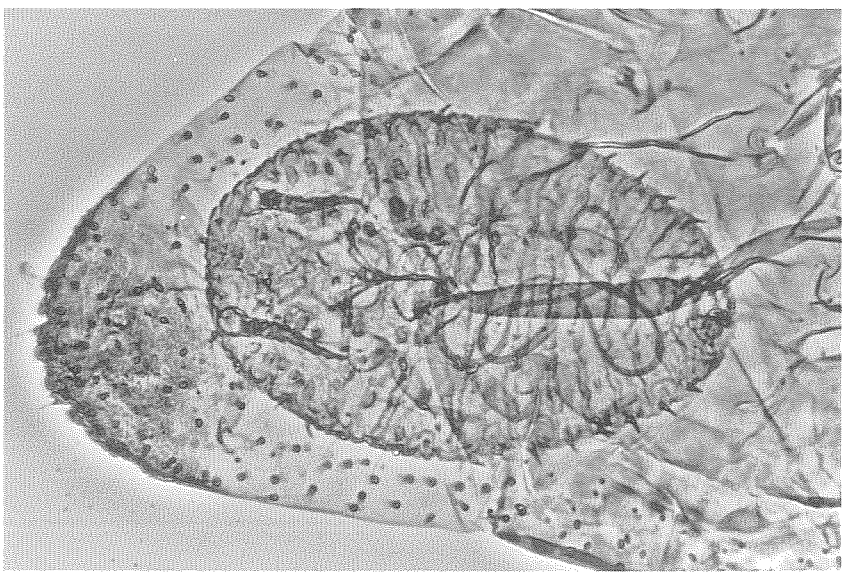

Fig. 26. *Pentacicola spinosus*, abdomen of adult female having a completed embryo within.

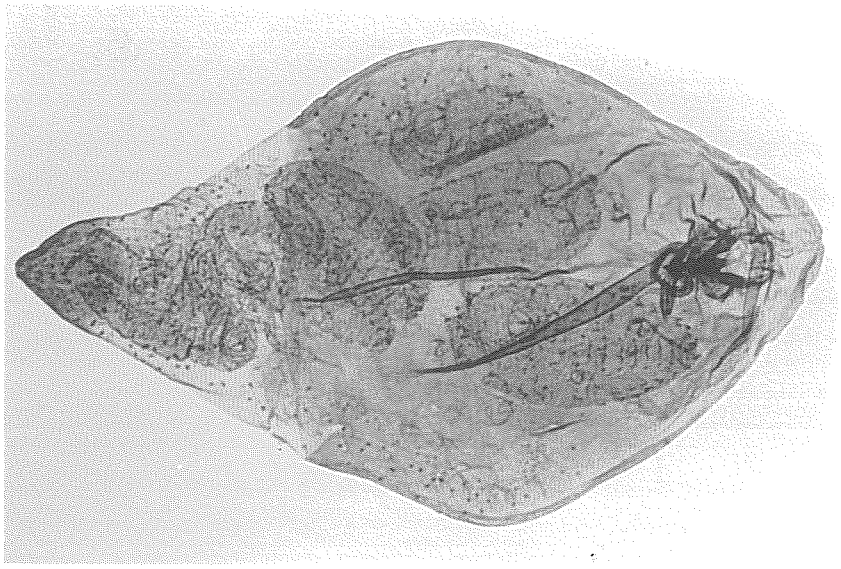

Fig. 27. *Pentacicola fimbriatus*, adult female, a full-grown specimen [86ML-413].

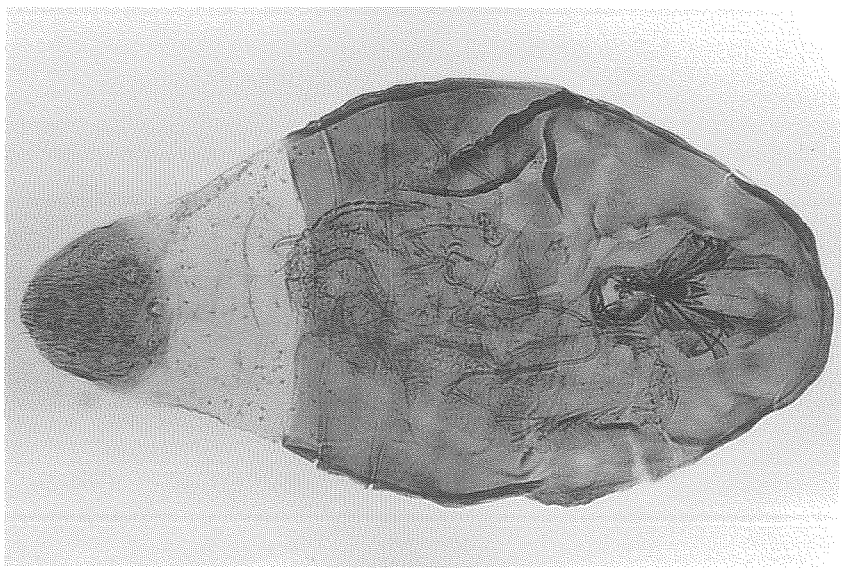

Fig. 28. *Pentacicola echinatus*, adult female, a full-grown specimen.

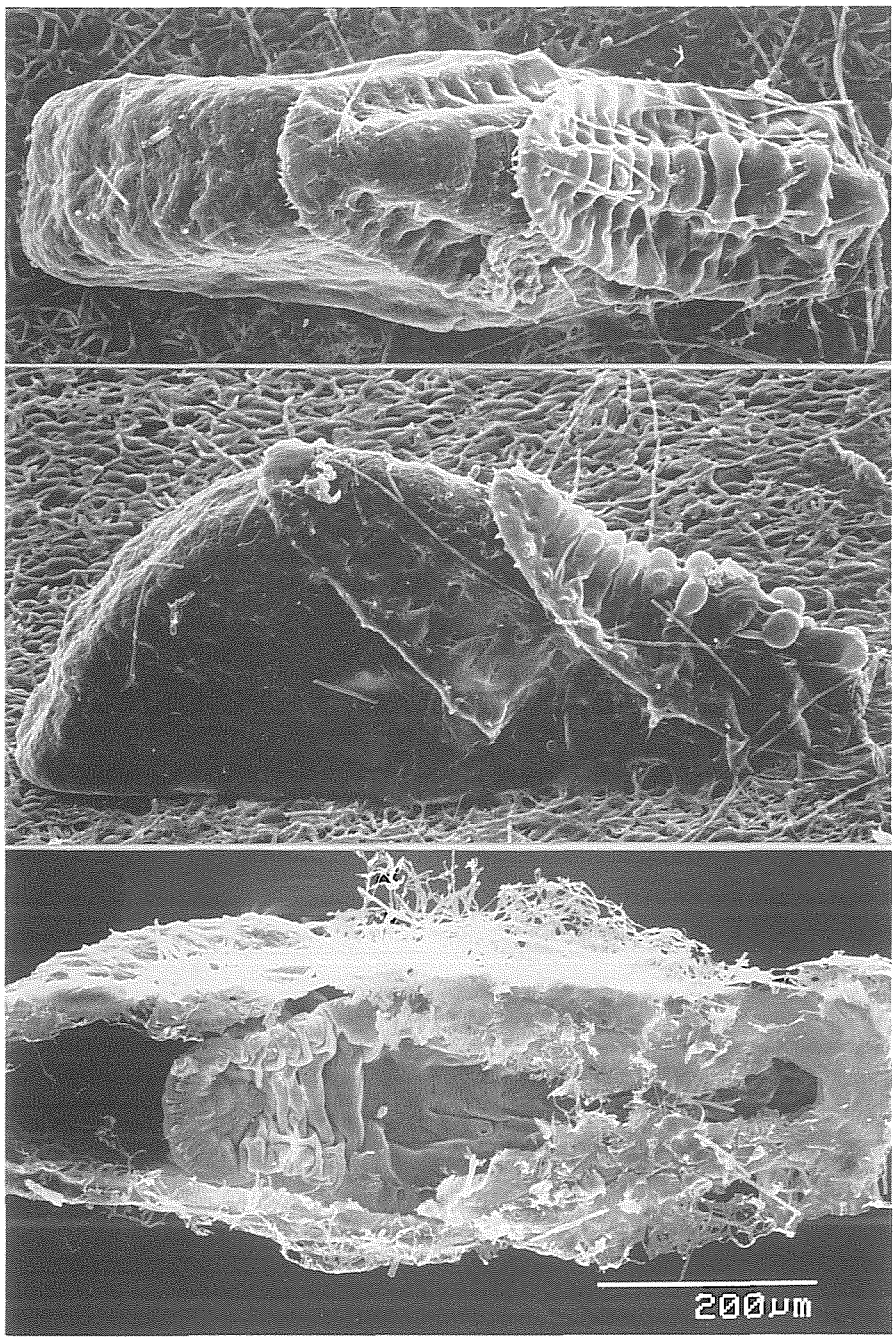

Fig. 29. *Kyphosoma kinabaluense*, female test, dorsal, lateral and ventral views [88ML-43].

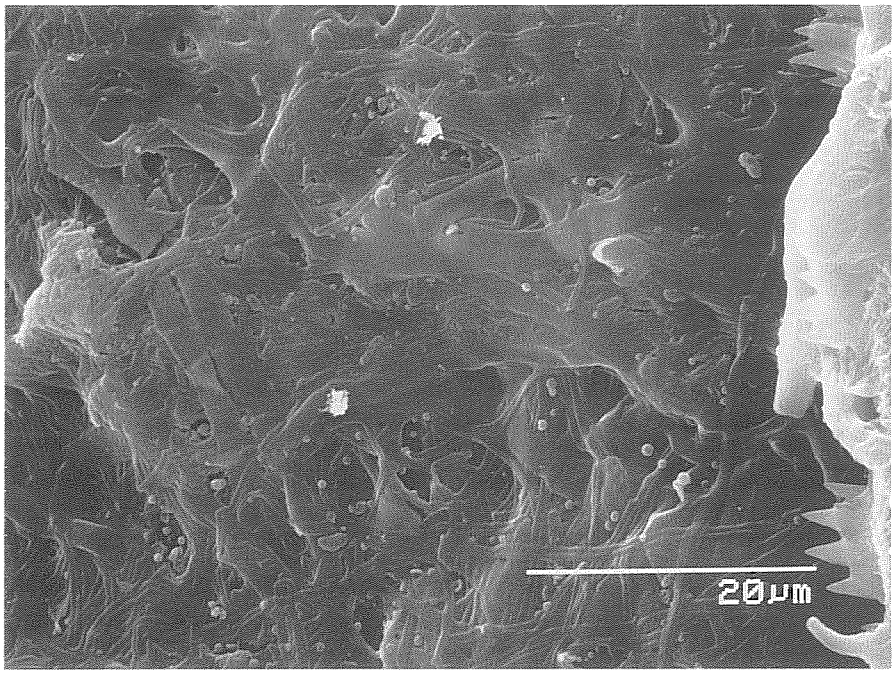

Fig. 30. *Kyphosoma kinabaluense*, female test, dorsal side [88ML-43]. Showing wax filaments laid irregularly ; right end : pygidial margin of 2nd exuvial cast.

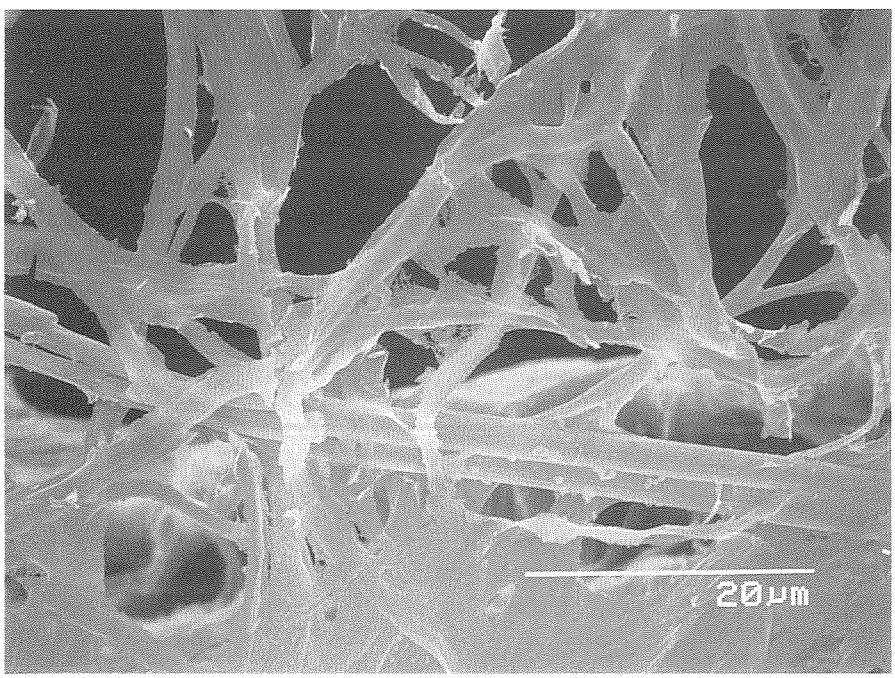

Fig. 31. *Kyphosoma kinabaluense*, female test, filaments on ventral portion [88ML-43].

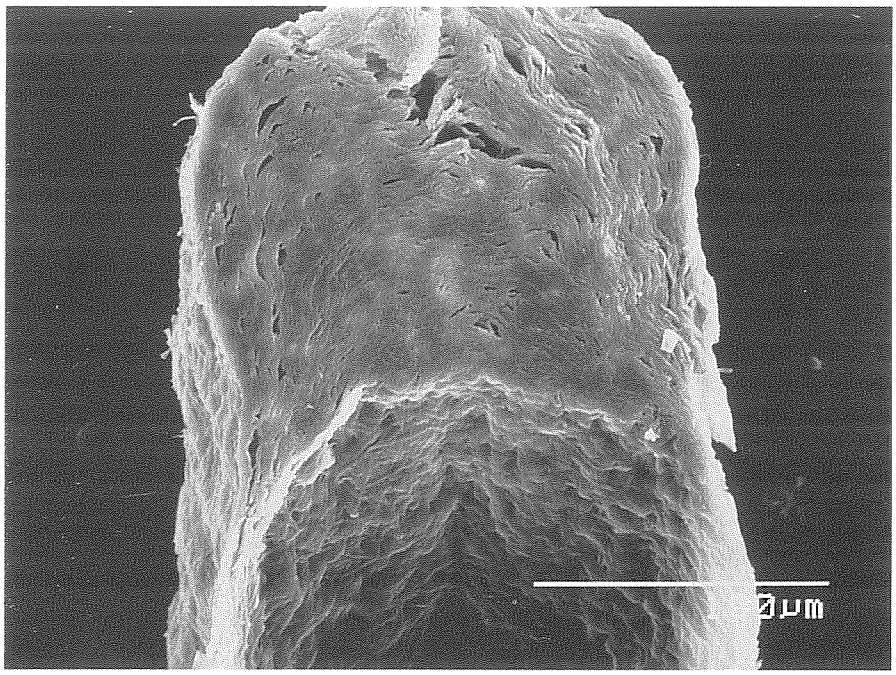

Fig. 32. *Kyphosoma kinabaluense*, female test, a cross section [88ML-63]. Showing thickened ridge.

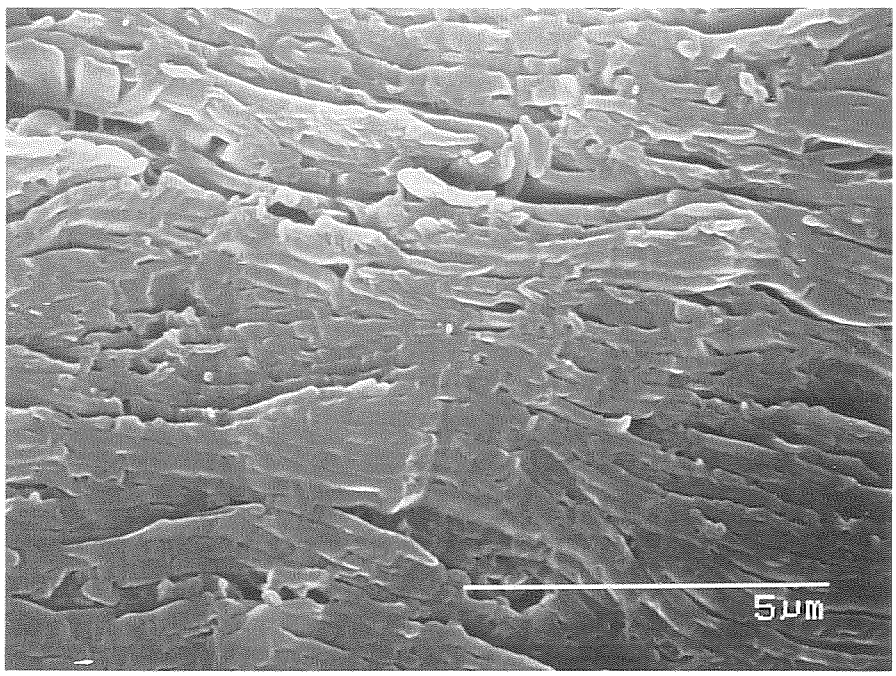

Fig. 33. *Kyphosoma kinabaluense*, female test. Part of Fig. 32, showing layers of wax filaments in thickened ridge.

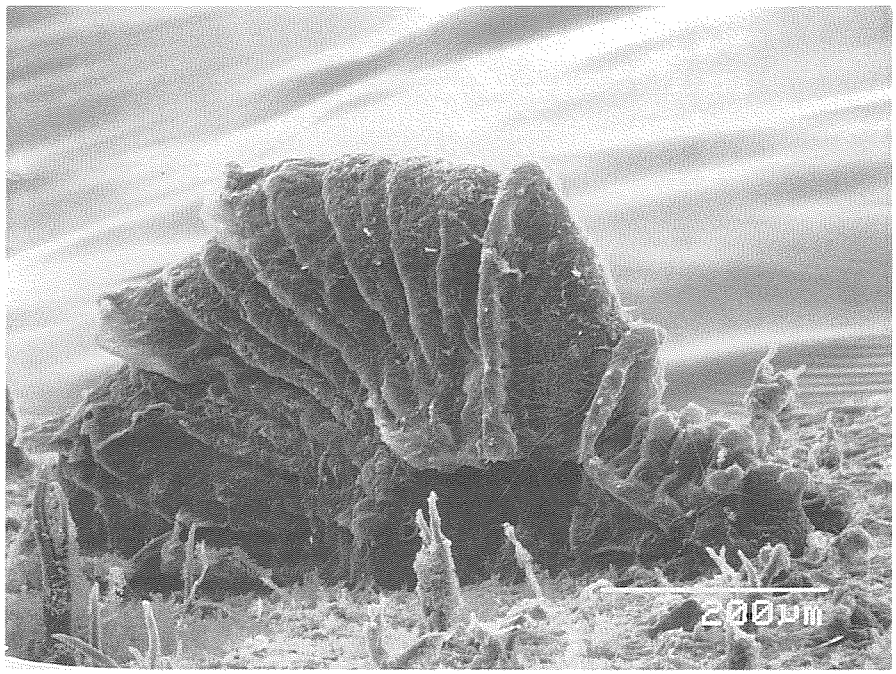

Fig. 34. *Kyphosoma melayuense*, female test, lateral view [91ML-374].

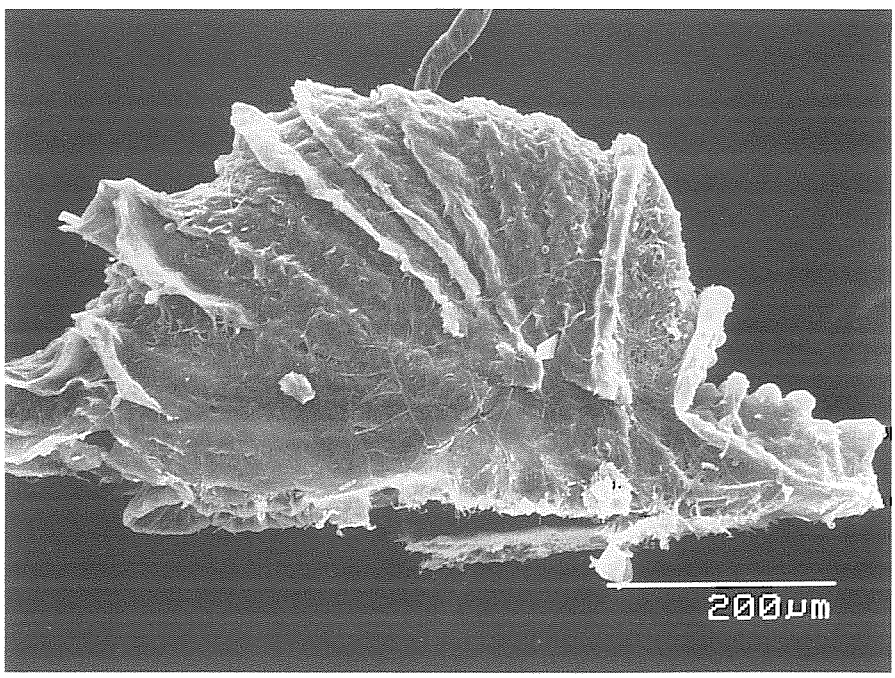

Fig. 35. *Kyphosoma melayuense*, female test : lateral view [91ML-374].

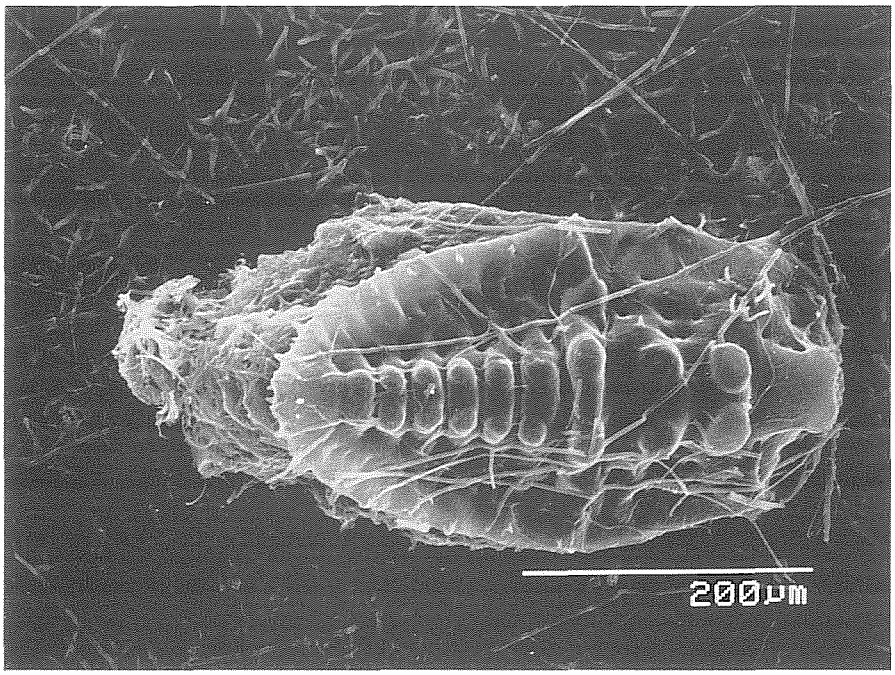

Fig. 36. *Kyphosoma kinabaluense*, male test, incipient stage [88ML-43].

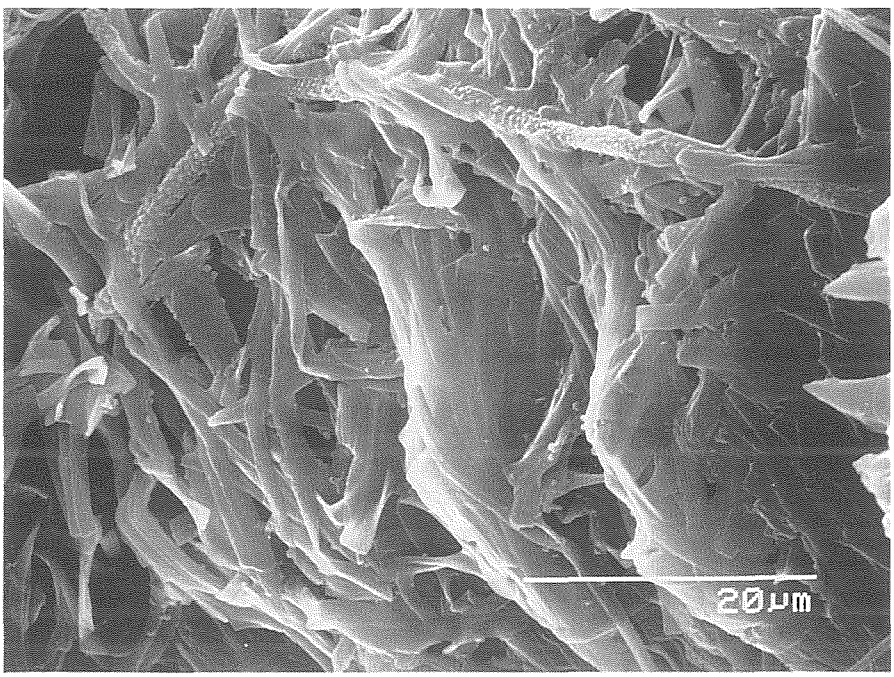

Fig. 37. *Kyphosoma kinabaluense*, male test [88ML-43]. Part of Fig. 36, showing wax filaments; right end: pygidial apex of 1st exuvial cast.

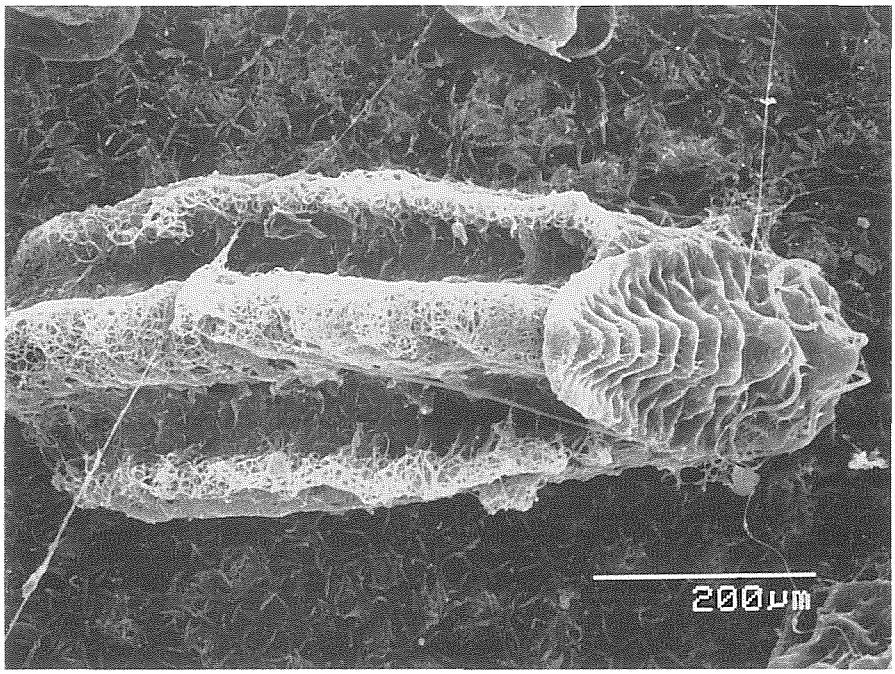

Fig. 38. *Kyphosoma pinosukense*, male test completed.

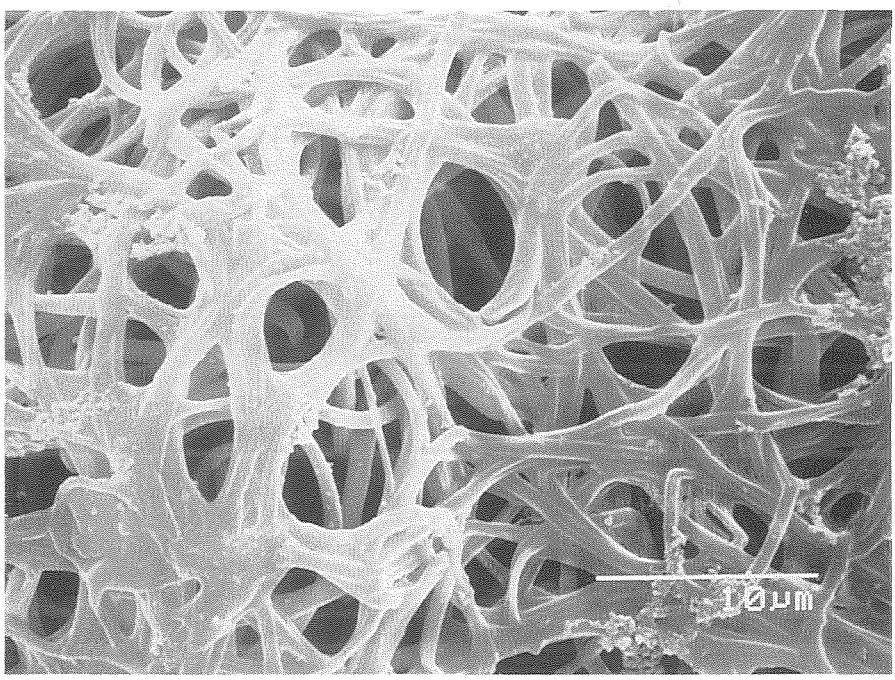

Fig. 39. *Kyphosoma pinosukense*, male test. Part of Fig. 38, showing filaments on median carina.

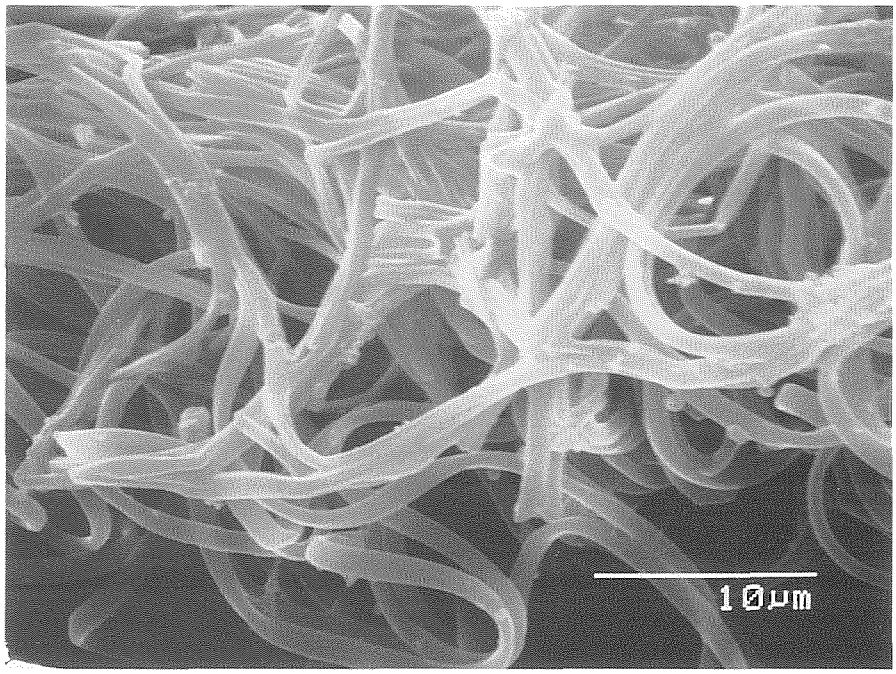

Fig. 40. *Kyphosoma pinosukense*, male test. Part of Fig. 38, showing wax filaments on lateral carina.

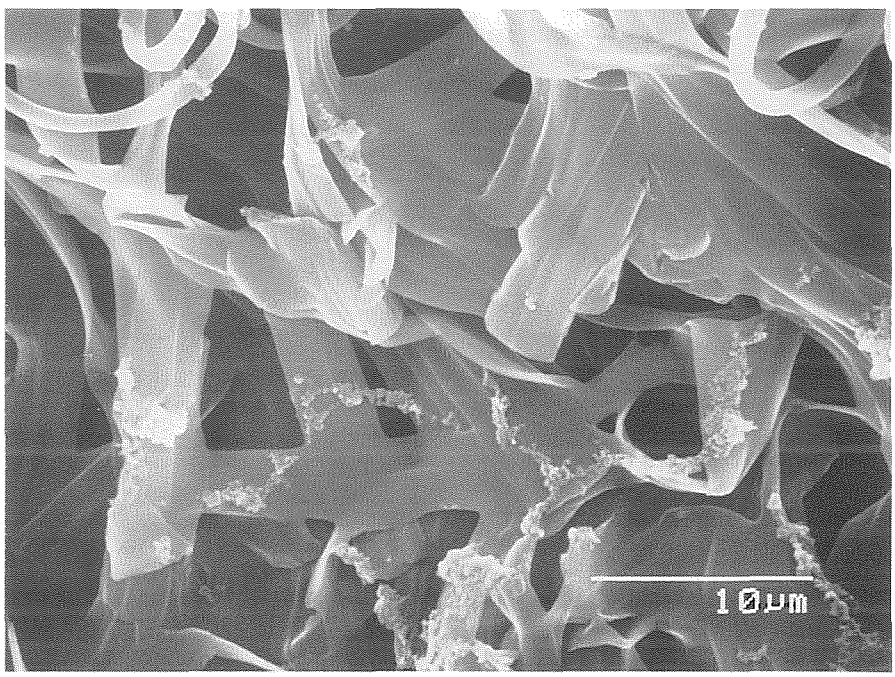

Fig. 41. *Kyphosoma pinosukense*, male test. Part of Fig. 38, showing wax filaments on groove between median and lateral carinae.

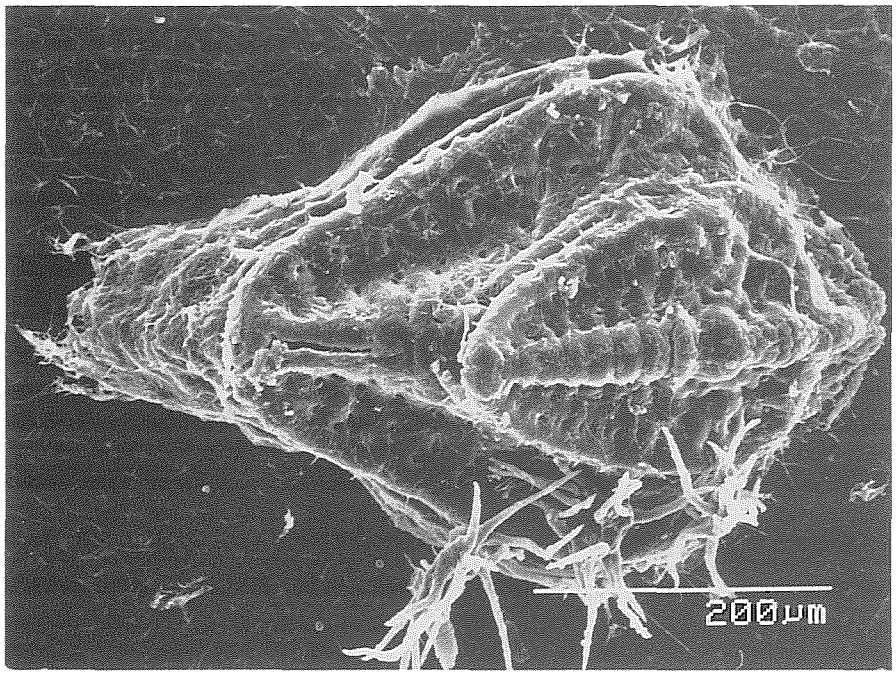

Fig. 42. *Pentacicola spinosus*, female test, dorsal view.

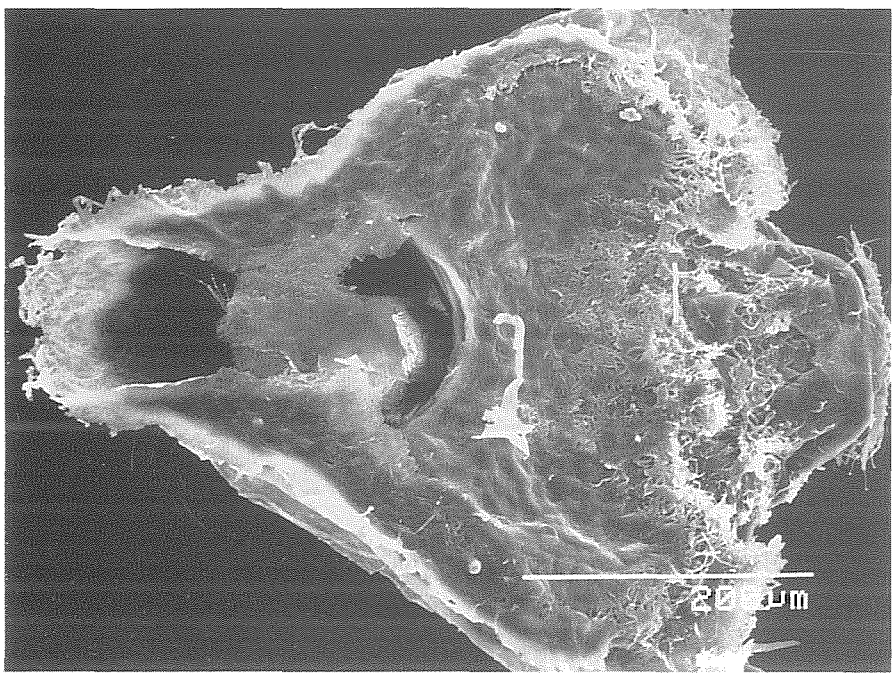

Fig. 43. *Pentacicola spinosus*, female test, ventral view.

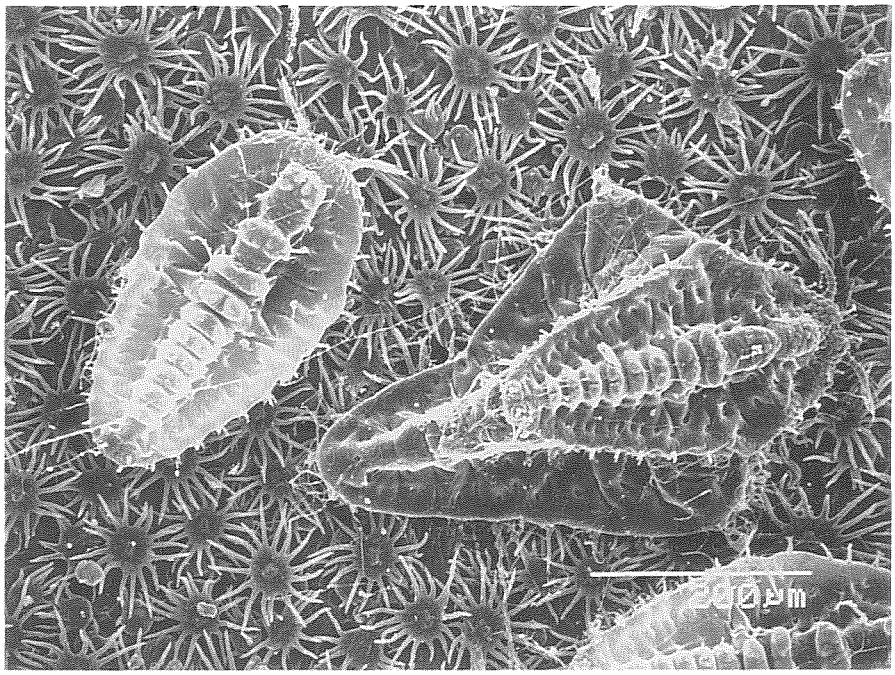

Fig. 44. *Pentacicola fimbriatus*, 1st instar male full-grown (left) and 2nd instar female full-grown with 1st exuvial cast (right) [90ML-23].

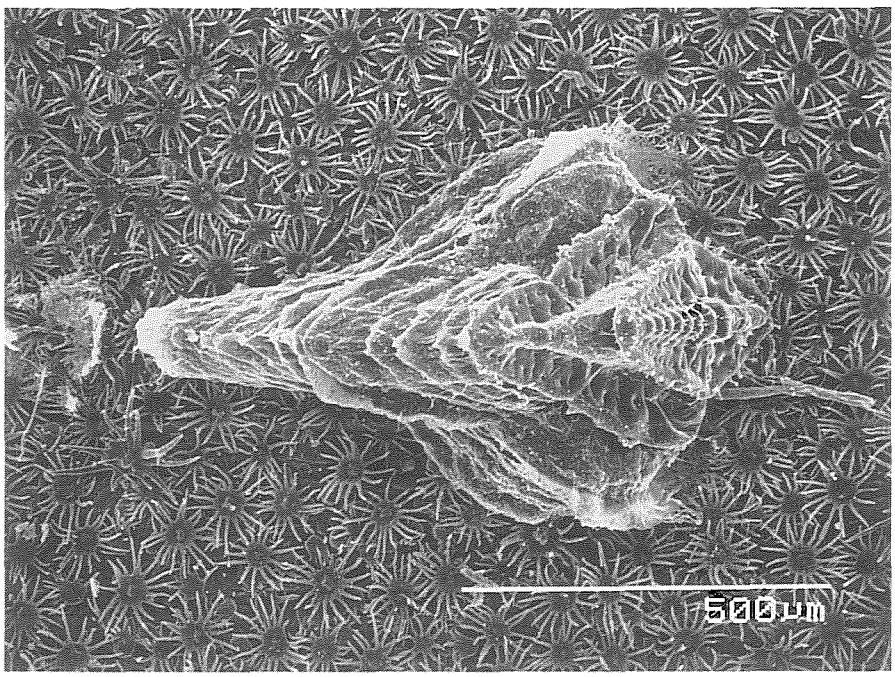

Fig. 45. *Pentacicola fimbriatus*, female test in dorsal view [90ML-23].

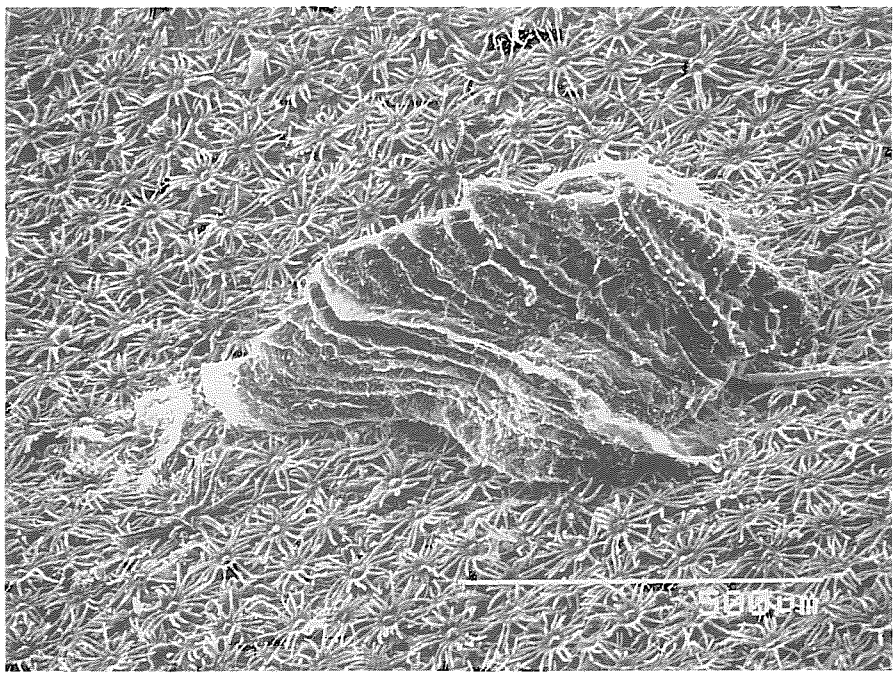

Fig. 46. *Pentacicola fimbriatus*, female test in lateral view [90ML-23].

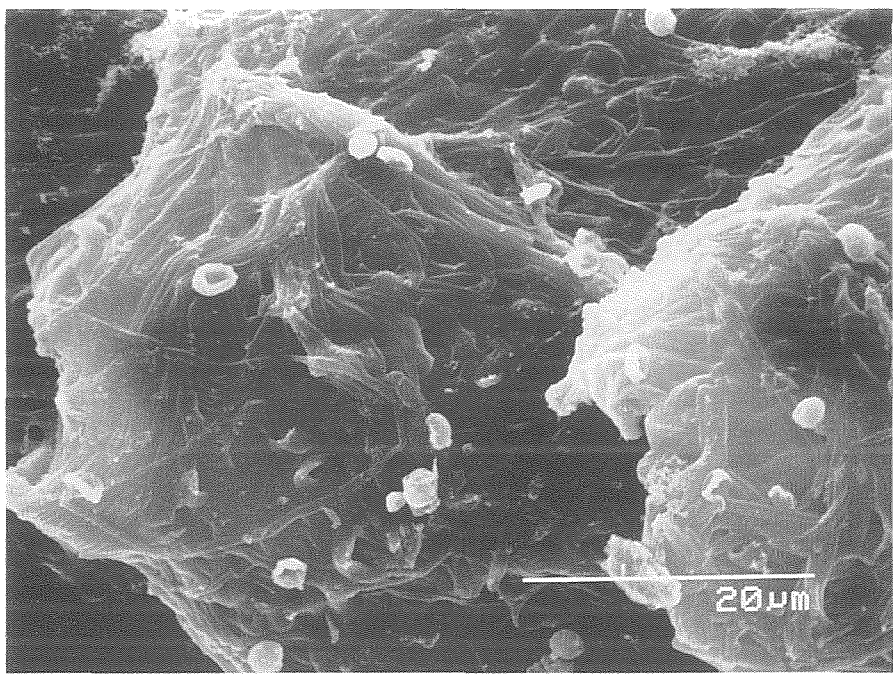

Fig. 47. *Pentacicola fimbriatus*, female test, dorsal surface [90ML-23]. Showing wax filaments.

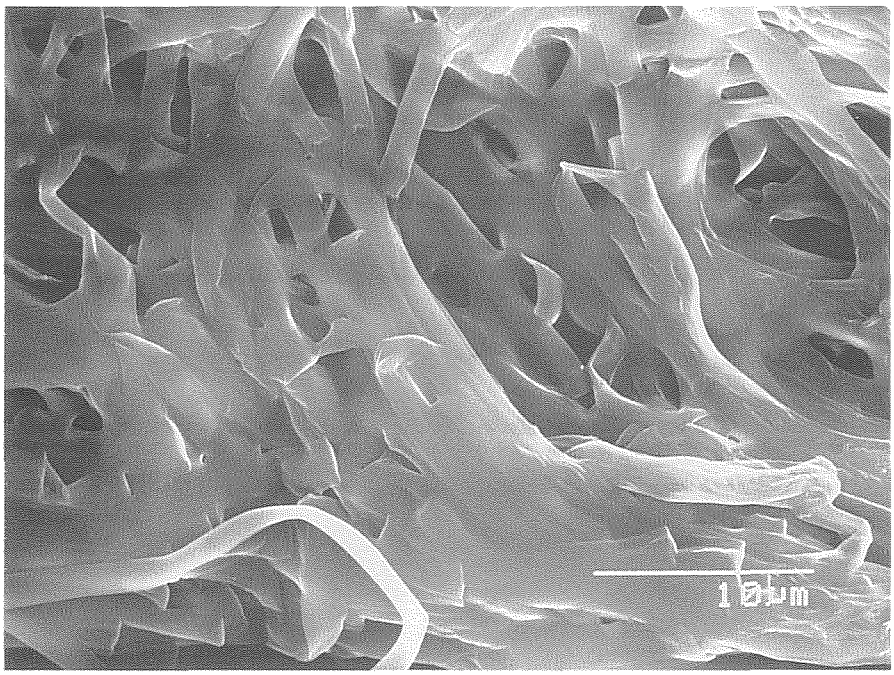

Fig. 48. *Pentacicola fimbriatus*, female test, inner surface [90ML-23]. Showing wax filaments.

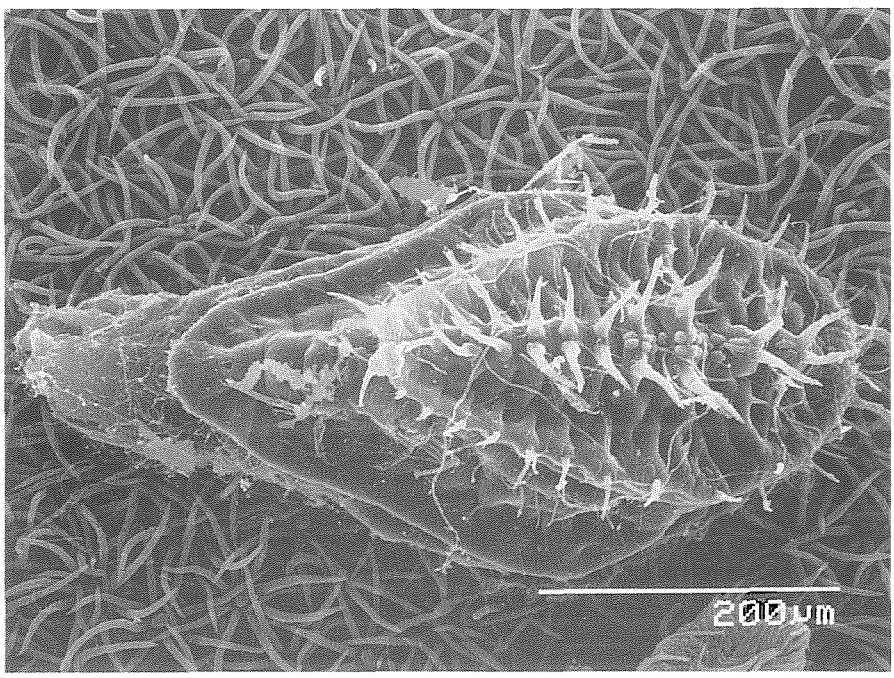

Fig. 49. *Pentacicola echinatus*, female test in dorsal view.

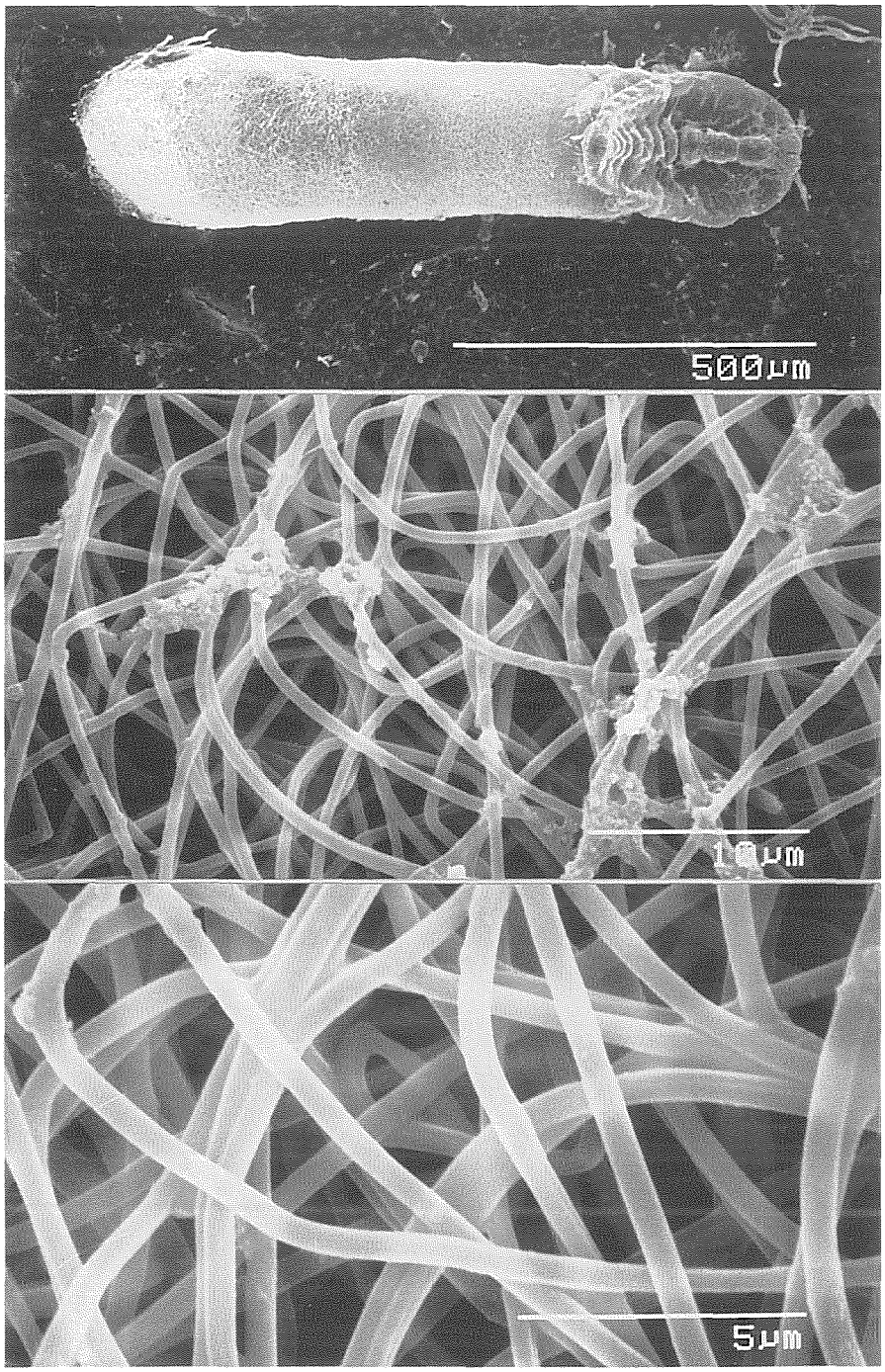

Fig. 50. *Pentacicola spinosus*, male test in dorsal view. Lower photographs showing wax filaments.

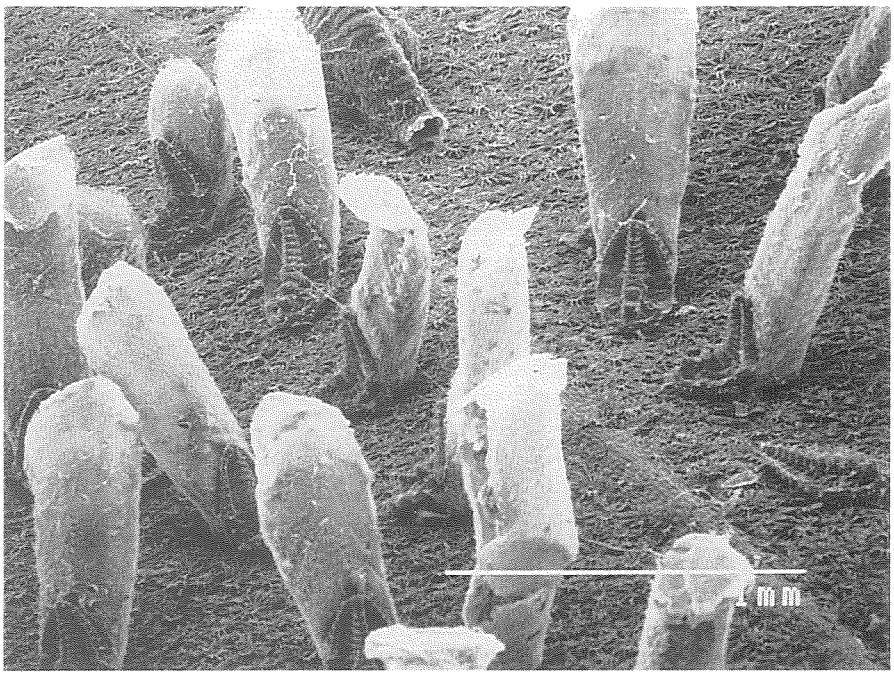

Fig. 51. *Pentacicola fimbriatus*, male tests in situ [90ML-23].

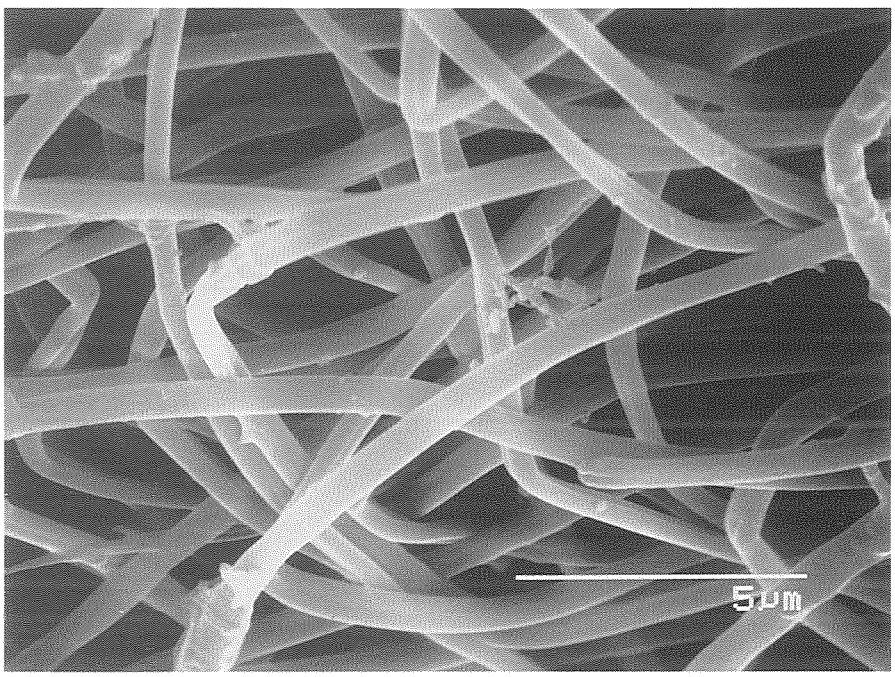

Fig. 52. *Pentacicola fimbriatus*, wax filaments of male test [90ML-23].

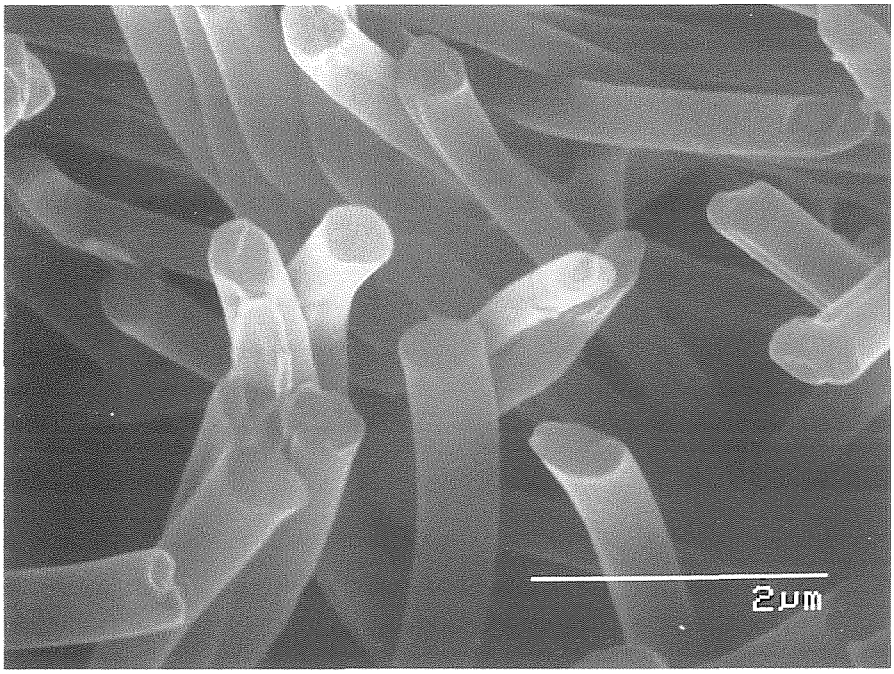

Fig. 53. *Pentacicola fimbriatus*, wax filaments of male test, cross-sectioned [90ML-23].

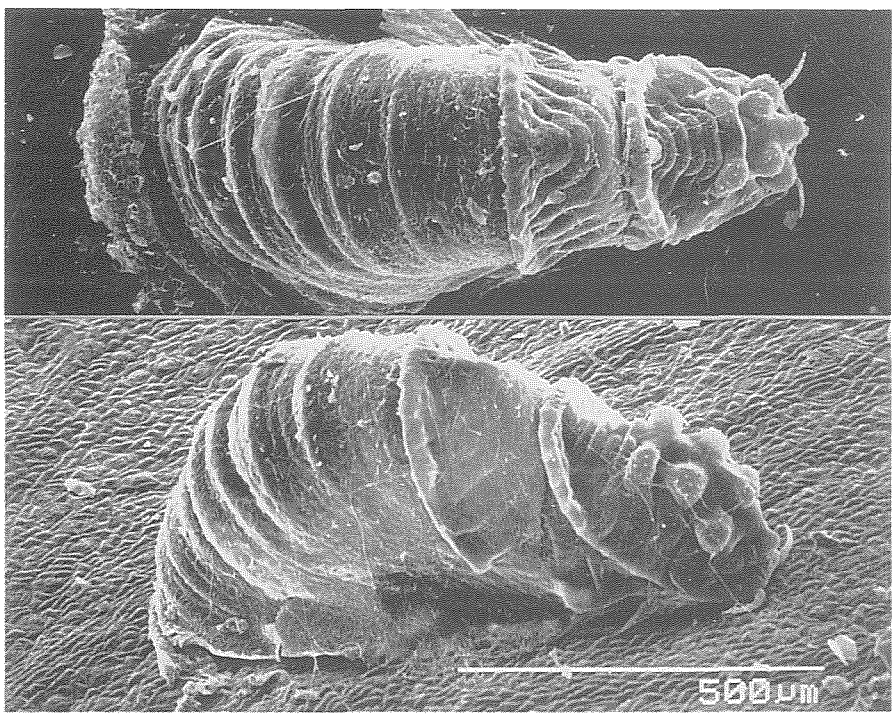

Fig. 54. *Thoa lophopetali*, female test in dorsal and lateral views.

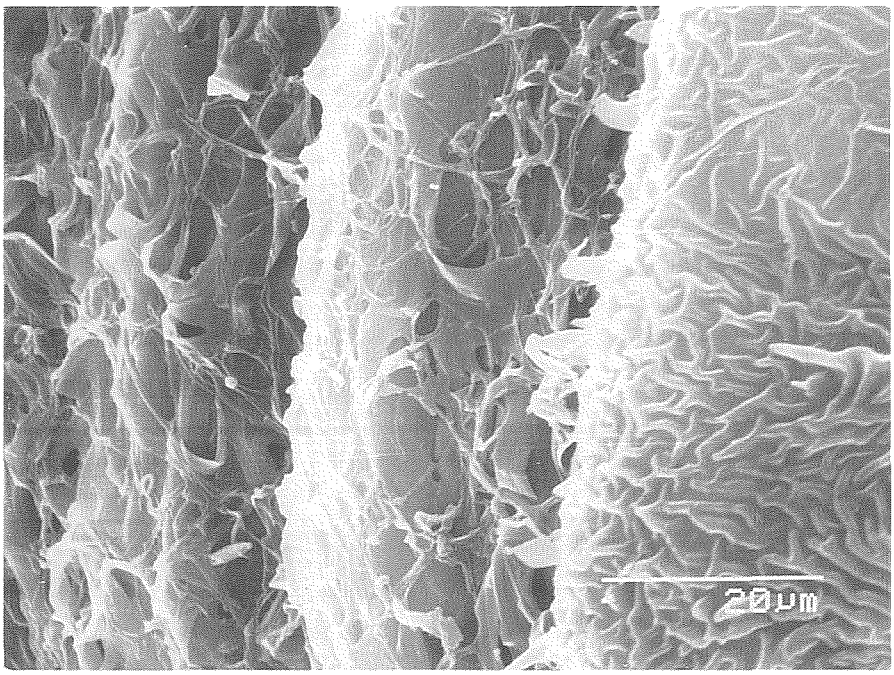

Fig. 55. *Thoa lophopetali*, female test, dorsal surface. Showing wax filaments; right: pygidial margin of 2nd exuvial cast.

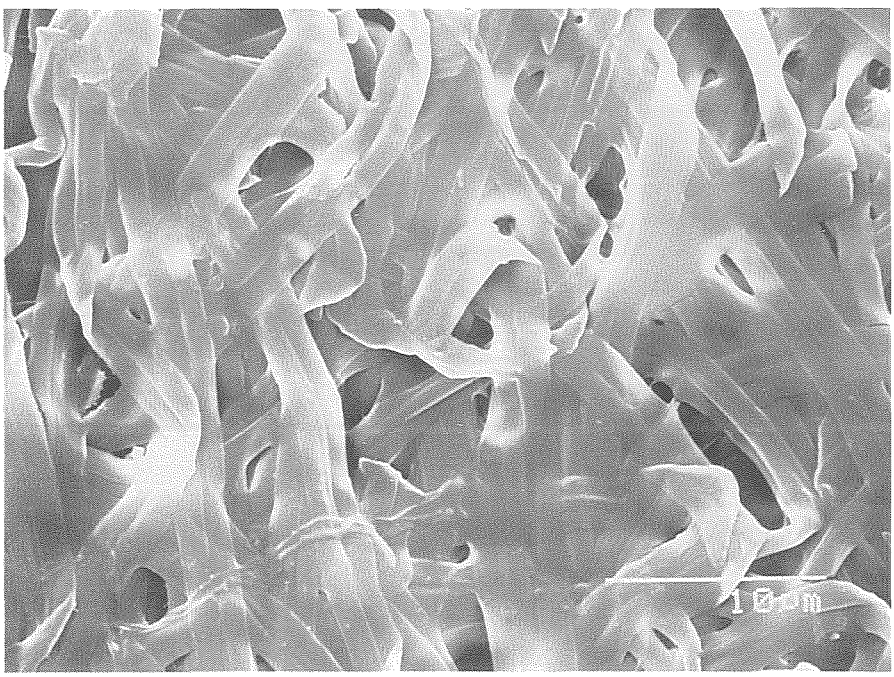

Fig. 56. *Thoa lophopetali*, female test, inner surface. Showing wax filaments.

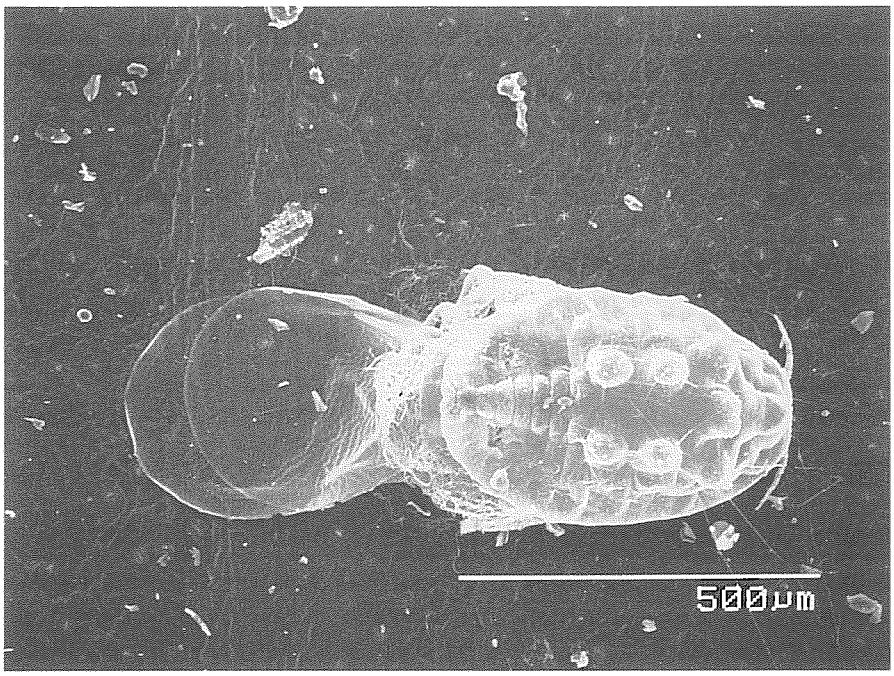

Fig. 57. *Thoa lophopetali*, male test completed, with wings of adult male extruded.

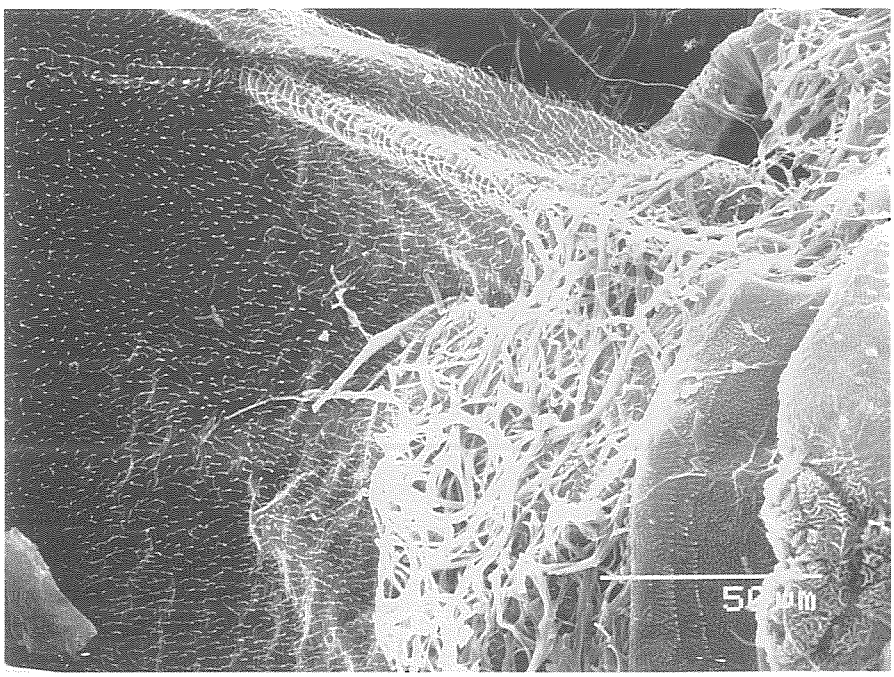

Fig. 58. *Thoa lophopetali*, male test. Part of Fig. 57, showing caudal end of 1st exuvial cast, with a small piece of ventral skin attached, and base of left wing.

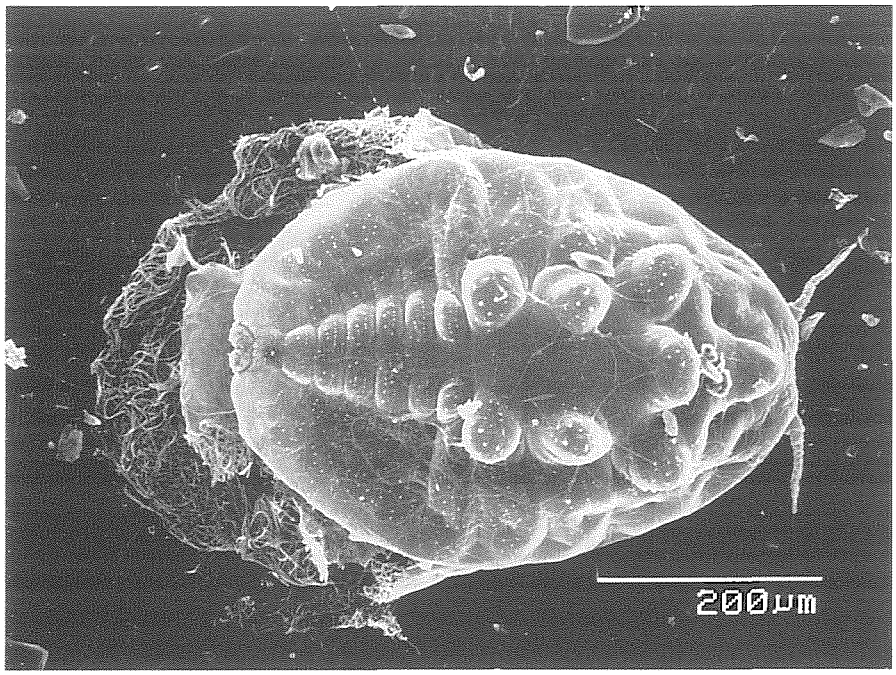

Fig. 59. *Thoa lophopetali*, another completed male test.

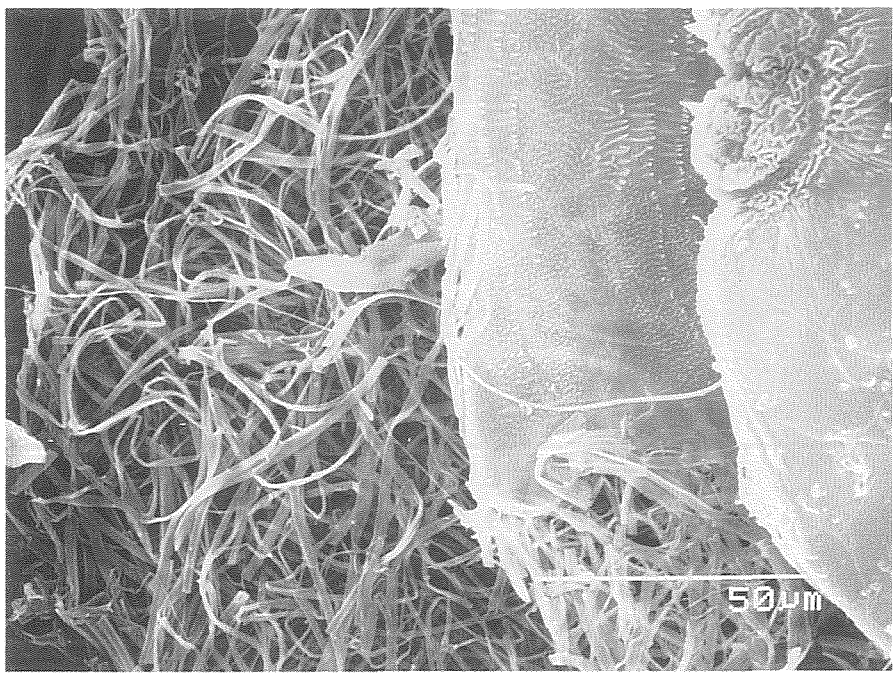

Fig. 60. *Thoa lophopetali*, male test. Part of Fig. 59, showing wax filaments; right: caudal end of 1st exuvial cast, with a small piece of ventral skin attached.