Title	AN APPROACH TO THE RUGASPIDIOTINI-PROBLEM [HOMOPTERA : COCCOIDEA : DIASPIDIDIAE]
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Citation	Insecta matsumurana. New series : journal of the Faculty of Agriculture Hokkaido University, series entomology., 52, 21-79
Issue Date	1995-12
Doc URL	https://hdl.handle.net/2115/9874
Type	departmental bulletin paper
File Information	52_p21-79.pdf

INSECTA MATSUMURANA

NEW SERIES 52 : 21-79 DECEMBER 1995

AN APPROACH TO THE RUGASPIDIOTINI-PROBLEM [HOMOPTERA : COCCOIDEA : DIASPIDIDAE]

By SADAO TAKAGI

Research Trips for Agricultural and Forest Insects in the Subcontinent of India, Scientific Report No. 49.
Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia, Scientific Report No. 21.

Abstract

TAKAGI, S. 1995. An approach to the Rugaspidiotini-problem [Homoptera : Coccoidea : Diaspididae]. *Ins. matsum. n. s.* 52 : 21-79, 1 tab., 52 figs. (33 pls.).

Five genera and 6 species of armoured scale insects were examined in connection with a pending problem concerning the composition of the tribe Rugaspidiotini. Emphasis was laid on characters of the 1st instar. The results combined with some published works have strengthened the supposition that the tribe as composed by authors is an assemblage of unrelated genera. *Nimbaspis molardi* and *Natalaspis* are revised ; *Anaimalaia scabra*, gen. et sp. nov., is described from South India as occurring on *Pterospermum*, and *Amphisoma erectum* and *Galeomytilus obesus*, genn. et spp. nov., from Palawan Is., the Philippines, on *Colona*. The latter two, while obviously belonging to the Diaspidini and Lepidosaphedini, are rough analogues to rugaspidiotines in pygidial characters, and suggest that the rugaspidiotine pattern of characters will evolve polyphyletically in such habitats as restrict horizontal movements of the insect body.

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Supported by Grants-in-Aid, Ministry of Education, Science and Culture, Government of Japan, No. 304108, 404307, 61041003, 62043003, 63041004, and 05041078.

Contents

2. Observations on 5 extraordinary genera

3. Some premises for discussion

4. Taxonomic positions of the 5 genera

5. Discussions

1. INTRODUCTION

The Rugaspidiotini-problem as here designated has been posed on the supposition that the tribe has largely been composed on the basis of similarities caused by convergence in the adult female (Howell, 1992 : Takagi, 1993). Indeed convergence may not be uncommon in adult female diaspidids, but the case is especially remarkable because the forms that have been referred by authors to the tribe (or the subtribe Rugaspidiotina) seem to have originated from diverse groups even belonging to different subfamilies.

Ferris (1938) placed *Rugaspidiotus arizonicus* in the tribe Odonaspidini and described 4 new species as members of *Rugaspidiotus*, but he suggested the possibility that the genus 'does not belong to the Odonaspidini' and also that 'four of the species referred to it are not congeneric with the type'. Balachowsky (1949) erected the subtribe Rugaspidiotina under the Odonaspidini, but Borchsenius (1966) recognized it under the Diaspidini, and recently the group has been treated as a tribe. Increasing genera have been referred to the group, making it appear more and more heterogeneous. The nomenclatorial nucleus of the tribe, *Rugaspidiotus arizonicus*, is characterized by having no distinct marginal appendages on the pygidium, by the ducts all small and strewn over both surfaces of the pygidium, and by the bivalve type of exuviation (Ferris, 1938). (In these characters it is similar to the Odonaspidini, but differs from the latter in lacking marginal scleroses marking intersegmental lines on the pygidium and in other characters.) Not all the forms referred to the Rugaspidiotini do agree with *R. arizonicus* in these characters : in some of them pygidial lobes are suggested by marginal prominences ; in other species, pygidial ducts are usual macroducts in size, which are absent on the ventral surface, or all ducts belong to the geminate-pore type. Not in all of them the 2nd instar exuvial cast is of the bivalve type. Furthermore, they are diverse in other details. It seems that the tribe Rugaspidiotini as composed by authors is a trash basket for diaspidids which cannot easily be assigned to any ordinary groups. Thus the Rugaspidiotini may be the worst case of confusion in the current diaspidid classification.

If convergence in the adult female is the main reason for the confusion, other stages and especially the larval stages may be worthy of study in approaching the problem. However, detailed and accurate larval studies are still meagre not only in the forms referred to the Rugaspidiotini but also in the whole family. Moreover, the state and role of larval forms in diaspidid taxonomy have not always been simple and clear. I (Takagi, 1983) found that the genus *Smilacicola*, referred by myself to the Rugaspidiotini, is polymorphic in the 2nd instar. The larvae of this instar are divisible into 2 distinct types. One of the types is definitely 'parlatoriine-patterned' and indicates that the genus is related to the Parlatoriini in some way. The other type is, however, quite different from the former, and the polymorphism requires a further explanation. Many Diaspidini have odd 2nd instar males, which must also be explained. The 1st instar larva, by contrast, may be expected to be stable phylogenetically in the pattern of characters. But this instar, too, sometimes shows an abrupt and remarkable change of characters between closely related species (Takagi et al., 1989 ; Takagi, 1993).

In this paper observations on 6 species belonging to 5 genera are given with emphasis on larval, especially 1st instar larval, characters in expectation of an approach to the Rugaspidiotini-problem. Two of the genera, *Nimbaspis* and *Natalaspis*, have been referred to the Rugaspidiotini. *Anaimalaia scabra*, gen. et sp. nov., is very similar to *Nimbaspis reticulata* in the adult female. *Amphisoma* and *Galeomytilus*, genn. nov., are referable to the Diaspidini and Lepidosaphedini, respectively, but are extraordinary for members of the tribes in some pygidial characters, which are similar to those of the rugaspidiotines.

2. OBSERVATIONS ON 5 EXTRAORDINARY GENERA

Abbreviations. Ll: median lobe ; abd I-IX: 1st to 9th abdominal segments; SEMy: scanning electron microscopy.

2.1. *Nimbaspis molardi*

Balachowsky, 1952: 128 ['Guinée forestière,... (vers 1.200 m alt.)'; 'Haute Côte d'Ivoire..., sur rameau semi-ligneux de *Macaranga huraefolia* (Euphorbiacée)']; Balachowsky, 1958 [original description reproduced].

Material. Twenty-six adult females and some exuvial casts mounted from material labelled '366, Nimba Guinée, 29. I. 1952, A. Balachowsky' (deposited in the Musée Royal de l'Afrique Centrale, Tervuren, except for 2 slides the Museum gifted to me). The insects were found on young shoots.

Adult female (Figs. 15 & 16). Balachowsky in his figure shows that the cephalothorax and 1st abdominal segment are sclerotized and in his description states that the cephalothorax is sclerotized or membranous. In all the specimens I have examined the derm is membranous in the prepygidial region, whereas it is well sclerotized throughout the pygidium. The spiracular disc pores are 3-locular.

Exuvial cast of 2nd instar female (Fig. 17). Irregularly ruptured on the ventral derm, of which most part is lost from the cast incorporated in the test; mouthparts and spiracles usually lost (when persisting, they are pushed back to near the posterior extremity of the cast as usual for a diaspidid). Spiracular disc pores 3-locular; anterior spiracle with 3 or 4 disc pores arranged in an arch, and the posterior with 1 or 2. Antenna with 2 short setae. Macroducts with inner end shaped like a geminate pore, strewn dorsally on abdominal segments and also on the remaining part of ventral derm (the remaining part belongs to the submarginal region of the cephalothorax and prepygidial abdomen); marginal macroducts of pygidium and also of some preceding segments (sometimes up to abd II) larger than the others.

Exuvial cast of 1st instar female (Fig. 2). The 1st instar exuvial cast is also irregularly ruptured on the ventral derm, of which most part, usually together with the mouthparts, spiracles and legs, is lost. Dorsal derm nearly elliptical. Antennae 5-segmented; terminal segment as long as segments III and IV combined, with some transverse or oblique irregular wrinkles, apically with a seta, which is much shorter than the segment; segment IV with a deep constriction halfway. Enlarged cephalic ducts present. No dorsal submedian ducts; no dorsal submarginal ducts on head and thorax. There are 10 small ducts on each side of the body on or near the margin, the anterior three (probably belonging to the meso- and metathorax and abd I) occurring on the ventral derm, and the rest mostly dorsally. Dorsal submedian setae occurring through thoracic and abdominal segments, the posteriormost on abd

VII. Anus situated at centre of pygidium (abd VII and succeeding segments). Anterior spiracle with 1 3-locular disc pore. Tibia with apical margin oblique and frayed ; tarsus about 3 times as long as tibia, also frayed apically, with a minute seta ventrally ; claw elongate. There are no marginal processes between the caudal setae ; a sclerotized conical process present laterally to caudal seta, slightly notched on each side, with a long sclerotized basal extension on ventral derm, accompanied laterally by 2 much smaller and rather membranous conical processes ; another set of similar processes on preceding segment, the sclerotized process with a weakly sclerotized basal extension.

2.2.1. *Anaimalaia scabra*, sp. nov.

Material. Collected at Top Slip, Anaimalai, alt. ca. 750 m., Tamil Nadu, India, on *'Pterospermum heyneanum ?'* [Sterculiaceae] (identified at the Botanical Survey of India Southern Circle, Coimbatore), December 2 and 3, 1978 [78IND-270 and -281]. Occurring on the undersurface of the leaves. Tests of female restricted to along the hairy veins, not easy to find ; it seems that the female test is largely composed of the exuvial casts, which are thin and brittle. Tests of male scattered, white, felted, elongate and parallel-sided, with no distinct longitudinal carinae ; 1st instar exuvial cast terminal. About 30 specimens of the adult female, several 2nd instar males, and exuvial casts were mounted. About half of the specimens including the name-bearing specimen [holotype] (adult female) are deposited in the collection of the Zoological Survey of India, Calcutta.

Adult female (Fig. 3). Body plump ; obovoid when mounted on slide ; derm remaining membranous in prepygidial region, or becoming sclerotized except for a membranous zone about base of pygidium. Pygidium with no marginal appendages, scabrous on both surfaces posteriorly to anus and vulva, which are situated near the base of the pygidium. Gland spines conical and sclerotized basally, extending apically into a long, slender process ; arranged in an irregularly double or triple row along body margin from head to base of pygidium ; the row is usually interrupted a little anteriorly to the anterior spiracle, with 4-15 gland spines in the anterior part thus delimited (on head and prothorax) and about 35-55 in the posterior part. Macroducts small, shaped like a geminate pore at inner end, scattered laterally to the row of gland spines on thorax and prepygidial segments and strewn on both surfaces of pygidium. Submedian microducts ventrally in prepygidial abdomen. Antennae situated just within anterior margin of head, separated from each other by a space a little narrower than mouthparts, each represented by a rather robust seta. Spiracular disc pores small, 3-locular ; anterior spiracle with 1-4 disc pores (rarely with no disc pore), the posterior occasionally with 1.

Second instar female exuvial cast. Dorsal derm elongate, elliptical, with part of ventral derm irregularly remaining around (the mouthparts and spiracles, together with a larger part of the ventral derm, are lost from the exuvial cast). Gland spines shaped like those of adult female, arranged in a row ventrally along margin from head to pygidium. Pygidium scabrous on dorsal surface posteriorly to anus ; ventral surface with many spinous processes irregularly laid marginally and submarginally. Ducts occurring dorsally along margin, mostly singly on abdominal and thoracic segments, the posterior two (probably belonging to abd VI and VII) larger than the others and obviously shaped like a geminate pore at inner end.

Second instar male (Fig. 4). Body elongate; no marginal process on abdomen, which is, however, slightly spiculate ventrally just within the posterior end. Gland spines similar to those of adult and 2nd instar female, 5 or 6 laterally to mouthparts (on supposed prothorax), 4-7 lateroposteriorly to anterior spiracle, 2 or 3 laterally to posterior spiracle, 1-3 on abd I and 1 or 2 on II submarginally, and 1 on each of succeeding segments near or on margin. Five marginal macroducts on each side, belonging to abd III-VII, somewhat modified in structure. Much smaller ducts strewn on both surfaces of abdomen, and also laterally on meso- and metathorax, 8-shaped at the inner end. Antenna with a short, thick seta. Anterior spiracle with 1-3 3-locular disc pores.

First instar exuvial cast (Fig. 5). Dorsal derm elongate, with part of ventral derm remaining around, and sometimes with mouthparts and legs attached to posterior end of abdomen. Antennae 6-segmented; terminal segment short, about as long as sgments IV and V united, not annulate, with a terminal seta. No enlarged dorsal ducts on head. Three pairs of submedian microducts dorsally on thorax, another pair laterally to anus. Ventral microducts occurring along marign on thorax (supposed meso- and metathorax) and abdomen (it seems that they vary in number from 5 to 8 on one side of the body). Submedian dorsal setae occurring through thorax and abdomen, the posteriormost occurring on abd VII. Tarsus twice as long as tibia, without a long seta ventrally.

2.2.2. *Anaimalaia*, gen. nov.

Name-bearing species [type-species]: *Anaimalaia scabra.*

In the adult female this genus is similar to *Nimbaspis* in the ducts, which are all shaped like a geminate pore at the inner end, and in having no marginal processes on the pygidium. Its resemblance to *N. reticulata* ['*N. reticulatus*' after Balachowsky] is especially close owing to the scabrous pygidium ['structure écailleuse' in *N. reticulata*]. In the 1st instar, however, *Anaimalaia scabra* has a pair of ducts laterally to the anus on the supposed abd VIII, whereas *N. molardi* has the ducts of the segment near the margin; the latter is different from the former also by having well-developed sclerotized marginal processes laterally to the caudal setae and is peculiar in the tibiae and tarsi, which are frayed on the apical margin; the antennae are 5-segmented in *Nimbaspis*, whereas 6-segmented in *Anaimalaia*; 3 pairs of submedian dorsal ducts occur on the thorax in *Anaimalaia* but none has been found in *Nimbaspis*. In the adult female, *Anaimalaia* is remarkably different from *Nimbaspis* in having well-developed gland spines occurring along the prepygidial body margin.

Anaimalaia scabra may be similar to *Eucleaspis imbricata* [=*Chionaspis* (*Dinaspis*) *imbricata*; =*Protodiaspis imbricata*], but, according to Munting (1968), the name-bearing species of *Eucleaspis, E. echinata*, has distinct lobes.

Anaimalaia is also very similar to *Pentacicola*, in which, however, the ducts are 2-barred at the inner end and the pygidium has at least 1 pair of pectinae. [See 4.2. for further discussion.]

2.3. *Natalaspis formosana*

Takahashi, 1930: 29 [*Odonaspis simplex* var. *formosana*; Taiwan, on *Dendrocalamus* and *Bambusa*]. Takagi, 1969: 58 [*Poliaspoides formosanus*; Taiwan]. Ben-Dov and Takagi, 1974:

46 [Taiwan, South Africa, and Reunion Island].

Material from Malaysia and the Philippines. Collected in grounds of the Forest Research Institute of Malaysia, Kepong, Selangor, Malaya, on *Bambusa vulgaris*, Sept. 26, 1986 [86ML-25] ; at Kuala Kubu Baharu, Selangor, Malaya, on an undetermined bamboo, Oct. 23, 1986 [86ML-301] ; at Ulu Gombak, Selangor, Malaya, on *Bambusa vulgaris*, Nov. 16, 1986 [86ML-495] ; at Sandakan, Sabah, on *Bambusa vulgaris*, Oct. 30, and on an undetermined bamboo, Nov. 18, 1988 [88ML-227 and -374] ; at Puerto Princesa, Palawan, on *Schizostachyum diffusum*, Aug. 9, 1993 [93PL-19] ; at Ipilan, Brooke's Point, Palawan, on *Schizostachyum lumampao*, Aug. 23, 1993 [93PL-135]. (Host plants were identified by Mr K.M. Kochummen [86ML-25 and -495] ; at Botany Section, Forest Research Centre, Sandakan [88ML-227] ; and by Dr Edwino S. Fernando [93PL-19 and -135]).

The examined specimens of the adult female are variable in the shape of the pygidium : in 86ML-25, -301 (Fig. 18), and -495 (Fig. 19) the pygidium tends to be rounded along the margin as in the form from Taiwan (Takagi, 1969 : Fig. 17), and in 88ML-227 and -374 and 93PL-19 and -135 (Figs. 20 & 21) it is almost straight on each side. The margin is almost smooth, with no prominent indentations or projections, in 86ML-301, whereas more or less indented in the others. The median area of the pygidium (abd IX) is scattered with ducts marginally and submarginally on both dorsal and ventral surfaces in 86ML-301, but with none or a few dorsal ones near the margin in the others. In 86ML-495 there is a pair of distinct intersegmental furrows towards the apex of the pygidium. In the larval stages, too, some variations, though not conspicuous, have been found. These forms may belong to more than 1 species, but here they are all referred to *N. formosana*.

Figures of the larval stages and the head of the adult male, all based on specimens mounted from 93PL-135, are here given to show larval and adult male characters of the genus (but not necessarily of *N. formosana*). The 2nd instar female (Fig. 6) has a pair of low but distinct marginal prominences at the apex of the pygidium. These prominences are serrate in 88ML-227 and -374 and 93PL-19 and -135, but in the others they are less serrate or not serrate, thus conical or rounded. They may represent median lobes. In the 2nd instar male (Fig. 7), at the corresponding position of the pygidium, occurs a pair of slender processes, which are dilated apically (some 2nd instar males have been available from 86ML-301, too ; in these specimens the processes tend to be frayed apically). Other characters of the 2nd instar male : large macroducts in oblique (on dorsal surface) or transverse (on ventral surface) rows across marginal and submarginal regions of meso- and metathorax and abd I ; smaller macroducts dorsally on abdomen ; slender ducts abundant on ventral surface ; abd II-VII each with a group of lateral ducts, which are short, each with a slender, slightly sinuate opening.

The 1st instar larva (Fig. 8) is elongate, with the lateral margins almost parallel. Antennae 5-segmented ; terminal segment as long as segments III and IV united, not annulate, with an apical seta. A pair of enlarged ducts on head. Three pairs of submedian dorsal ducts on thorax ; 10 ducts on each side of body along margin, the posteriormost opened dorsally (on supposed abd VIII) and the others ventrally. Submedian dorsal setae occurring through thorax and abdomen, the posteriormost on abd VII. Anterior spiracle with 1 3-locular disc pore. Tibiae and tarsi very short, the latter without a distinct seta ventrally. A pair of sharp sclerotized processes between caudal setae ; a broader, tricuspid, sclerotized process laterally to caudal seta (on abd VII), with a long sclerotized base, accompanied laterally by a much less sclerotized tricuspid process ; 7 processes, similar to the outer process on abd VII, occurring along margin in preceding segments, the anteriormost being supposed to belong to metathorax. (The outer process of abd VII is rudimentary or absent in 86ML-301 and -495.)

The head of the adult male (Fig. 1), depressed dorsoventrally on slide, is roughly conical. Midcranial ridge represented by slender dorsal branches. Postoccipital ridge slender ; transverse median part short ; anterior arms divergent. Preoral ridge absent.

In SEMy the spiracular disc pores of the adult female (Fig. 22) are 3-locular, with the septa a little swollen but not produced to form distinct septal processes, and the perivulvar disc pores (Figs. 23 & 24) belong to the capitate type. The female apparently moves when forming its test, because the test is much broader than the insect body. The dorsal surface of the test, however, shows no regular arrangement of wax filaments, which are laid coarsely and disorderly (Figs. 25 & 26).

2.4. *Natalaspis* sp.

Material. Collected at Bukit Tapah, alt. ca. 650 m., Perak, Malaya, on *Schizostachyum* sp. (identified by Mr K.M. Kochummen), Oct. 19, 1986 [86ML-247]. Only 1 adult female was mounted from a mixture of some coccoids occurring together under the leafsheath (its presence was not noticed when the mixture was processed for mounting, and its exuvial casts were lost during the process).

Adult female (Fig. 27). Differing from *N. formosana* in having a pair of round processes at apex of pygidium ; another pair of similar processes laterally to the apical pair, separated from the latter by a space as wide as one of the processes ; dorsal ducts of pygidium more numerous than in *N. formosana* ; anterior spiracle with 5 and 6 disc pores ; perivulvar disc pores in 5 groups. [See 4.3. for further discussion.]

2.5.1. *Amphisoma erectum*, sp. n.

Material. Collected at Salogon, Batarasa (or Bataraza), Palawan, Philippines, on '*Columbia serratifolia*' = *Colona serratifolia* [Tiliaceae] (identified by Dr Edwino S. Fernando), Aug. 17, 1993 [93PL-78]. Occurring on twigs and petioles, among dense erect hairs, and also on the undersurface of the leaves on the densely hairy base. Tests of both sexes standing on the anterior end among the dense hairs of the host (Figs. 32 & 33). Test of female (Figs. 34 & 35) nearly ovoid, bivalve, the ventral portion being formed like the dorsal one ; light brown ; 2nd instar exuvial cast (Fig. 31) bivalve, being split along margin of thorax and abdomen, and, thus, incorporated in bivalve test. Test of male (Fig. 40) elongate, felted, with a slight median carina dorsally, white, with 1st instar exuvial cast terminal. A number of adult females, some larvae, and exuvial casts were mounted. The name-bearing specimen [holotype] (adult female) and about half of the mounted specimens are deposited in the collection of the Museum of Natural History, University of the Philippines at Los Baños.

Adult female (Figs. 9 & 28). Body ovoid to elongate ovoid. Derm remaining membranous in prepygidial region. Pygidium (abd V and succeeding segments) roundish on margin, slightly recessed apically to receive small and low L1s, which are set close, with the mesal margins short, parallel to each other and separated from each other by a slender space. No lateral lobes. Small marginal gland spines on pygidial margin, 1 just laterally to L1 (on abd VIII) and on each of 4 preceding segments (abd IV-VII). Macroducts occurring marginally, submarginally and submedially on both surfaces of pygidium and abd IV, and laterally on preceding segments. Dorsal macroducts: marginal macroducts 1 on abd VII and 2 on each of IV-VI; submarginal macroducts 1 on VI and 2 or 3 on IV and V each; submedian macroducts 0-2 on VI, 1 or 2 on V and 1-3 (rarely 0) on IV, tending to be smaller (sometimes another small one on III). Ventral macroducts: marginal macroducts 2 on abd VII, 2 on VI and 2 or sometimes 1 on V; submarginal macroducts 1 on VII just anteriorly to the marginal macroducts (sometimes, further anteriorly, another macroduct occurring submarginally or submedially), 2-5 on V and VI each, and 3-6 on IV (the outermost may be regarded as marginal); submedian macroducts 0-2 on IV-VI each (small especially on IV). Lateral macroducts 5-10 on abd III, 3-6 on II, 4-7 on I, 5-9 on metathorax, and 4-8 on mesothorax (sometimes 1-3 very small ones on prothorax). Ventral microducts 2-5 on prothorax (or combined head and prothorax), about 10-18 on mesothorax just posteriorly to anterior spiracle, 6-11 on metathorax just posteriorly to posterior spiracle, 6-13 mediosubmedially across abd I, 1-4 submedially on II, and 1 or 2 submedially on III. Antennae on or just within anterior margin of head, separated from each other by a space narrower than mouthparts, each composed of a tubercle and a seta. Spiracular disc pores 3-locular; anterior spiracle with 2-6 disc pores; posterior spiracle without disc pore or with 1 disc pore or rarely 2. Perivulvar disc pores in 5 groups; 4-10 in median group, 8-16 in the anterolateral, and 4-13 in the posterolateral; 44-58 in total. Anus situated anteriorly to centre of pygidium. A pair of sclerotized bars anteriorly to anus, usually gently curved (preanal scleroses). Another bar occurring between submedian and submarginal dorsal macroducts of abd V, crossing intersegmental furrow between abd V and VI (intersegmental sclerosis). A small submarginal boss dorsally between abd III and IV; another one on mesothorax.

Second instar female (Fig. 10). Nearly obovoid. L1s as in adult female. Lateral lobes absent. Marginal gland spines: 1 laterally to L1, minute; 1 on abd II-IV each; a few small gland spines laterally to anterior spiracle, a similar one laterally to posterior spiracle and submarginally on abd I. Dorsal macroducts: 4 marginal ones on each side, belonging to abd IV-VII; 3 submarginal ones on I-III (at times the anteriormost absent), becoming smaller anteriorly. Ventral macroducts: 3 marginal on abd V-VII, and 1 near margin on IV; 1 submarginal on VI just anteriorly to the marginal one, usually also on V; usually 3 submedian ones belonging to V-VII, the anteriormost or anterior two sometimes small. Ventral microducts scattered on head, posteriorly to each spiracle, and medially across abd I; 1 submedian one usually present on II-IV each, abd III sometimes with another duct (micro- or macroduct) submarginally. Anterior spiracle with 1 or 2 (usually 2) disc pores.

Second instar male (Fig. 11). Body ovoid; margin of abd V and succeeding segments rugged, having small processes, but no distinct lobes are identifiable. Marginal gland spines minute on abd III-VIII; larger gland spines on preceding segments: 2 or 3 posteriorly to anterior spiracle, 1 or 2 laterally to posterior spiracle, and 1 submarginally on abd I and II each. Macroducts rather abundant on both surfaces of abdomen; on dorsal surface, arranged in a partly double longitudinal row submedially, and scattered submarginally; on ventral surface, arranged in a single submedian and a double submarginal longitudinal row. Six modified macroducts marginally on each side, belonging to abd II-VII; 2 or 3 submarginally, belonging to abd IV (or V)-VI. Ventral microducts scattered on head and posteriorly to each spiracle. Anterior spiracle with 2 or 3 (usually 2) disc pores.

First instar larva (Fig. 12). Body elongate obovoid. Antenna 5-segmented; terminal segment as long as segments I-IV united, not annulate, apically with a long seta. A pair of enlarged dorsal ducts on head. Three submedian dorsal microducts on each side of thorax; 1 submedian duct laterally to anus; 9 ventral microducts along margin, probably belonging to meso- and metathorax and abd I-VII, the abdominal ones each opened at apex of a small tubercle. Submedian dorsal setae occurring through thorax and abdomen, the posteriormost on abd VII. Anterior spiracle with 1 3-locular disc pore. Tarsus about twice as long as tibia, without a long seta ventrally. A pair of small, pointed processes between caudal setae; a sclerotized bi- or tricuspid process just laterally to caudal seta, accompanied laterally by a small pointed process; a similar pointed process on preceding segment.

In SEMy the spiracular disc pores (Fig. 29) of the adult female are 3-locular, with the septa a little swollen but not produced to form distinct processes. The perivulvar disc pores (Fig. 30) belong to the capitate type. The test of the female shows wax filaments running transversely in a curve on both the dorsal and ventral portions (Figs. 36 & 37). The inner surfaces of both the portions are lined with fine filaments, which are tangled together to form a number of small clumps (Figs. 38 & 39). The male test (Figs. 41 & 42) shows no regular running of filaments.

2.5.2. *Amphisoma*, gen. nov.

Name-bearing species [type-species]: *Amphisoma erectum*.

This genus belongs to the Diaspidini and probably to the Chionaspidina, but is quite peculiar and unique in having marginal, submarginal and submedian macroducts on the ventral as well as dorsal surface. [See 4.4. for further discussion.]

2.6.1. *Galeomytilus obesus*, sp. nov.

Material. Collected at Salogon, Batarasa (or Bataraza), Palawan, Philippines, on '*Columbia serratifolia*' = *Colona serratifolia* [Tiliaceae] (identified by Dr Edwino S. Fernando), Aug. 17, 1993 [93PL-78]. Occurring on twigs and petioles, among dense erect hairs; scattered, sometimes among tests of *Amphisoma erectum* [2.5.1.]. Female test (Fig. 48) brown; elongate, slender, parallel-sided, cylindrical with ventral portion complete, the dorsal surface with transverse curved ribs; 2nd exuvial cast swollen to form a helmetlike covering at anterior end of test; 1st exuvial cast often absent on test (easy to drop out of the place probably owing to the swollen 2nd cast). Test of male (Fig. 51) similar to test of female, but light in colour and with transverse ribs more prominent. Twenty-nine adult females, exuvial casts of female, and some 1st instar larvae were mounted. Not all of the adult females were mounted right (exactly dorsoventral) owing to the plump body; 2nd casts mostly mounted as in Fig. 47. The name-bearing specimen [holotype] (adult female) and about half of the specimens are deposited in the collection of the Museum of Natural

History, the University of the Philippines at Los Baños.

Adult female (Figs. 13, 43, & 44). Body not depressed dorsoventrally as usual in the family, but plump and cylindrical; when flattened on slide dorsoventrally, obovoid to elongate obovoid, sometimes nearly oblong, expanding anteriorly. Derm membranous except for a weakly sclerotized narrow median area of dorsal pygidium. Pygidium (abd V and succeeding segments) round marginally, with no prominent processes. L1s discernible, but very low and almost confounded with pygidial margin, set close, flat or broadly round apically, often notched at mesal corner, not particularly sclerotized. No lateral lobes discernible. A pair of minute gland spines between L1s (on abd IX), a similar one just laterally to L1 (on VIII), the 3 preceding segments (V-VII) each with 1 rudimentary gland spine. Prepygidial gland spines well developed, sclerotized basally, with a long membranous extension apically: 0-3 between anterior and posterior spiracles, 6-19 just posterolaterally to posterior spiracle (on metathorax); 3-9 on abd I, 2-5 on II, 0-3 on III, and 0-1 (usually 0) on IV, all being submarginal in position in the flattened specimens. Macroducts thickly rimmed around orifice, generally rather strewn than arranged in definite rows; dorsally 50 or so distributed over pygidium and some on preceding abdominal segments, 1 usually present submarginally in front of space between L1s (on abd IX); many strewn between anterior and posterior spiracles (on mesothorax) and laterally to gland spines of metathorax and abd I, 50 or so in total. Much larger dorsal macroducts marginally on pygidium, 4 on each side belonging to abd IV-VII, none of them produced to form a pore prominence. On the ventral surface of the pygidium, there are submarginally in front of L1 2 or 3 enlarged ducts which are as large as the dorsal marginal macroducts and very thickly rimmed around the orifice, accompanied anteriorly by several much smaller ducts, all these forming a short longitudinal row; a similar row on each of 2 preceding segments (abd VI and VII), 1 or 2 ducts at the posterior end of the row being enlarged and thickly rimmed around orifice. Antennae on or just within anterior margin of head, separated from each other by a space narrower than mouthparts, each composed of a robust tubercle and 2 thick setae. Anterior spiracle with 5-8 3-locular disc pores; posterior spiracle with none. Perivulvar disc pores in 5 groups arranged in a shallow arch, the median group and one or both of the anterolateral groups often united together; 3-5 in median group, 3-6 in the anterolateral, and 2-5 in the posterolateral, 16-22 in total. Anus subbasal, being situated near intersegmental furrow between abd V and VI. There is a short crescent-shaped sclerotization submarginally between abd V and VI.

Second instar female exuvial cast (Fig. 47). Sclerotized and swollen, when mounted tending to be folded in two longitudinally. Similar to adult female in general characters, but with much fewer macroducts. Dorsal macroducts occurring submarginally up to thoracic region; submedially on abd IV (or V)-VII, 1 on each segment. Ventral macroducts present at least submarginally on abd V-VII, a few being seen on each of these segments on remaining fragments of the derm, as large as dorsal macroducts. Four enlarged marginal macroducts on each side of pygidium, 1 on abd IV-VII each, thickly rimmed around orifice. Pygidial margin as in adult female, with retracted L1s and very small gland spines. Prepygidial gland spines similar to those in adult female, 2-4 on meso- and metathorax each, 1-3 on abd I, and 1 on II-IV each. Antenna composed of a flat tubercle and 2 setae.

First instar larva (Fig. 14). Elongate. Antenna 6-segmented, terminal segment short, as long as segments III-V united, not annulate, apically with a seta. No enlarged dorsal ducts on head; instead, there is near the eye a duct, which is not particularly enlarged; 2 similar ducts present on thorax on or near lateral margin; 5 similar, a little smaller ducts on abdomen marginally, each opened at apex of a small tubercle. Submedian dorsal setae occurring through thorax and abdomen, the posteriormost belonging to abd VII. Anterior spiracle with 1 3-locular disc pore. Tarsus twice as long as tibia, with a strong seta ventrally; claw short, directed downwards, making a nearly right angle with tarsus. A pair of processes present between caudal setae, sclerotized and rather prominent; another sclerotized process just laterally to caudal seta, notched on each side, accompanied laterally by a much smaller process; a marginal prominence just anteriorly to the posteriormost gland tubercle, little sclerotized. Sclerotized patches of derm dorsally on thorax and abdomen, 1 submarginally on prothorax to abd VII each, another patch mesally to the submarginal one on prothorax.

In SEMy the spiracular disc pores (Fig. 45) of the adult female is definitely 3-locular, with no septal processes. The perivulvar disc pores (Fig. 46) belong to the capitate type. The tests of both sexes (Figs. 48-52) show wax filaments running transversely in a curve.

2.6.2. *Galeomytilus*, gen. nov.

Name-bearing species [type-species]: *Galeomytilus obesus.*

This genus belongs to the Lepidosaphedini, in which it may be distinguished from other genera by the combination of the following characters in the adult female: body plump, cylindrical; L1s retracted within pygidial margin; lateral lobes absent; enlarged marginal macroducts single on pygidium; prepygidial gland spines prolonged apically to form a membranous extension; ventral submarginal ducts much enlarged and thickly rimmed around orifice. It is somewhat similar to *Mercetaspis*, but the resemblance is largely due to loss or reduction (concerning the development of lobes and the number of marginal macroducts) and, therefore, may be superficial. [See 4.5. for further discussion.]

3. SOME PREMISES FOR DISCUSSION

3.1. Major subdivisions of the Diaspididae

No classificatory scheme of the Diaspididae has yet found a general agreement. For years I have adopted a simple scheme based on the occurrence of marginal appendages of the pygidium (Table 1). I do not think that this scheme covers all the described forms of diaspidids. However, at least the bulk of the 2 main subfamilies, the Diaspidinae and the Aspidiotinae (both interpreted broadly), may be fitted in. The diaspidids are essentially characterized by their manner in forming the test, and the marginal appendages, as well as the body shape and wax-secreting organs, are assumed to have evolved in association with test formation. The scheme, therefore, may not be insignificant ecologically and evolutionarily. Moreover, the marginal appendages comprise some features (lobes, gland spines, pectinae, pore prominences), so that they must have a great phylogenetic significance.

Forms primarily without pygidial appendages are lumped together and referred

Table 1. Major subdivisions of the Diaspididae.

	Diaspidinae	Aspidiotinae
Level III	[LLDS] Diaspidini Lepidosaphedini	[LPg] Aspidiotini Odonaspidini Parlatoriini *Smilacicola*
Level II	[LLPS] Diaspidini : Kuwanaspidina	[LP] Leucaspidini
Level I	[PS] Diaspidini : Protodiaspidina	[P] *Thysanaspis*
Level 0	[0 or S] *Ulucoccus* [S] *Phoenicococcus* *Comstockiella* *Xanthophthalma* • • • • • • • • • •	

Pygidial appendages in brackets. L : lobes, all unilobed. LL : lobes, divided into lobules except the median pair. D : pore prominences. S : gland spines. P : non-glandular pectinae. Pg : glandular pectinae. 0 : no appendages (or no well-differentiated ones). The Odonaspidini and *Smilacicola* are referred to Level III on the basis of their parlatoriine-patterned 2nd instar larvae.

to Level 0. (However, *Ulucoccus* has gland spines, and *Comstockiella* shows lobelike prominences in the 1st instar.) Only several genera are mentioned in the table as belonging to this level. Apparently they have no relationship to each other. It is almost certain that other forms will be referred to this level [see also 7.1.].

Rugaspidiotines typically have no trace of pygidial appendages in the adult female, but in at least some of them this state is probably secondary as will be discussed [4.1., 4.2., 4.3., & 5.1.]. Many of them may, therefore, be referred not to Level 0 but to higher levels.

3.2. Disc pores

Until several decades ago the spiracular disc pores of the Diaspididae had long been supposed to be 5-locular and only occasionally 3- or 4-locular. It seems now that usually they are 5-locular in the Aspidiotinae and 3-locular (occasionally 4-locular) in the Diaspidinae. Exceptions are known, and slowly increasing in my observations, so that the number of loculi should be adopted as a taxonomic character with some reservation.

The perivulvar disc pores are 5-locular. However, pores abnormal in the number of loculi are sometimes found among 5-locular ones, and in *Ulucoccus* the abdominal disc pores (not perivulvar in position) are 3- or 4-locular. This may demand careful examination as to the loculi of the perivulvar disc pores, too. Apart from the number of loculi, SEMy has revealed the presence of some types of perivulvar disc pores in the structure of the septa separating the loculi: the 'capitate type' has been found in the Diaspidinae and the 'sulcate type' (and 2 other types) in the Aspidiotinae (Takagi, 1990). It should be kept in mind, however, that the species examined for the septal structure are still very few.

In the 5 genera under discussion the spiracular disc pores are 3-locular in the adult female and larvae. Three of the genera have perivulvar disc pores, and in all of them the disc pores belong to the capitate type. Thus the disc pores suggest that the 5 genera belong to the Diaspidinae. It will be shown that this relationship finds support in other features, especially of the 1st instar [4.].

3.3. Ducts

'One-barred' macroducts, usually very long, occur in the Aspidiotini, and '2-barred' ones, not so long, in the other tribes of the Aspidiotinae and in the Diaspidinae. Macroducts of another type show an 8-shaped structure at the inner end. They are supposed to be primitive in comparison with the 1- and 2-barred ducts, because the structure of the inner end is similar to geminate pores and tubular geminate pores occurring in the Asterolecaniidae and other families of the Coccoidea (Stickney, 1934). In fact, in the Diaspididae, macroducts of this type usually occur in the 1st instar larva. It seems that microducts are also 8-shaped at the inner end. It is noteworthy that *Nimbaspis* and *Anaimalaia* have macroducts of the geminate-pore type even in the adult female. Further, modified macroducts, appearing more or less deformed in structure, are seen mainly in the 2nd instar males of the Diaspidini.

3.4. First instar larval characters

Howell and Tippins (1990) in their revision of the 1st instar larvae of the Diaspididae recognized some patterns of characters associated with higher taxa. Among the genera under discussion, *Nimbaspis, Anaimalaia, Natalaspis*, and *Amphisoma* have some 1st instar larval characters in common with some well-studied species of the Diaspidini, and *Galeomytilus* does with the Lepidosaphedini. The Diaspidini may usually be characterized by the following characters: antennae with a single apical seta (instead of 2); tarsi without a strong seta ventrally; spiracular disc pores 3-locular; dorsal submedian setae occurring through thorax and abdomen as posteriorly as abd VII; ventral submedian setae absent on prepygidial abdomen; dorsal ducts absent submarginally on head and mesothorax and submedially on abd II. The Lepidosaphedini differ from the Diaspidini as follows: antennae with a subapical seta often almost apical in position, thus appearing to have 2 apical setae; tarsi with a strong seta ventrally; prepygidial abdomen ventrally with submedian setae; spiracular disc pores occasionally 5-locular. In these characters the Lepidosaphedini are similar to the Aspidiotinae.

The 1st instar larvae generally have marginal appendages around the caudal setae, and some of the appendages are assumed to be homologous with lobes and pectinae occurring in the adult females and the 2nd instar larvae. There is often a pair of processes, usually small and pointed, between the caudal setae. Although they may occasionally be shaped like lobes or pectinae, I do not think that they are true lobes or pectinae. In fact, sometimes they are absent in larvae which have well-sclerotized processes (supposed lobes) laterally to the caudal setae.

I agree with Stickney (1934b, but not 1934a) in the view that the median lobes are not manifested in the 1st instar. The supposed lobes occurring just laterally to the caudal setae belong to the 7th abdominal segment and should correspond to the 2nd lobes in the adult female, and those occurring on the preceding segment, to the 3rd. Sometimes the inner lobule of the 2nd lobe is much enlarged, apparently corresponding to, and substituting for, the enlarged median lobes in the adult female and the 2nd instar (Takagi, 1992).

It is the opinion here adopted that the marginal appendages evolved primarily in the adult female and in association with test formation. Usually they are manifested in the 1st instar, too, but the role of this instar in test formation, if any, may be negligible, because the test is largely formed by the adult in the female (except in the pupillarial forms) and by the 2nd instar in the male. Obviously the main function of the 1st instar in the life history is dispersal. On this supposition the occurrence of marginal appendages in the 1st instar is incidental to their development in the adult female. As a corollary the presence of marginal appendages in the 1st instar combined with their absence in the adult female should mean that they have been lost in the adult female.

4. TAXONOMIC POSITIONS OF THE 5 GENERA

4.1. *Nimbaspis*

This genus was referred by Balachowsky (1952; 1958) to the subtribe Rugaspidiotina, the tribe Odonaspidini. It deviates remarkably from the typical rugaspidiotine pattern as represented by *Rugaspidiotus arizonicus* in the macroducts being all of the geminate-pore type and lacking on the ventral surface of the pygidium. It has no trace of marginal appendages on the pygidium. The adult female and also the 2nd instar female, thus, appear very primitive, and, based on these instars alone, the genus is referable to Level 0 (Table 1), an assemblage of very primitive diaspidids. The 1st instar, however, has 2 pairs of well-sclerotized marginal appendages (which are the inner lobules of the supposed 2nd and 3rd lobes), and this strongly suggests that the absence of lobes in the 2nd instar and adult females is secondary [3.4.]. The 1st instar shares some characters with Diaspidini, while there is nothing to suggest a relationship to Aspidiotinae. It is strange in the tibiae and tarsi, which are frayed on their apical margins. This state is puzzling, but at least there is no evidence to show that it is a primitive character in the family.

It seems, therefore, that the adult female *Nimbaspis* is an atavistic form originated from a diaspidine with well-developed lobes. The 2nd instar female is a simplified copy of the adult female as usual in the family, while the 1st instar is supposed to have remained relatively unchanged. However, no specified image of the ancestral diaspidine is obtainable. The 2nd instar male may be worthy of study for proceeding with the possible ancestral form.

4.2. *Anaimalaia*

The primary purpose of my examination of *Nimbaspis molardi*, the name-bearing species of *Nimbaspis*, was to compare *Anaimalaia scabra* with it, because *A. scabra* appeared very close to *Nimbaspis* in the adult female except for the presence of gland spines occurring along the prepygidial body margin. However, in the 1st instar I have found definite differences between *A. scabra* and *N. molardi* [2.2.2.], and I have concluded that the two are not so closely related to each other as suggested by the similarity in the adult female.

Anaimalaia, like *Nimbaspis*, appears very primitive in the adult female in having geminate-pore type ducts and in having no marginal appendages on the pygidium. It differs from *Nimbaspis* in having no marginal appendages in the 1st instar, either, which, however, has some characters common to Diaspidini. Especially noteworthy is the presence of a pair of ducts laterally to the anus, which agree in position with the suranal ducts occurring in the subtribes Chionaspidina and Protodiaspidina [both belonging to the Diaspidini] (see Takagi, 1993, for the Protodiaspidina). In fact, the similarity between the adult females of *Anaimalaia* and *Pentacicola* [Protodiaspidina] is very close, the latter differing in having 2-barred ducts and in having pectinae on the pygidium. In two of the 3 known species of *Pentacicola*, however, the pectinae are reduced to 1 pair in the adult female and are lost in the 1st instar. We may easily imagine a *Pentacicola* species with no pectinae in the adult female as well as in the 1st instar. *Anaimalaia*, therefore, should essentially differ from the Protodiaspidina not in lacking pectinae but in having ducts of the geminate-pore type.

Here I adopt the view that all these similarities between *Anaimalaia* and *Pentacicola*, including the agreement in the presence of suranal ducts, are not superficial. Then 2 interpretations are possible: 1) the absence of marginal appendages is primary, and *Anaimalaia* is a primitive relative of the Protodiaspidina ; 2) the absence of marginal appendages is secondary, and the genus is an atavistic form originated probably from within the Protodiaspidina. The 2nd instar male of *Anaimalaia scabra* has modified macroducts marginally on the abdomen as usual in the Diaspidini, and this may support the latter interpretation.

4.3. *Natalaspis*

This genus, too, has been referred to the Rugaspidiotini. In the 1st instar, it substantially agrees with some well-studied Diaspidini, but differs from the latter in the elongate body and, especially, in the occurrence of tricuspid processes on the lateral sides of the body. Such processes may not be usual in the Diaspidini, yet similar ones are seen in, for example, *Kyphosoma* [Diaspidini: Protodiaspidina], and also in leucaspidines and odonaspidines [both belonging to the Aspidiotinae]. The inner lobule of the supposed 2nd lobe is well represented and strongly sclerotized, so that *Natalaspis* may have originated from a species with well-developed lobes in the adult female [3.4.]. In the 2nd instar female the lobes are suggested by serrate or round prominences. In the 2nd instar male, there is a pair of slender processes at the apex of the pygidium where the median lobes should be expected. These processes are similar to gland spines or pectinae in shape, but have no microduct. I am inclined to believe that they are modified median lobes.

The 2nd instar male is also characterized by having short ducts which are similar to those in the '*xerospermi*-type' 2nd instar males (see Takagi et al., 1989, for this type of the 2nd instar male). These ducts, however, occur not in a large cluster on each side of the abdomen as in the *xerospermi*-type, but in small groups on the 2nd to 7th abdominal segments just within the margin. Their positions correspond to those of the frame ducts in Chionaspidina [Diaspidini].

I have prepared a figure (Fig. 1) and a brief description of the head of the adult male [2.3.], but would like to avoid discussion on its characters primarily because of our poor knowledge on this stage. However, it seems that there is no character in disagreement with the supposition that *Natalaspis* has arisen from within the Diaspidini.

The adult female of the unnamed species mentioned in Section 2.4. differs from *N. formosana* and *N. simplex* in having obvious prominences on the pygidium, which can be regarded as lobes. Thus, it may represent a relatively primitive form of *Natalaspis*. Unfortunately, no larval specimens have been available, so that the generic position of the species is not definitely unquestionable. In fact, there is another species of *Natalaspis* which may be doubted about its generic position: *N. leptocarpi*. This species was transferred from *Odonaspis* to the genus by Ben-Dov (1976), but is quite different from *N. formosana* and *N. simplex* as well as from the odonaspidines in host association.

4.4. *Amphisoma*

This is a surprising form, having a set of differentiated marginal, submarginal and submedian macroducts on the ventral as well as dorsal surface of the pygidium. In spite of this quite extraordinary character and also of the rudimentary median lobes *Amphisoma erectum* undoubtedly belongs to the Diaspidini; there is no other character which contradicts this view. The species even gives an impression that it is a member of the Chionaspidina. This is partly due to the preanal and intersegmental scleroses [2.5.1.], which remind me of *Pinnaspis* species. The 1st instar has a pair of ducts laterally to the anus [suranal ducts], and the 2nd instar male is very similar to the 2nd instar males of some chionaspidines. Thus these instars support the view that *Amphisoma* belongs to the Chionaspidina.

4.5. *Galeomytilus*

The adult female has very large marginal macroducts [megaducts] dorsally on the pygidium as in many lepidosaphedines. It is peculiar in having on the ventral surface of the pygidium, too, enlarged ducts submarginally, of which several ones are as large as the megaducts. These ventral ducts occur in longitudinal segmental rows in the positions where microducts are expected to occur in other lepidosaphedines.

The 1st instar represents a lepidosaphedine pattern in the combination of the following characters: the occurrence of submedian dorsal setae through the thorax and abdomen, the occurrence of submedian ventral setae on the prepygidial abdomen, and the presence of a strong seta on the tarsus. The occurrence of 3 ducts near the margin on each side of the cephalothoracic region (1 posteriorly to the eye or between the head and prothorax, 1 between the pro- and mesothorax, and 1 between the meso- and metathorax) is also common at least to *Lepidosaphes*. However, it has also the following characters, which may be exceptional or uncommon in the lepidosaphedines: presence of small dorsal patches on the thorax and abdomen; shortened claws, which make a nearly right angle with the tarsus.

5. DISCUSSIONS

5.1. Rugaspidiotini : an artefact

Howell et al. (1986) examined the 1st instar of *Rugaspidiotus arizonicus*, and concluded that it is similar in several important characters to the Odonaspidini ['Odonaspidinae' according to them ; referable to the Aspidiotinae in the scheme adopted in this paper]. Howell (1992) described the 1st instars of 3 species of *Rugaspidiotinus*, and stated that 'they form a separate branch between *Comstockiella* (Group III) and Groups I and II' [Group I and II correspond to the Aspidiotinae and Diaspidinae in Table 1].

Based on the description mentioned above, *R. arizonicus* certainly has some characters in common with the Aspidiotinae. It shows no trace of marginal appendages. If this state in the 1st instar (and also in the 2nd instar and adult female) is primary, *R. arizonicus* should be a primitive diaspidid having some relationship to the Aspidiotinae. On the other hand, the patterns in the 3 species of *Rugaspidiotinus* are, so far as based on the descriptions, almost certainly lepidosaphedine [see also 7.2.]. 'No clearly defined pygidial lobes' are found in *R. circumdatus*, but 'Lobes 2 and 3' are 'well developed' in *R. sculpturatus* and *R. nebulosus*. The absence of marginal appendages in the 1st species may probably be due to a secondary loss so far as based on the general similarity among the 3 species.

Smilacicola is another genus referred to the Rugaspidiotini. The 2nd instar larvae are divisible into 2 distinct types, the parlatoriine type and the geminate-pore type. The former type shows that the genus shares an ancestor with the Parlatoriini, and the latter may approximate to an earlier ancestral form (Takagi, 1983). In the pattern of the 1st instar the genus agrees with Aspidiotinae except for the presence of submedian dorsal setae on the abdomen which occur as posteriorly as the 7th segment [see also 7.3.].

Protodiaspis was placed in the Rugaspidiotina by Borchsenius (1966). The subtribe Protodiaspidina, comprising the American *Protodiaspis* and 5 Asian genera, is now recognized under the tribe Diaspidini (Takagi, 1993).

In the present work 2 other genera, *Nimbaspis* and *Natalaspis*, which have been referred to the Rugaspidiotini, are revised. These genera, bearing no relationship to each other, are supposed to have originated from some forms of the Diaspidini with well-developed lobes in the adult females [4.1. and 4.3.]. In the opinion adopted in this paper, *Anaimalaia* resembles *Nimbaspis* only superficially in the adult female, and is related to *Pentacicola* [Diaspidini : Protodiaspidina].

We can, therefore, conclude that the genera mentioned in this section have no relationship to each other and that their proper taxonomic positions, when fully clarified, will be scattered in the family.

5.2. *Amphisoma* and *Galeomytilus* : incipient rugaspidiotines

Undoubtedly *Amphisoma* belongs to the Diaspidini and *Galeomytilus* to the Lepidosaphedini, yet they share a character quite unusual in these tribes : the occurrence of macroducts on both the surfaces of the pygidium. Their pygidial lobes are much reduced : the lateral lobes are completely lost and the median lobes are nearly merged into the pygidial margin. In all these characters they are rough analogues to rugaspidiotines. In *Amphisoma* even the exuvial cast of the 2nd instar female is bivalve as in *Rugaspidiotus arizonicus*. Thus these genera are harmonious with the conclusion of the preceding section that the rugaspidiotine pattern has evolved in different groups of diaspidids.

In *Galeomytilus* the ventral macroducts of the pygidium occur in the positions where microducts are expected to be found in other lepidosaphedines. In *Amphisoma*, on the other hand, the ventral macroducts are arranged not only in submedian and submarginal series but also marginally in the definite positions, while no microducts are expected to occur on the pygidial margin in ordinary diaspidines. Thus, there being no precursors, the emergence of the ventral marginal macroducts appears mysterious. It seems as if the ventral surface of the pygidium had gained the nature of the dorsal, but ventral features other than the macroducts—vulva, perivulvar disc pores, setae, apical sclerosis of the derm—are all normal in appearance and position.

5.3. Why has the rugaspidiotine pattern evolved so many times?

In *Galeomytilus obesus* several ventral macroducts of the pygidium are so enlarged as to equal the megaducts (occurring dorsally on the margin) in size, and, though situated ventrally and submarginally, they should be megaducts functionally. In *Amphisoma erectum* the ventral set of macroducts is as complete as the dorsal one, indicating that both the pygidial surfaces function the same in secreting wax filaments for test formation.

The pygidial lobes are much reduced in these species, and it is doubtful that the remaining median lobes, almost merged into the pygidial margin, still have any function. It has been supposed that, in diaspidids with well-developed sclerotized lobes, the female uses these appendages to pare or saw an upper layer of the surface tissue of the host plant, moving horizontally in oscillation or rotation to form the test.

Amphisoma erectum and *Galeomytilus obesus* occur on the hairy surface of the host plant, where horizontal movements of the body are impeded by dense and long standing hairs. *A. erectum* forms tests standing on the anterior end in both sexes. The female, however, still moves right and left in oscillation, and constructs a test with the ventral portion formed as complete as the dorsal. Probably the growing test gives support to the moving insect body, which, standing on the head, is held vertical to the surface of the plant body. In this position of the body the lobes are probably useless. There is nothing particular in the male test. In fact, standing male tests are occasionally found in other Diaspidini, of which the female tests are formed horizontally. (Generally in this tribe, the 2nd instar male has abundant ducts on the ventral surface as well as on the dorsal and secretes wax to form a tubular test without moving.)

Galeomytilus obesus, on the other hand, does not stand but lies. The adult female is a small and cylindrical insect, apparently in accord with the narrow space among the dense hairs of the host plant. It certainly does not make horizontal movements; in spite of this, the wax filaments on the test run transversely. The insect is assumed, therefore, to roll around the longitudinal body axis when forming the test. It seems, in this species, too, that the ventral surface of the pygidium takes part in test formation, and that the lobes are of no use. No specimen of the 2nd instar male has been available, but the male test is similar to the female one, so that the 2nd instar male should move the same way.

These examples will suffice to show that the rugaspidiotine pattern of characters will evolve in such habitats as restrict horizontal movements—in cracks on the bark, under the stipules, under the leaf-sheaths, etc., as well as in dense erect hairs, of the host plant. Under such a condition the pygidial appendages may be useless (however, the functions of the pectinae and gland spines in test formation are unknown). In the typical rugaspidiotine pattern these appendages are completely absent and the pygidium has abundant ducts on the ventral surface as well as on the dorsal. The loss of the pygidial appendages can be atavistic, and, therefore, may easily occur in various groups of the family. Some habitats may require the augmentation of ducts on the ventral surface of the pygidium, and *Amphisoma erectum* and *Galeomytilus obesus* suggest that females in different groups of the family can meet this requirement. After all, we may reasonably conclude that the rugaspidiotine pattern of characters can evolve polyphyletically in diverse habitats.

The Rugaspidiotini have been recorded from a wide range of habitats, and this fact probably reflects their diverse origins and diverse ecological requirements. The Odonaspidini, occurring under the leaf-sheaths of bamboos and other Poaceae, are parallels to the Rugaspidiotini in the cryptic mode of life and in the pattern of the adult female pygidial characters. They may be regarded as representing another case of the evolution of the rugaspidiotine pattern—a case of a fairly successful taxon as compared with the rugaspidiotines, which are now to be disassembled into unrelated genera [see also 7.4.].

6. CONCLUSIONS

6.1. This work covers only a small part of the Rugaspidiotini, yet may be sufficient to show that the tribe as composed by authors is an assemblage of unrelated forms. I myself referred *Natalaspis* and *Smilacicola* to the Rugaspidiotini and even discussed the evolution of the Rugaspidiotini. Needless to say, any argument based on such a false composition is meaningless.

The relationships suggested in this paper are, however, still very crude and rough. There seems to be no described species closely related to *Rugaspidiotus arizonicus*. Its relationship to the Aspidiotinae seems undeniable, but no taxon within the subfamily is specified as its relative. *Rugaspidiotinus* is assumed to have arisen from within the Lepidosaphedini, and *Nimbaspis* and *Natalaspis* are supposed to be related to the Diaspidini, but no further analysis has been made. *Smilacicola* evidently has a relationship to the Parlatoriini, probably sharing an ancestor with the latter, but no real organism is known which may represent or approach the supposed common ancestor in the pattern of characters.

6.2. In concluding this paper I cannot evade the question: how to treat these genera formally. If *Rugaspidiotus* lacks pygidial appendages primarily, it should be referred to Level 0; if it does secondarily, it may have its own tribe Rugaspidiotini in the subfamily Aspidiotinae. *Smilacicola* may also have its own tribe in the subfamily. *Rugaspidiotinus, Nimbaspis* and *Natalaspis* appear in the adult females too much changed from their supposed ancestral tribes to be included within the latter. Then they, too, may have their own higher taxa, say tribes. However, this procedure, when extended to other rugaspidiotines, will result in a number of monotypic tribes.

The odonaspidines are parallels to the rugaspidiotines, but, in contrast to the latter, they form a compact group both in morphology and in host association. It should be emphasized that they have their own characters in the 1st instar (Howell and Tippins, 1990). Thus the tribe Odonaspidini appears to be a distinct, well-stabilized taxon.

Distinctness in the 1st instar among others may be convincing on the validity of diaspidid higher taxa, and I adopt it as a criterion here [see also 7.5.]. In this instar *Rugaspidiotinus* seems to agree with the Lepidosaphedini and *Nimbaspis* and *Natalaspis* are not substantially different from the Diaspidini. Hence they should be included within these tribes. *Anaimalaia* may be referred to the Protodiaspidina [Diaspidini] especially on the basis of the presence of suranal ducts in the 1st instar [4.2.].

6.3. The adult female of *Nimbaspis molardi* appears very primitive, not only lacking pygidial appendages but also having geminate-pore type macroducts. It is, however, interpreted to be atavistic, and the genus is assumed to have arisen from an advanced form of the Diaspidini. Adopting this interpretation, we have another question: how to treat such apparently primitive forms produced by reversal of evolution. Obviously their primitive patterns of characters had been held cryptic in their genomes until they again manifested them. Their advanced patterns of characters once achieved are now ancestral, and may not be lost but just suppressed. It follows that they have not returned to the primitive ancestral taxa.

We do not know how exactly the apparently primitive atavistic forms reveal the patterns of their primitive ancestors. In this connection it is noteworthy that the adult and 2nd instar females of *Nimbaspis molardi* are similar to the geminate-pore type 2nd instar larvae of *Smilacicola* in spite of the fact that these genera belong to the different subfamilies Diaspidinae and Aspidiotinae. This suggests that they have reproduced the pattern of the common ancestor of these subfamilies to some degree. It should be added that there are various forms of supposedly primitive diaspidids, all referable to Level 0 in Table 1. Among them, *Ulucoccus*, having gland spines, is supposed to approach the ancestral form of the Diaspidini. However, not all of them may represent patterns ancestral to extant advanced forms.

6.4. For years I have been arguing that atavistic patterns in the 2nd instar larvae (especially of the male) are manifested incidentally to the evolving adult females (the latest paper on this subject: Takagi, 1993). In *Nimbaspis molardi*, however, the stage that is atavistic is the adult female (and the 2nd instar female, which is a simplified copy of the adult female)—a phenomenon not attributable to incidental atavism. The atavistic adult female should have its own adaptive significance. This species occurs on soft shoots of the host plant, but I am not sure whether this habitat is relevant to the atavistic manifestation.

6.5. In conclusion, the Rugaspidiotini-problem is deeply concerned in a unifying idea in biology—phenotypic potential. This idea is still difficult to explain in terms of mechanisms underlying phenomena that can be relevant to it. It is, however, useful not only in arguing about atavistic organisms or 'living fossils of another kind' (Takagi, 1993) but also in understanding why convergent forms should strictly be discriminated. Convergent forms, however similar in the manifested phenotypes, are different in their ancestral phenotypes now held cryptic—evidence that they have different genomes. Mereover, 'Cryptic maintenance of phenotypic potential can only be one side of the coin. Changes in regulatory schemes…can result in entirely new, large-scale phenotypic experiments' (Hunkapillar et al., 1982). Convergent forms with their own genomes will not necessarily agree in further phenotypic experiments—in other words, they differ in evolutionary potential.

7. SUPPLEMENTARY NOTES

7.1. [for 3.1.]. In the view here adopted the diaspidids of Level 0 are remnants of the earliest evolution of the family and suggest the appearance of a wide variety of forms at that time—a small-scale version of 'disparity' (Gould, 1990 ; 1991) or the 'old-fashioned meadow'-like effect of evolution (Willmer, 1990), both the terms having been applied to the emergence of phyla. The formal classification of the Level 0 forms is beyond the scope of the present paper, but it is obvious that they cannot be lumped together in the same higher taxon (a subfamily or a tribe).

7.2. [for 5.1.]. As to the proposed transference of *Rugaspidiotinus* to the Lepidosaphedini, Prof. James O. Howell wrote to me as follows: 'Your idea that *Rugaspidiotinus* is related to the Lepidosaphedini is, I believe, a very good one. I, too, had similar thoughts, at least based on the first instars. Their general characters fit those of the Lepidosaphedini, including their lack of dorsal ducts on the thorax.' (Jan. 15, 1995).

7.3. [for 5.1.]. The drawing of the 1st instar of *Smilacicola heimi* in Takagi (1983: Fig. 6) is probably inaccurate in the occurrence of ducts on the dorsal and ventral surfaces. This has been found in comparing the drawing with the exuvial cast of *S. crenatus*, in which the 4 pairs of submedian ducts, occurring on the thoracic segments and the 2nd abdominal segment, are all opened dorsally and the prothoracic submarginal duct is situated ventrally as in some well-studied species of the Aspidiotinae.

7.4. [for 5.3.]. There is another example of the evolution of the rugaspidiotine or odonaspidine pattern: *Antakaspis terminaliae*, for which Mamet (1959) proposed the tribe Antakaspidini. This species is especially similar to the Odonaspidini, but probably in convergence with the latter. As to the habitat, however, the species was stated only as occurring on the trunk of *Terminalia* sp.

7.5. [for 6.2.]. Thus many of the 'rugaspidiotine' genera may be referred to their supposed ancestral tribes. It should be emphasized that the criterion (distinctness in the 1st instar) is adopted for assuring the distinctness of higher taxa and not for avoiding paraphyly. 'Heteromorph speciation' (Endrödy-Younga, 1981)—rising of a new species from one of the subspecies of a polytypic species—evidently makes the parental species paraphyletic with respect to the daughter species (Bremer and Wanntorp, 1979 ; Patton and Smith, 1981). Species—biological entities as currently understood—do not necessarily coincide with cladistic clusters. Generally, no taxa of higher categories are considered to be real in the same sense as species are. However, the view is adopted that higher taxa are also biological phenomena rather than methodological devices and that all taxa, specific or supraspecific, should represent *stabilized evolutionary stages* or *grades*. In this view, paraphyletic taxa can be sound biologically. The tribe Parlatoriini is probably paraphyletic with respect to the Odonaspidini, but authors (although most of them may not be aware of this relationship) recognize both the tribes as good taxa.

ACKNOWLEDGEMENTS

This paper is based on material collected in India in connection with the project 'Research Trips for Agricultural and Forest Insects in the Subcontinent of India' and in Malaysia and the Philippines under the project 'Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia'. I express my thanks to the concerned Authorities in these countries for the approval for our surveys and to many people who helped us.

The latter project came to an end with the trips carried out in 1994 in the Philippines with the cooperation of staff members of the University of the Philippines at Los Baños. Dr Venus J. Calilung, Department of Entomology, cooperated for our project and joined some trips. Dr William Sm. Gruezo, Director of the Museum of Natural History, approved our project. Dr Edwino S. Fernando, Department of Forest Biological Sciences, identified a number of host plants. Mr Ireneo L. Lit, Mr Orlando Eusebio and Mr Edison Cosico, all from the Museum of Natural History, helped us in carrying out the trips in the country. Many students in the Department of Entomology and other departments helped us in various ways.

I am grateful to the Authorities of the Musée Royal de l 'Afrique Centrale, Tervuren, Belgium, for making available to me type material of *Nimbaspis molardi*.

I am thankful to Prof. James O. Howell, University of Georgia, U.S.A., for his helpful information.

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APPENDIX : GENERA PLACED IN THE RUGASPIDIOTINI

Rugaspidiotini Balachowsky, 1949
[Originally Rugaspidiotina, Odonaspidini]

Adiscodiaspis Marchal, 1909. *A. ericicola* (Marchal, 1909) [=*Diaspis* (*Adiscodiaspis*) *ericicola*] and *A. tamaricicola* Malenotti, 1916, were referred to the Rugaspidiotina, Diaspidini, by Borchsenius (1966). Tang (1986) erected *Circodiaspis* for *A. tamaricicola* and another species, while Danzig (1993) synonymized *Circodiaspis* with *Adiscodiaspis* [but see *Circodiaspis*], referring the genus tentatively to the Diaspidini.

Annulaspis Ferris, 1938. Erecting the genus for *A. polygona* Ferris, 1938, the author referred it to the Odonaspidini. Balachowsky (1949) proposed to establish the subtribe Rugaspidiotina under the Odonaspidini, and included *Annulaspis* in it.

Circodiaspis Tang, 1986. The author proposed this genus for *Adiscodiaspis tamaricicola*

Malenotti, 1916 ['*A. tamaricola*'] and *C. sinensis* Tang, 1986, and referred it to the Rugaspidiotini. These species may rightly be separated from *Adiscodiaspis*, but, on the other hand, they may be congeneric with *Prodiaspis tamaricicola* Young, 1984, which was described as belonging to the Xanthophthalminae. On this supposition, *Circodiaspis* is a junior synonym of *Prodiaspis* Young, 1984, and *P. tamaricicola* Young is a junior homonym of *C. tamaricicola* Malenotti.

Crassaspis Ferris, 1941. Erecting the genus on the basis of *C. multipora* (Ferris, 1919) [=*Pseudodiaspis multipora*] and *C. maculata* Ferris, 1941, the author referred it to the Diaspidini. Borchsenius (1966) placed it in the Rugaspidiotina, Diaspidini.

Discodiaspis Koronéos, 1934. The genus was based on *D. suaedae* Koronéos, 1934, which is a junior synonym of *Protargionia salicorniae* Gómez-Menor, 1928. Balachowsky (1953) transferred *Rugaspidiotus numidicus* Balachowsky, 1949, to *Discodiaspis* and, thus, recognized the genus as a member of the Rugaspidiotina, Odonaspidini. According to Ben-Dov (1974), the following 4 species are also referable to this genus: *D. consolidata* (Ferris, 1941) [=*Chortinaspis consolidata*]; *D. globosa* Munting, 1968; *D. janinae* Balachowsky, 1970; *D. gallamformans* Ben-Dov, 1974.

Natalaspis MacGillivray, 1921 [=*Poliaspoides* MacGillivray, 1921]. *Natalaspis* was based on a form unnamed at that time, now *N. formosana* (Takahashi, 1930). It includes *N. simplex* (Green, 1899), and, according to Ben-Dov (1976), also *N. leptocarpi* (Brittin, 1916) [= '*Odonaspis ? leptocarpi*']. As stated in the text another species (unnamed) may be referred to the genus. Balachowsky (1949) recognized the genus [*Poliaspoides*] as a member of the Rugaspidiotina, Odonaspidini.

Nimbaspis Balachowsky, 1952. Erecting the genus on the basis of *N. molardi* Balachowsky, 1952, and *N. reticulata* Balachwosky, 1952 ['*N. reticulatus*'], the author referred it to the Rugaspidiotina, Odonaspidini. *N. squamosa* Balachowsky et Ferrero, 1967 ['*N. squamosus*'] was added to the genus.

Osiraspis Hall, 1923. This genus was established on the basis of *O. balteata* Hall, 1923. Balachowsky (1953) referred it to the Rugaspidiotina, Odonaspidini.

Protodiaspis Cockerell, 1898. Borchsenius (1966) referred this genus to the Rugaspidiotina, Diaspidini. Takagi (1993) associated it with 5 other genera in the subtribe Protodiaspidina, Diaspidini, though he recognized that the 14 species referred to the genus are far from uniform in the adult females.

Pygalataspis Ferris, 1921. This genus was proposed for *P. miscanthi* Ferris, 1921. Borchsenius (1966) placed it in the Rugaspidiotina, Diaspidini.

Ramachandraspis Rao, 1953. This genus was erected on the basis of *R. fenestrata* Rao, 1953, and referred to the Rugaspidiotina, Diaspidini, by Borchsenius (1966).

Rugaspidiotinus Balachowsky, 1953. This genus was originally proposed for part of *Rugaspidiotus*, and now comprises *R. circumdatus* (Ferris, 1938), *R. fuscitatis* (Ferris, 1938), *R. nebulosus* (Ferris, 1938) and *R. sculpturatus* (Ferris, 1938).

Rugaspidiotus MacGillivray, 1921. This genus was erected on the basis of *R. arizonicus* (Cockerell, 1900) [=*Diaspis arizonica*]. At least 8 other species were referred to the genus and later removed to other genera. Another species, *Rugaspidiotus communis* Hu, 1987, was also described in the genus.

Rugpapuaspis Ben-Dov, 1991. This genus is based on *R. proxantennata* Ben-Dov, 1991. According to the author, it is referable to the Rugaspidiotini.

Smilacicola Takagi, 1969. Erecting the genus on the basis of *S. apicalis* Takagi, 1969, the author placed it in the Rugaspidiotini. Later, *S. heimi* (Balachowsky, 1947) [=*Rugaspidiotus heimi*] and *S. crenatus* Takagi, 1983, were added to the genus.

PLATES

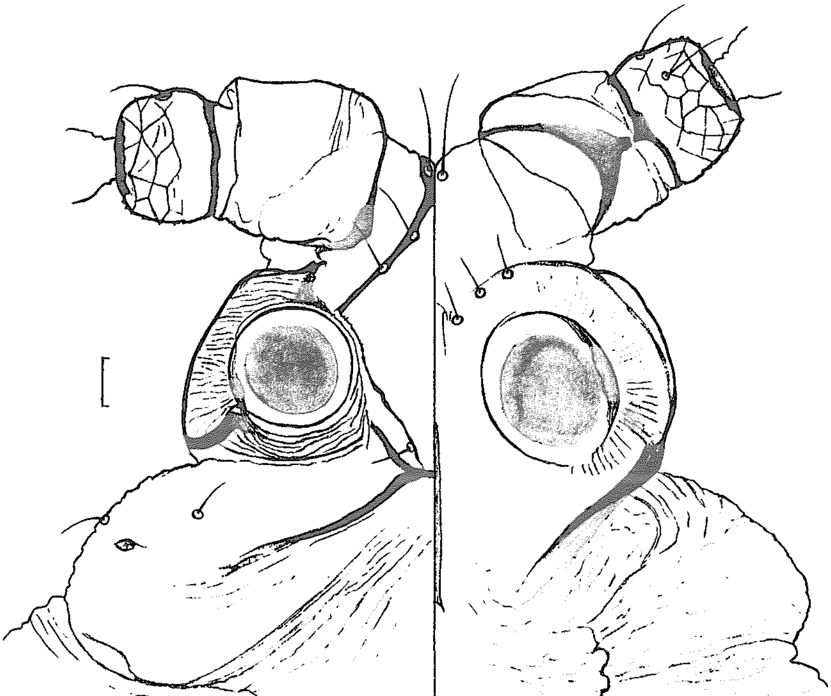

Fig. 1. *Natalaspis formosana*, adult male: head [93PL-135]. Scale: 0.01 mm.

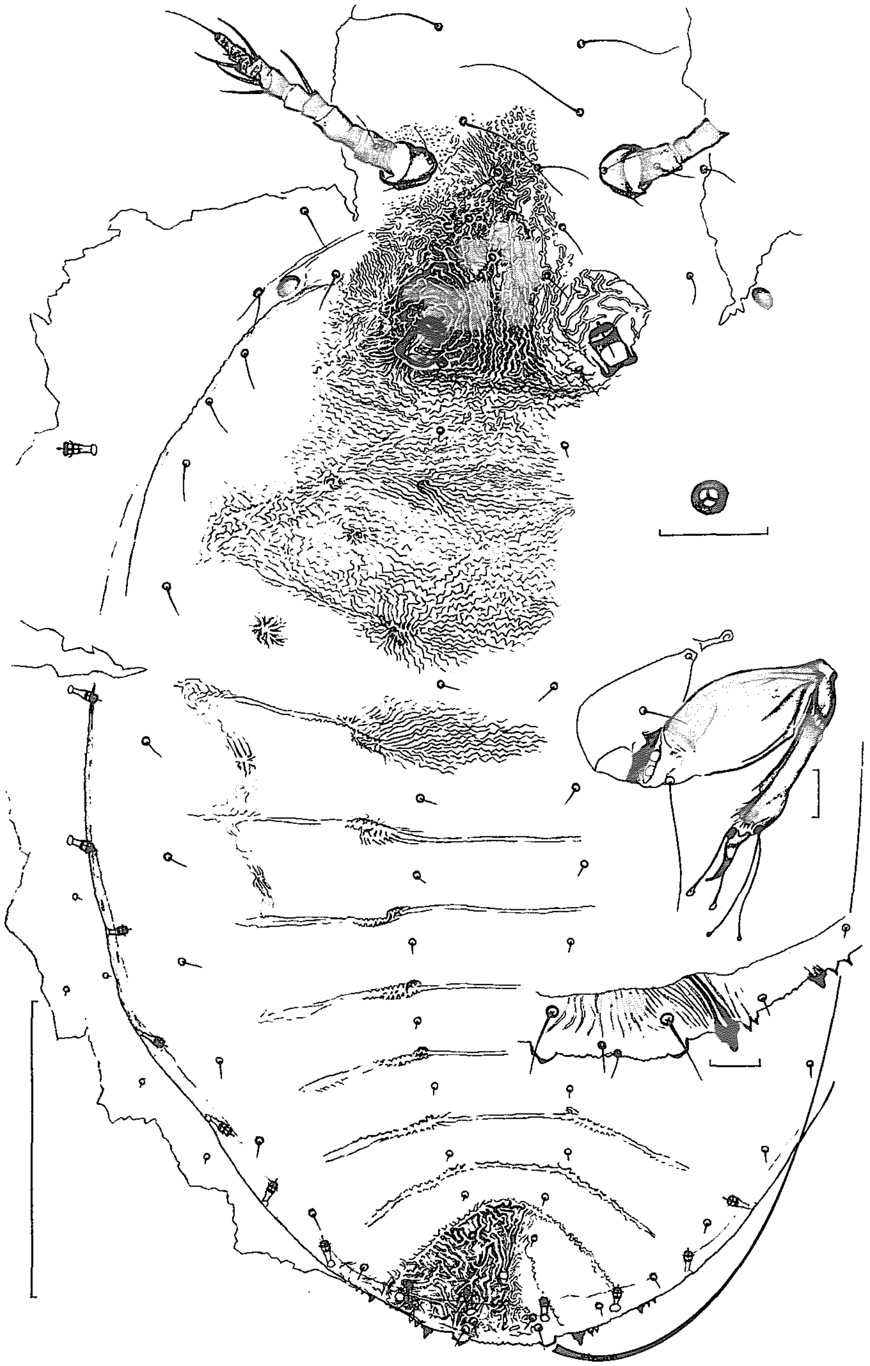

Fig. 2. *Nimbaspis molardi*, exuvial cast of 1st instar female. Scale for exuvial cast: 0.1 mm; scales for parts: 0.01 mm.

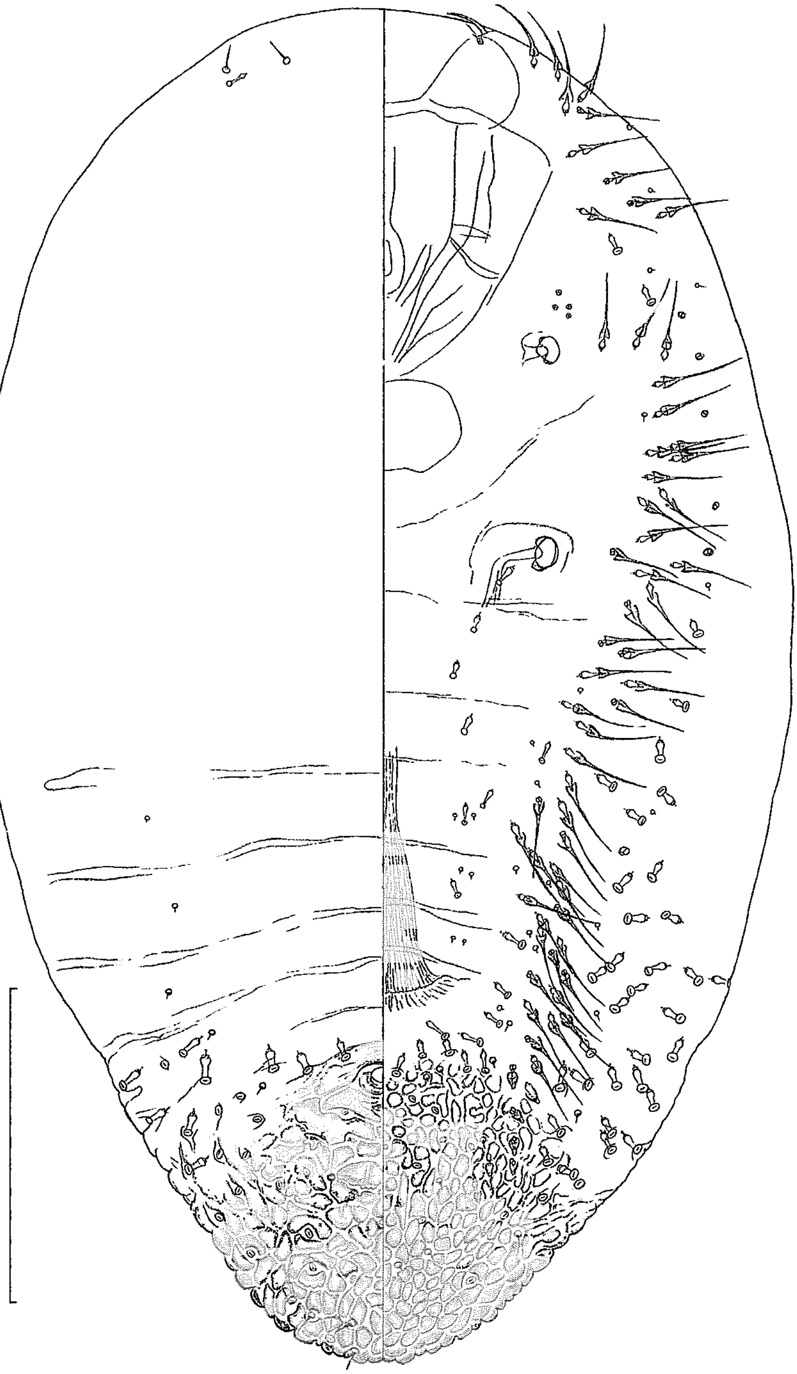

Fig. 3. *Anaimalaia scabra*, adult female. Scale: 0.1 mm.

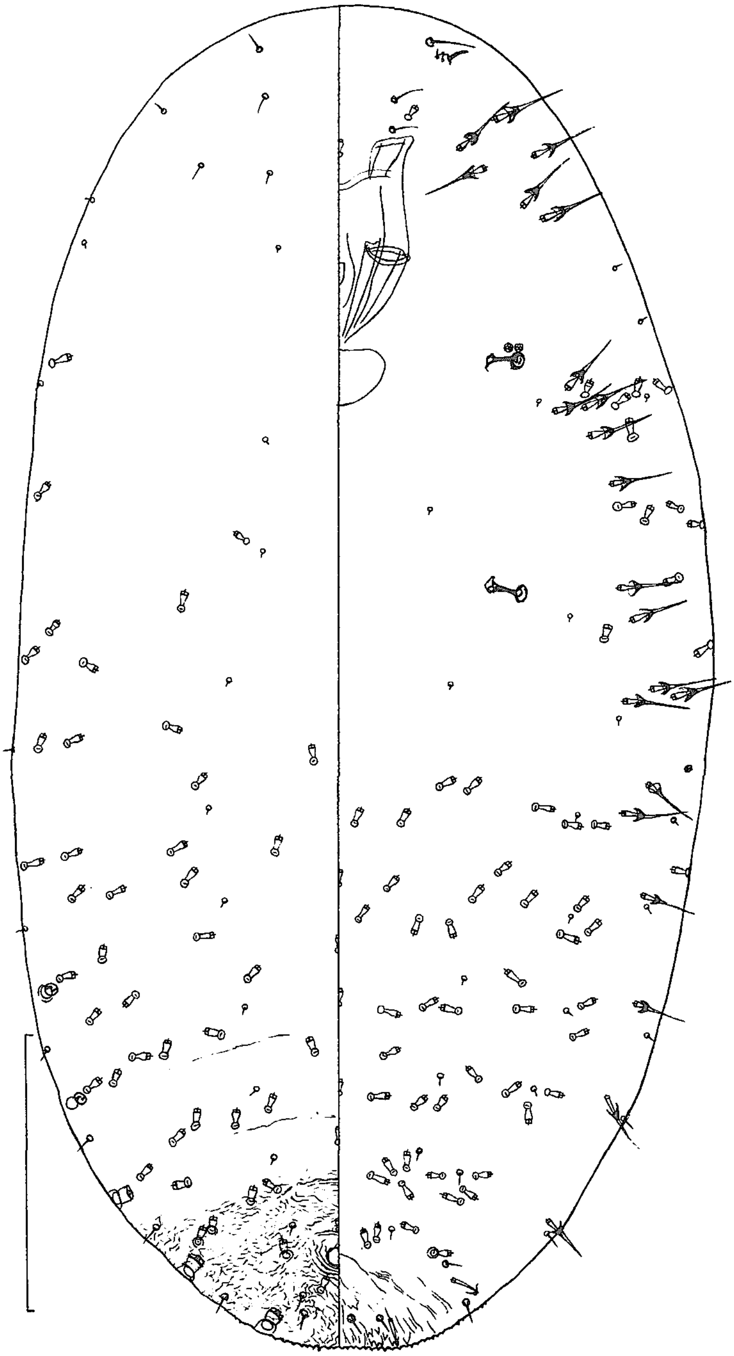

Fig. 4. *Anaimalaia scabra*, 2nd instar male. Scale: 0.1 mm.

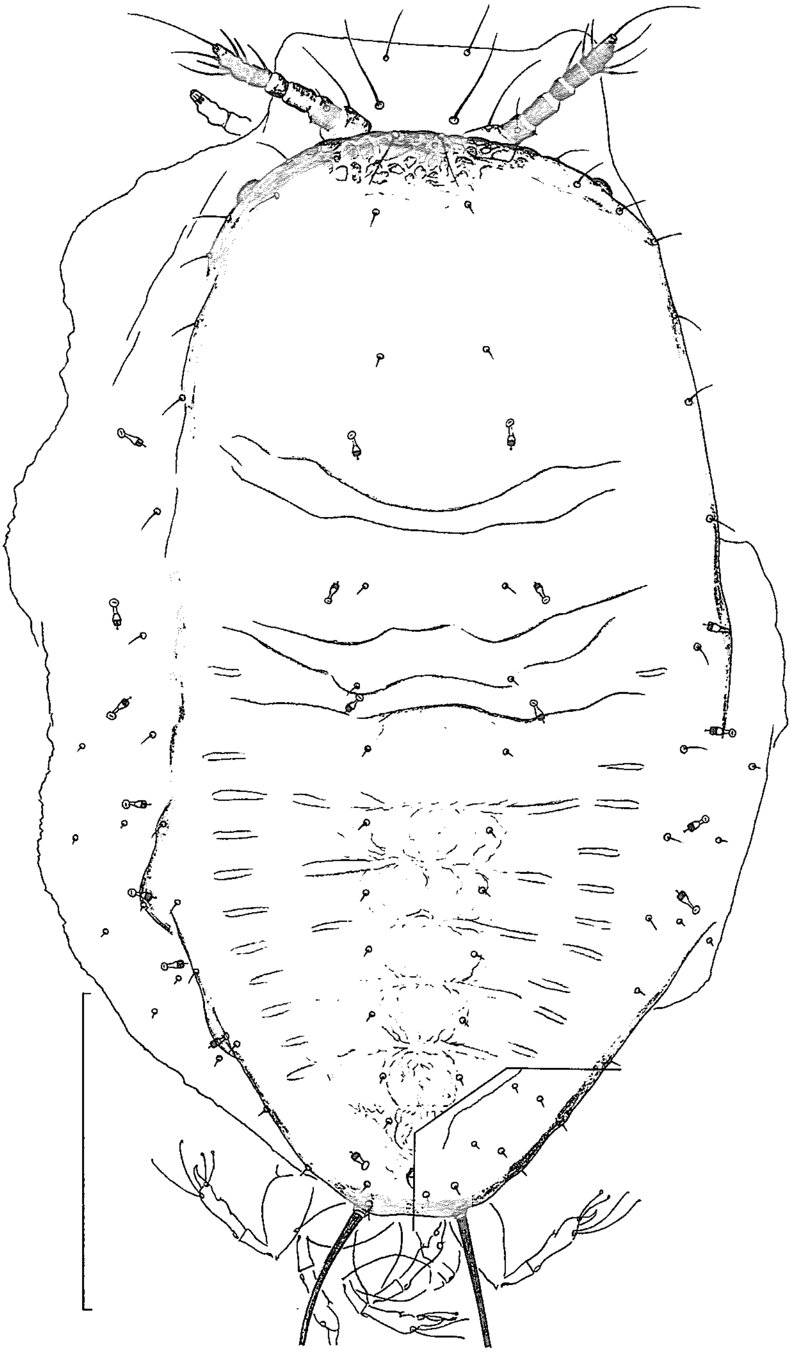

Fig. 5. *Anaimalaia scabra*, exuvial cast of 1st instar. Scale : 0.1 mm.

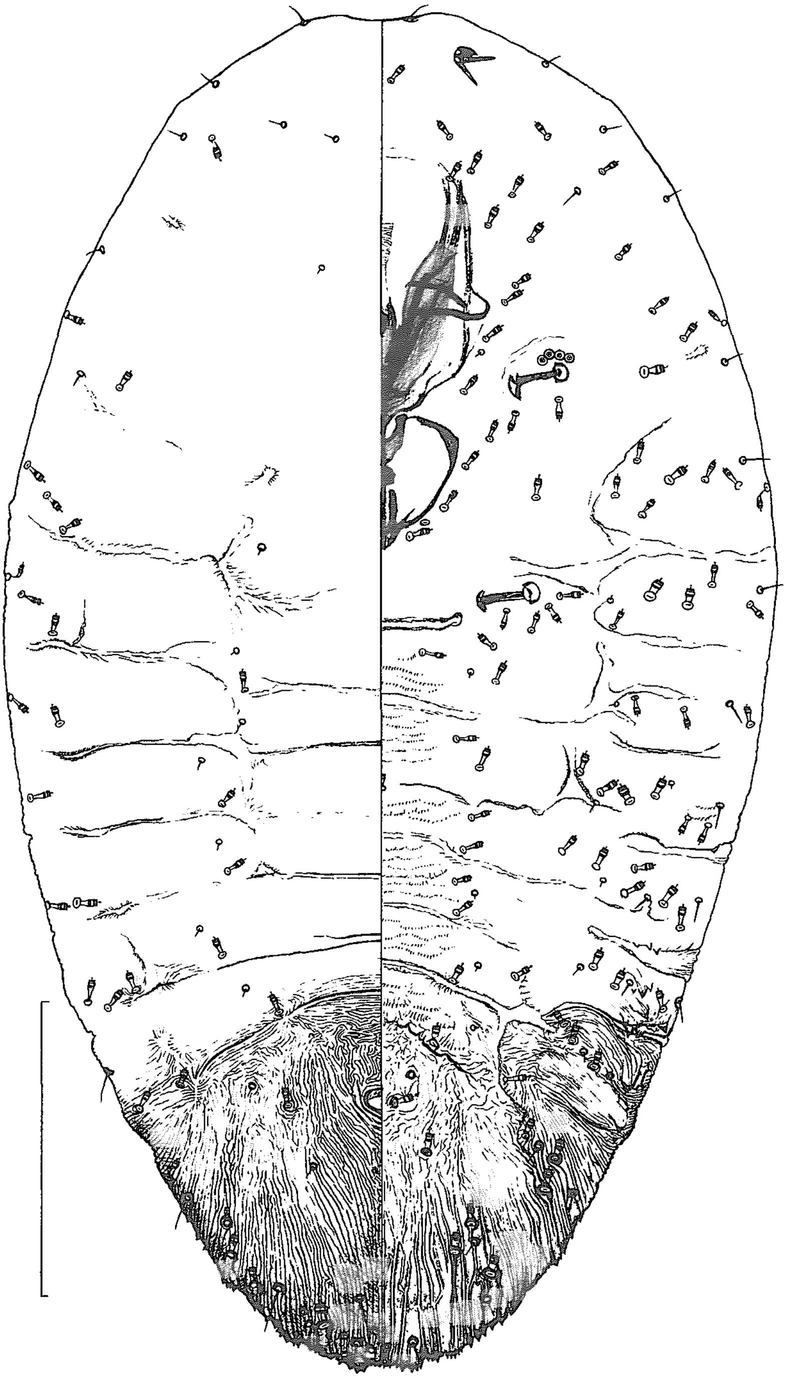

Fig. 6. *Natalaspis formosana*, 2nd instar female [93PL-135]. Scale: 0.1 mm.

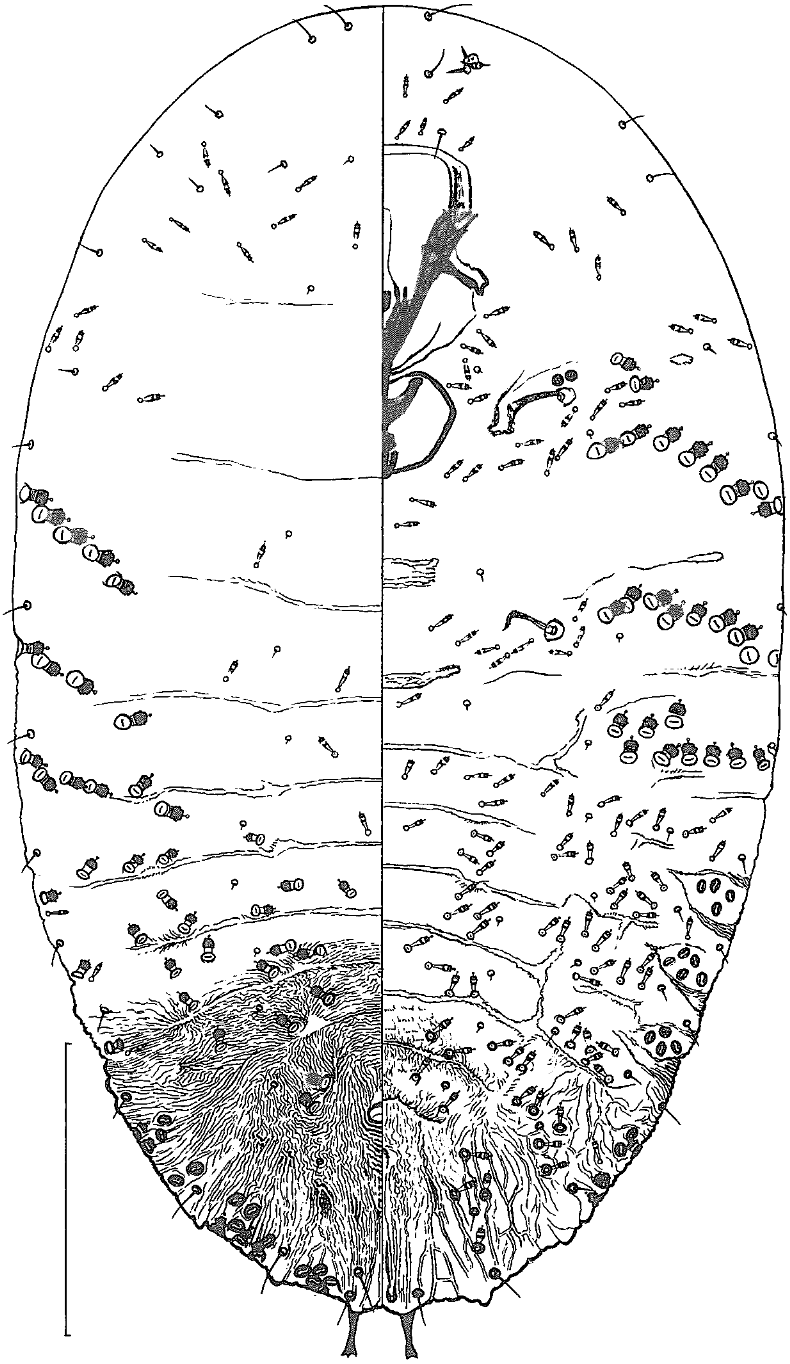

Fig. 7. *Natalaspis formosana*, 2nd instar male [93PL-135]. Scale: 0.1 mm.

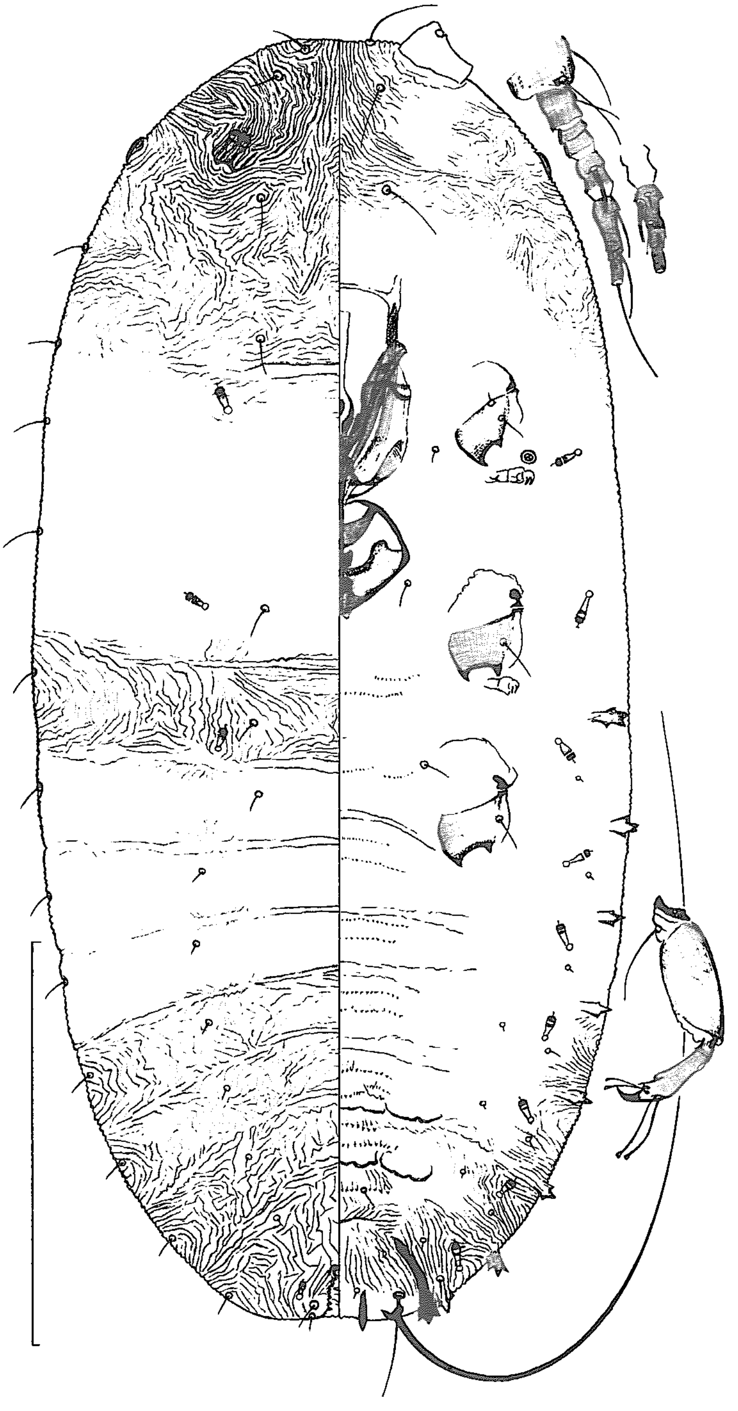

Fig. 8. *Natalaspis formosana*, 1st instar [93PL-135]. Scale: 0.1 mm.

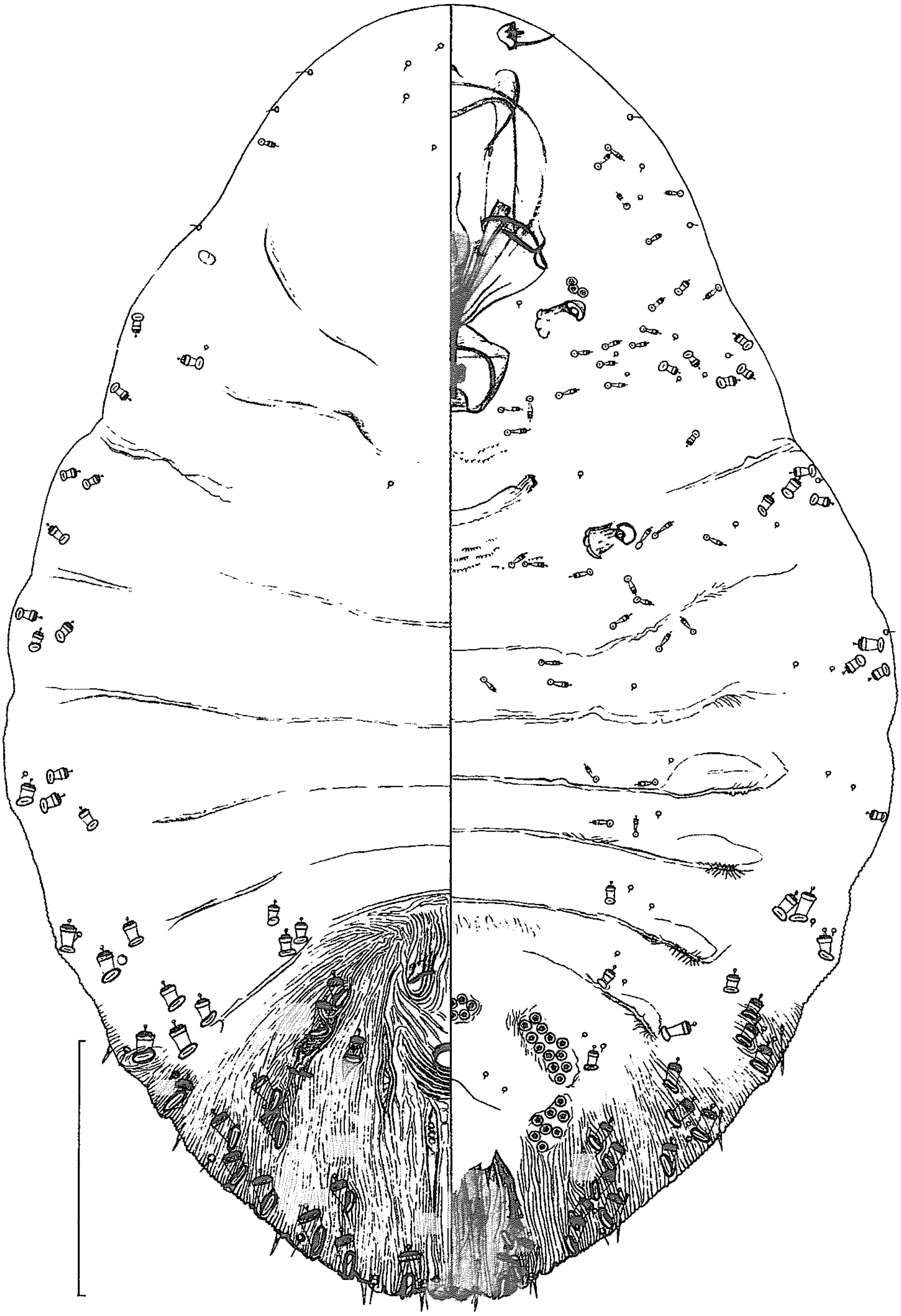

Fig. 9. *Amphisoma erectum*, adult female. Scale: 0.1 mm.

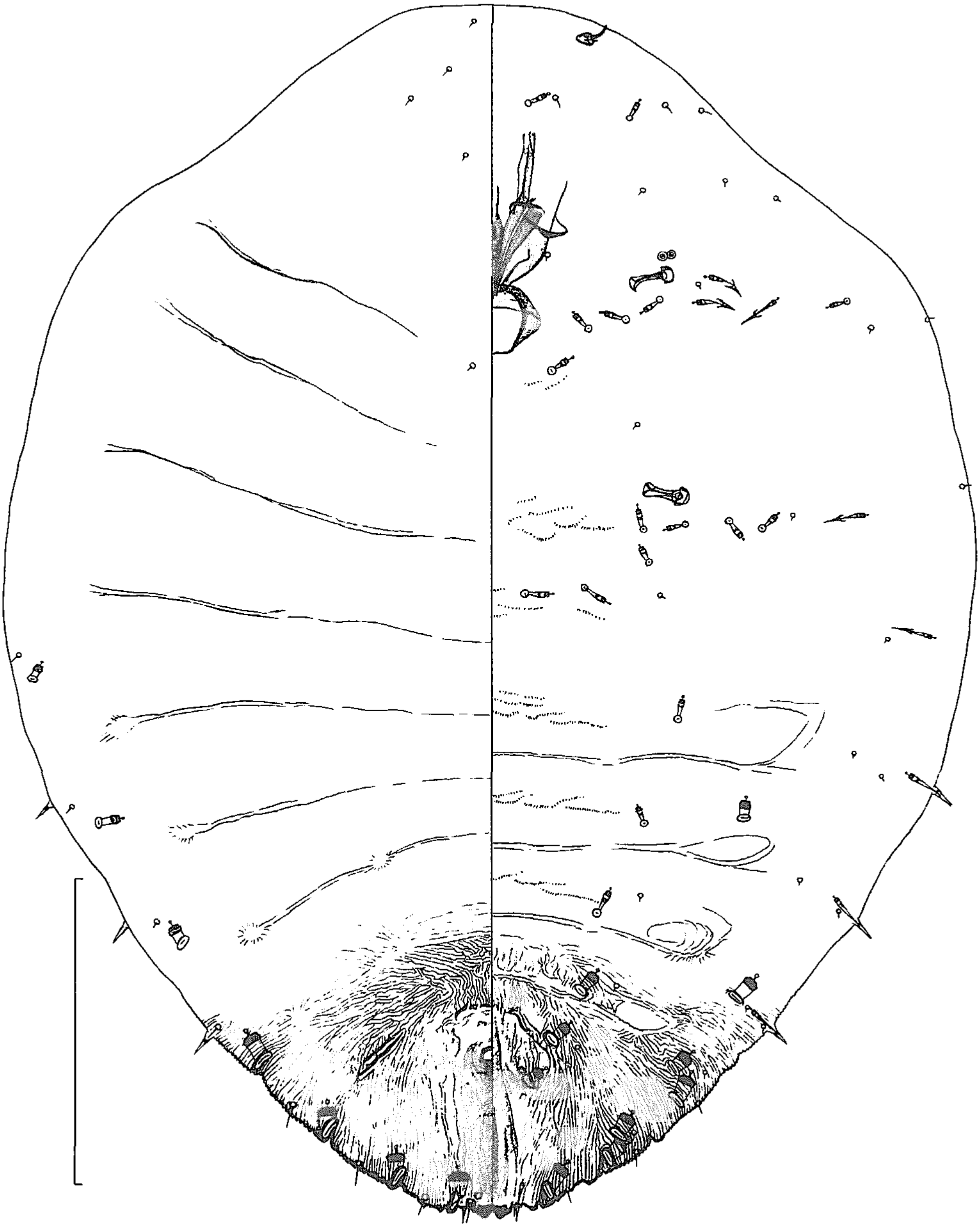

Fig. 10. *Amphisoma erectum*, 2nd instar female. Scale: 0.1 mm.

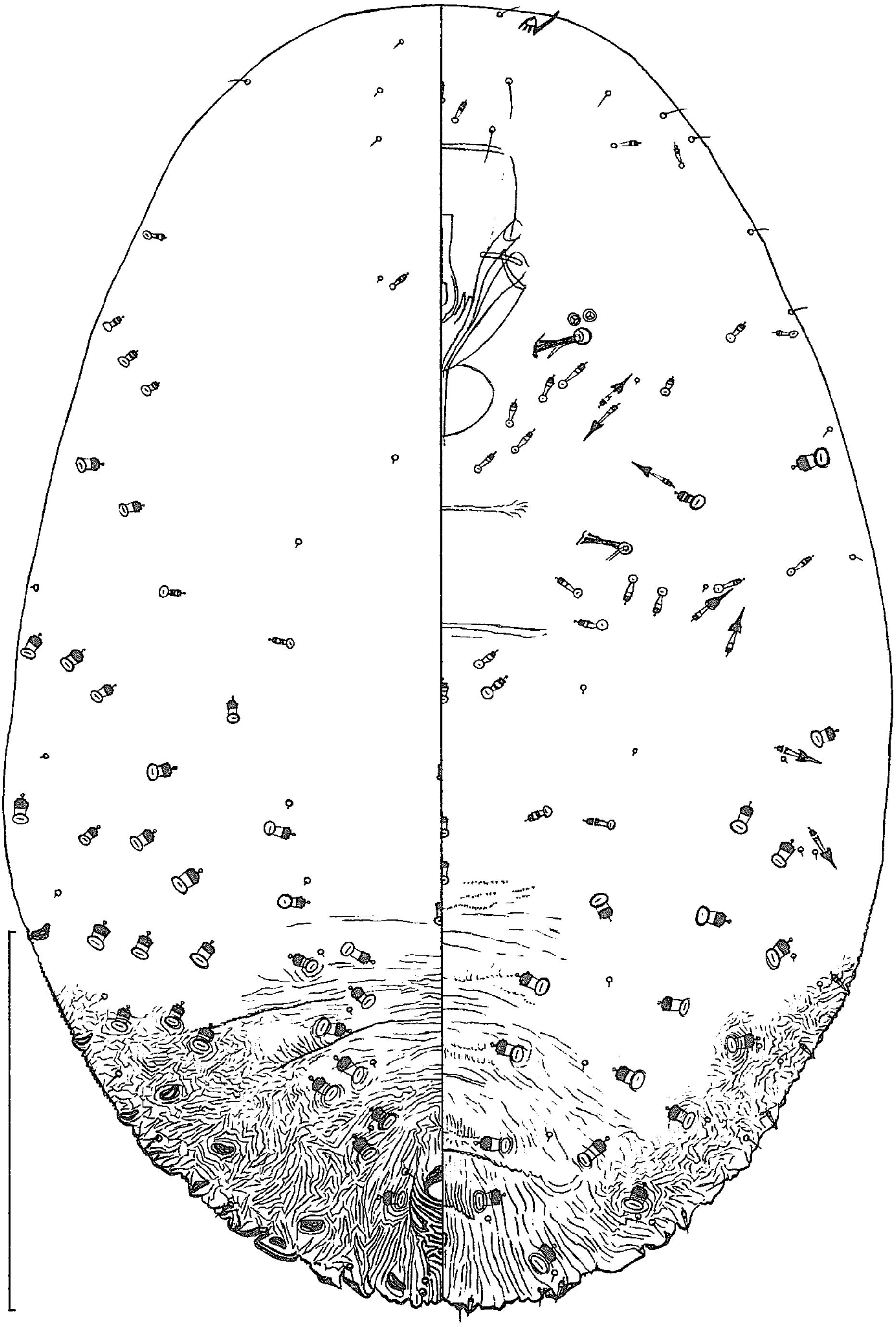

Fig. 11. *Amphisoma erectum*, 2nd instar male. Scale: 0.1 mm.

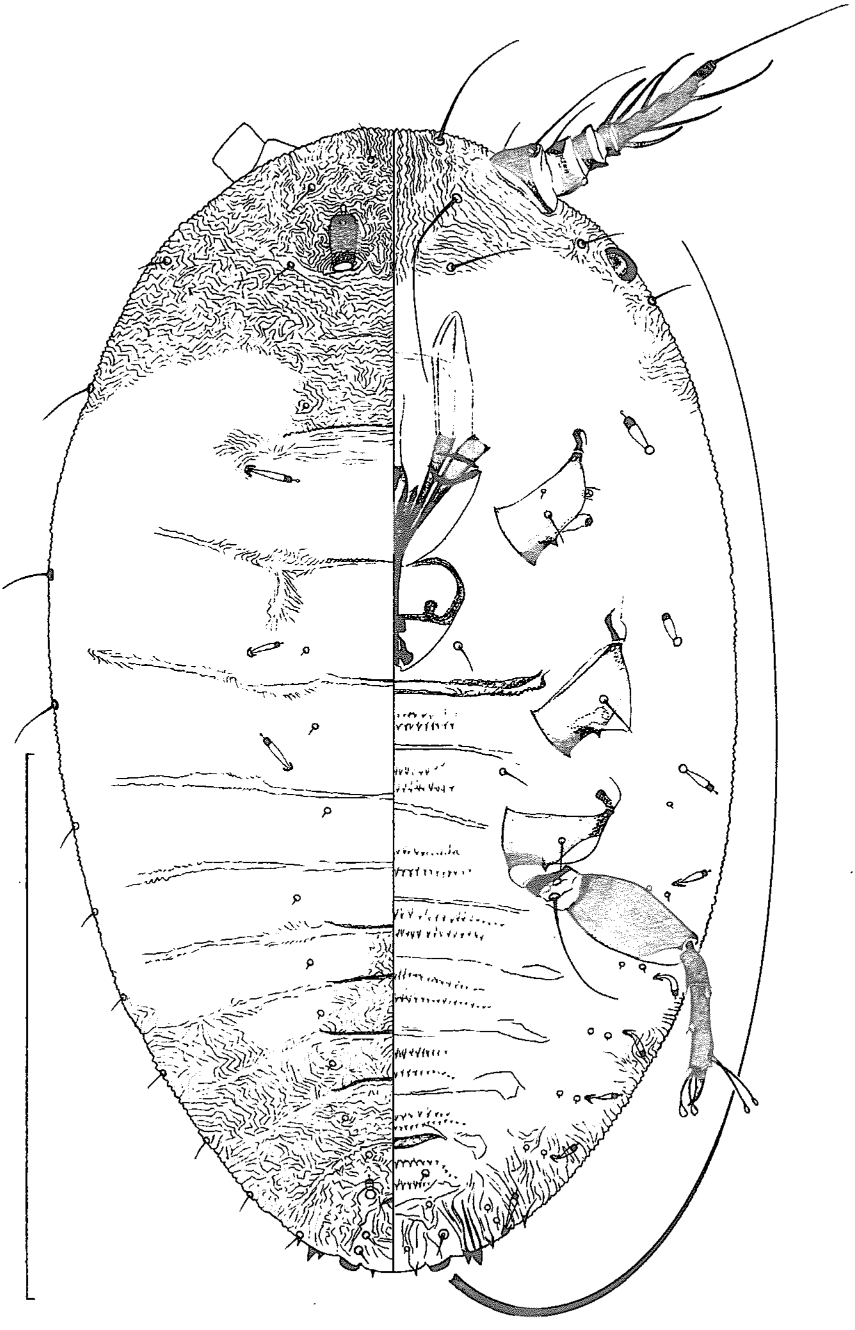

Fig. 12. *Amphisoma erectum*, 1st instar. Scale: 0.1 mm.

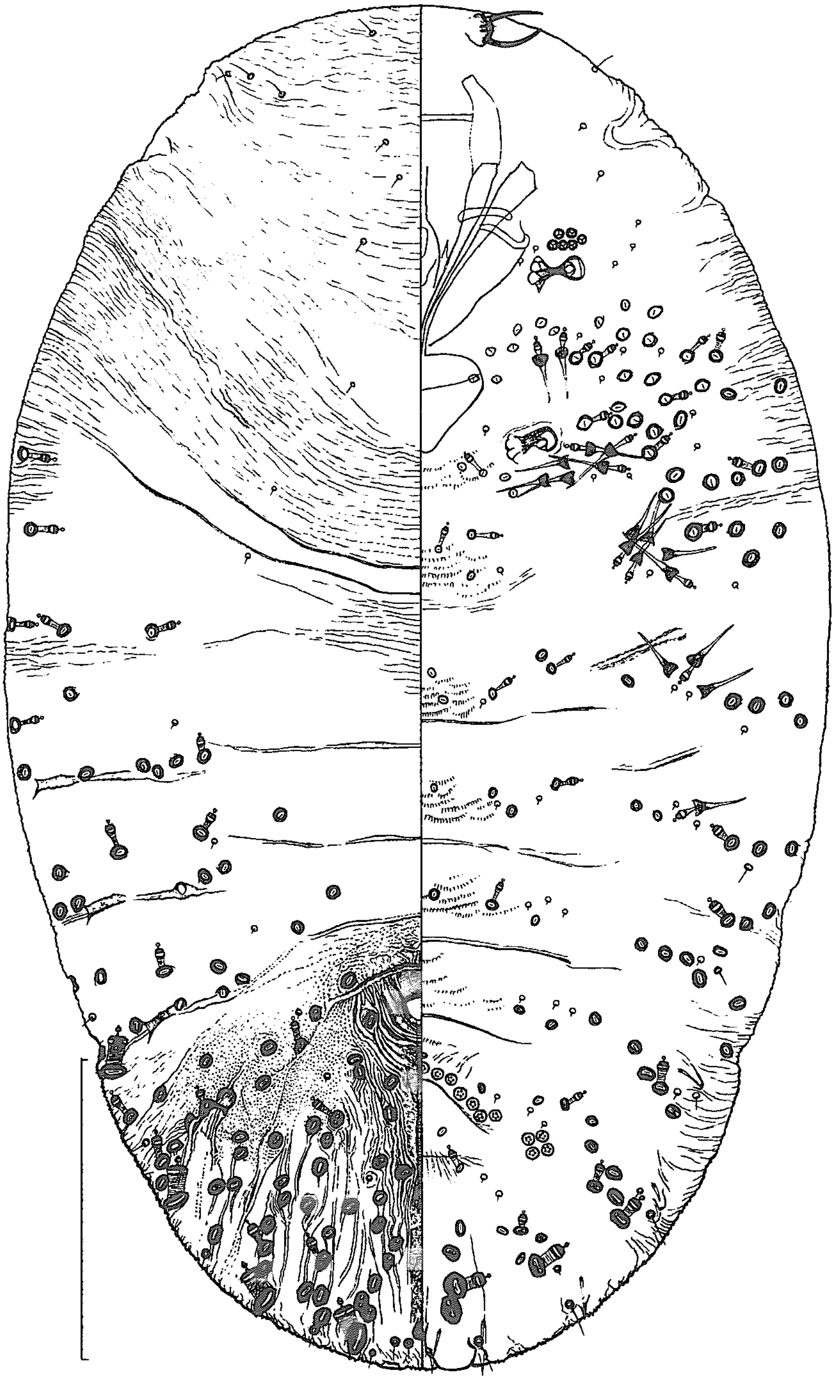

Fig. 13. *Galeomytilus obesus*, adult female. Scale: 0.1 mm.

Fig. 14. *Galeomytilus obesus*, 1st instar. Scale: 0.1 mm.

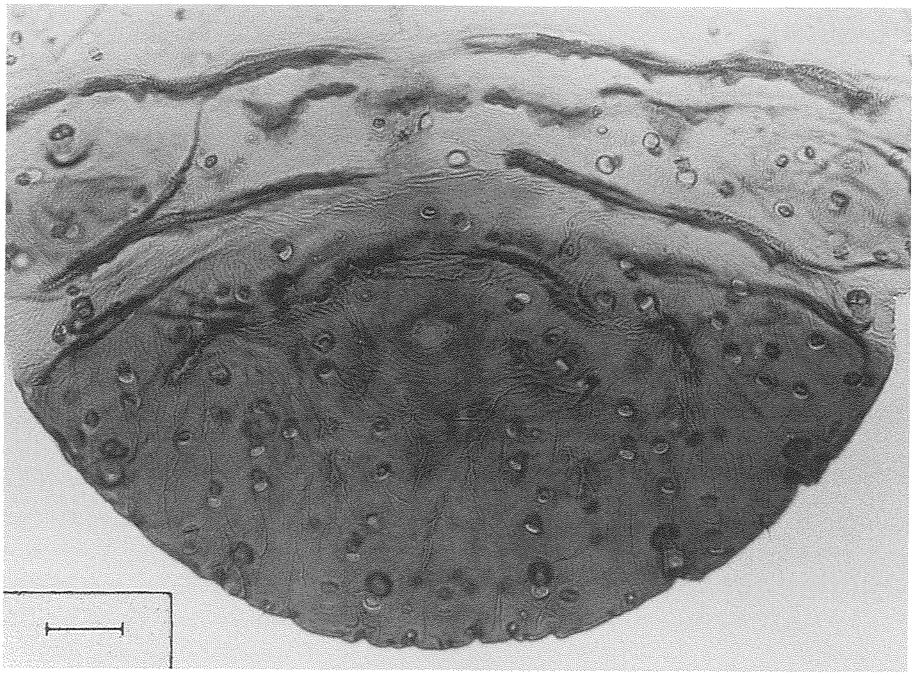

Fig. 15. *Nimbaspis molardi*, adult female: pygidium, dorsal surface. Scale: 25 μm.

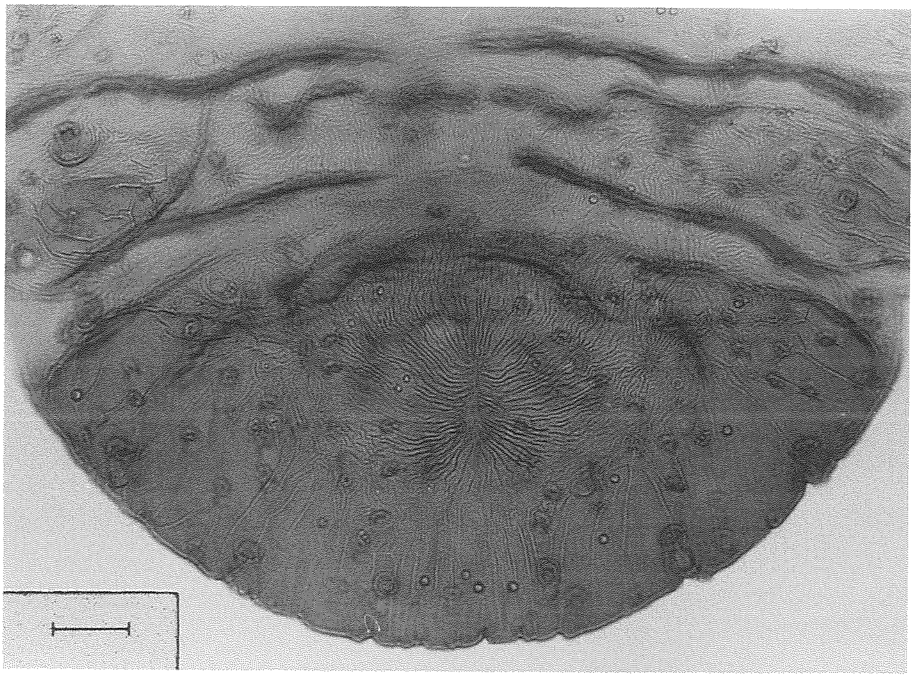

Fig. 16. Same as Fig. 15, ventral surface.

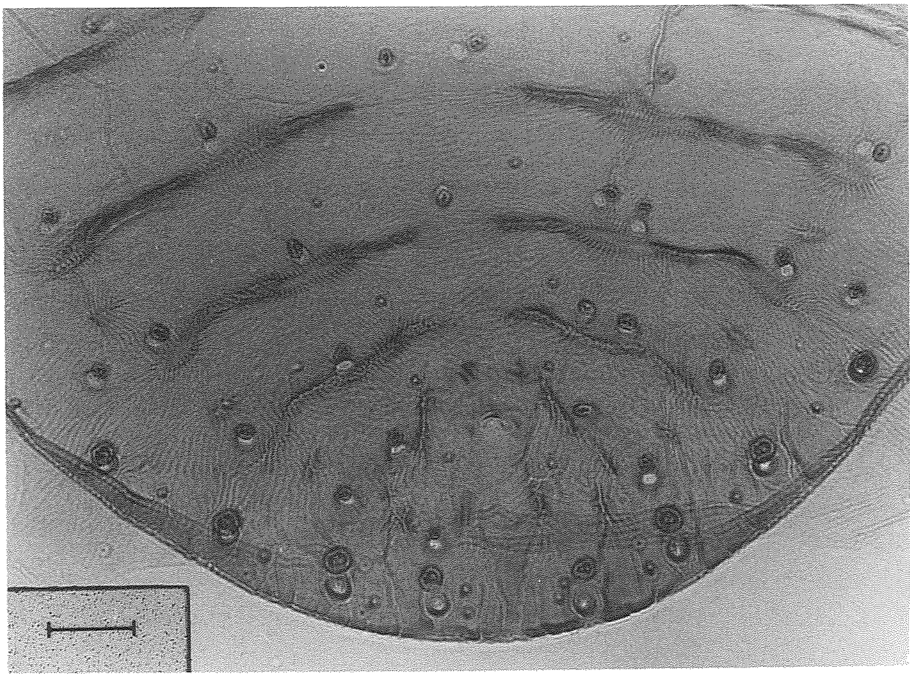

Fig. 17. *Nimbaspis molardi*, exuvial cast of 2nd instar female: pygidium. Scale: 25 μm.

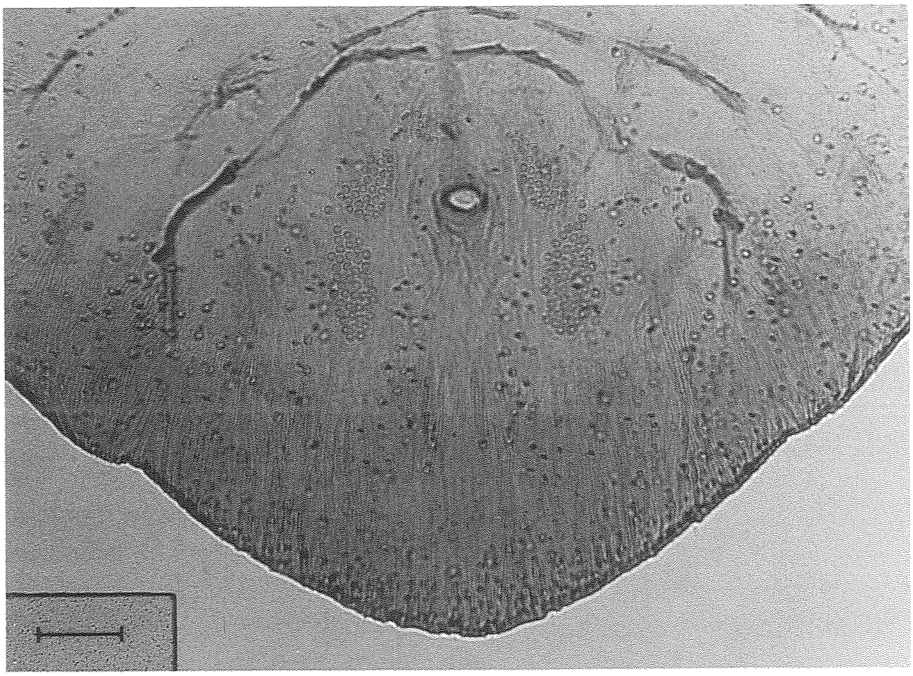

Fig. 18. *Natalaspis formosana*, adult female: pygidium [86ML-301]. Scale: 50 μm.

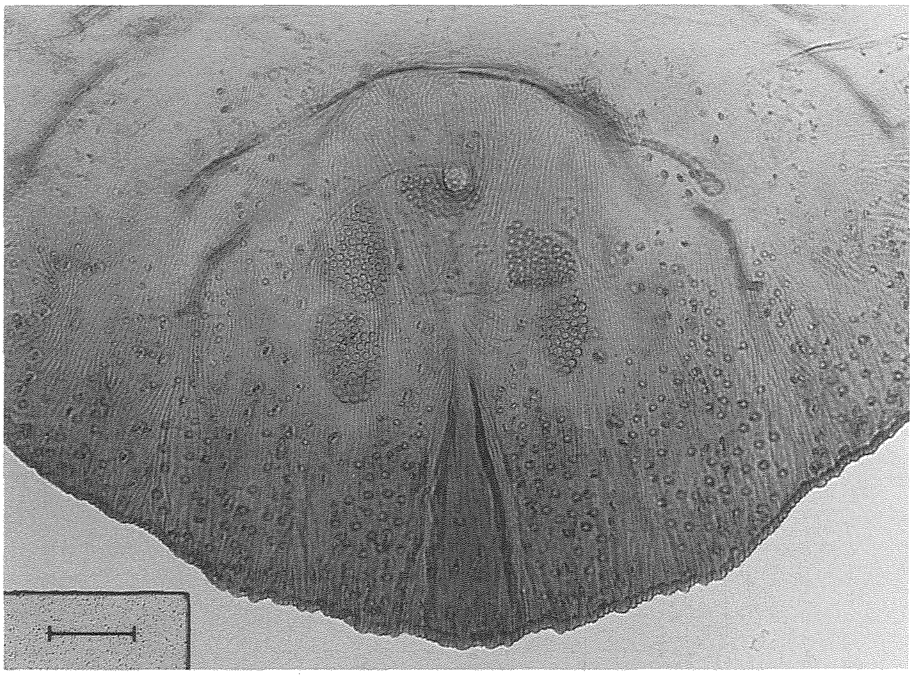

Fig. 19. *Natalaspis formosana*, adult female: pygidium [86ML-495]. Scale: 50 μm.

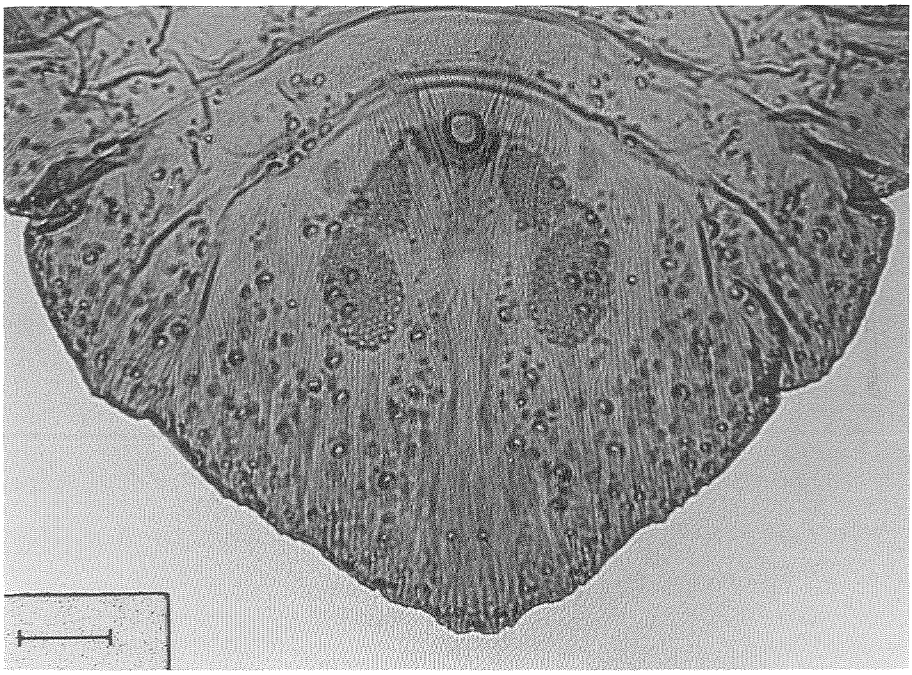

Fig. 20. *Natalaspis formosana*, adult female: pygidium, dorsal surface [93PL-135]. Scale: 50 μm.

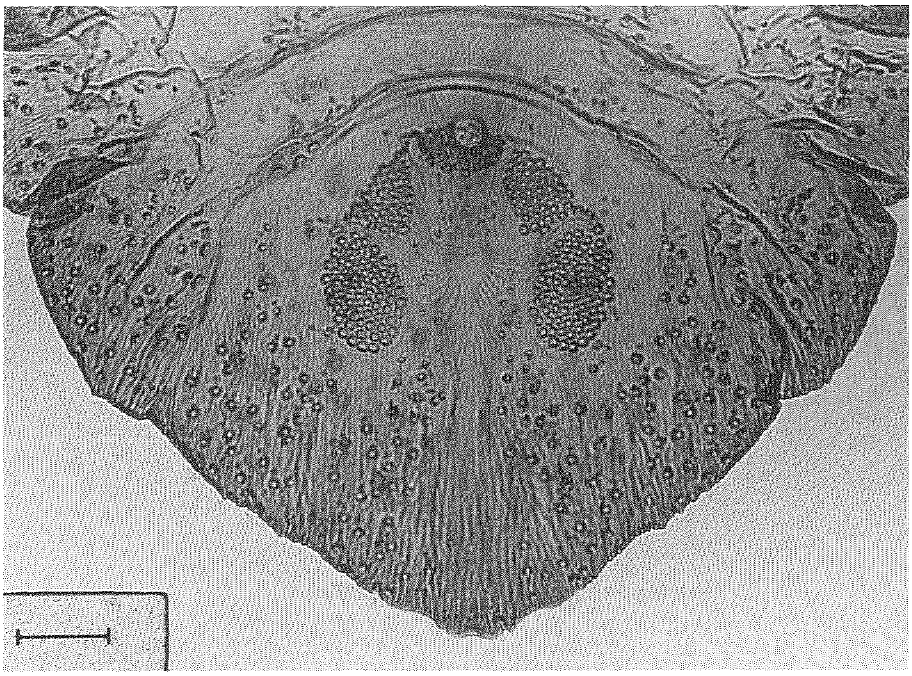

Fig. 21. Same as Fig. 20, ventral surface.

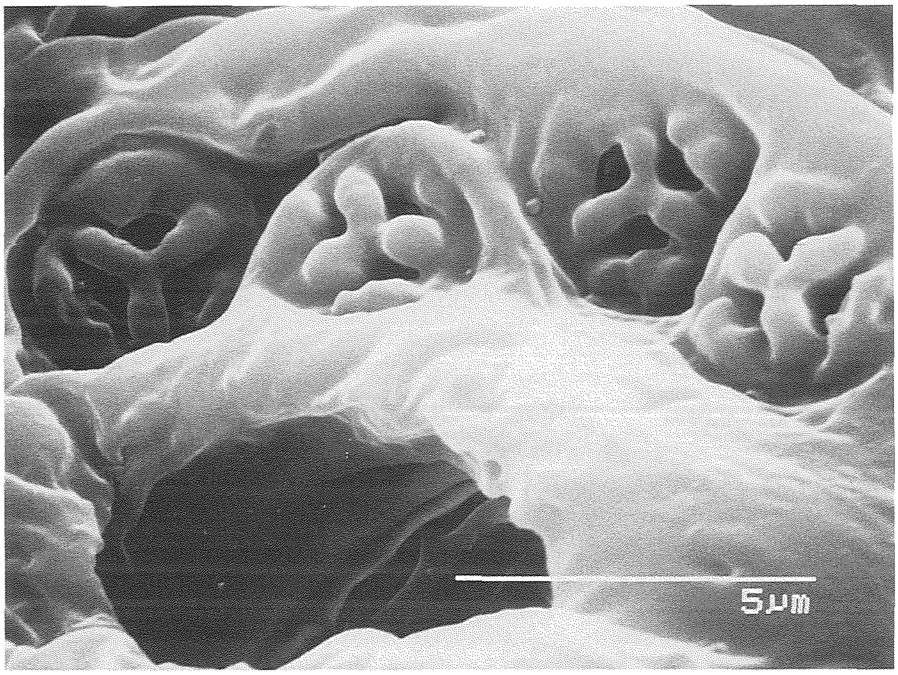

Fig. 22. *Natalaspis formosana*, adult female: anterior spiracular disc pores [93PL-135].

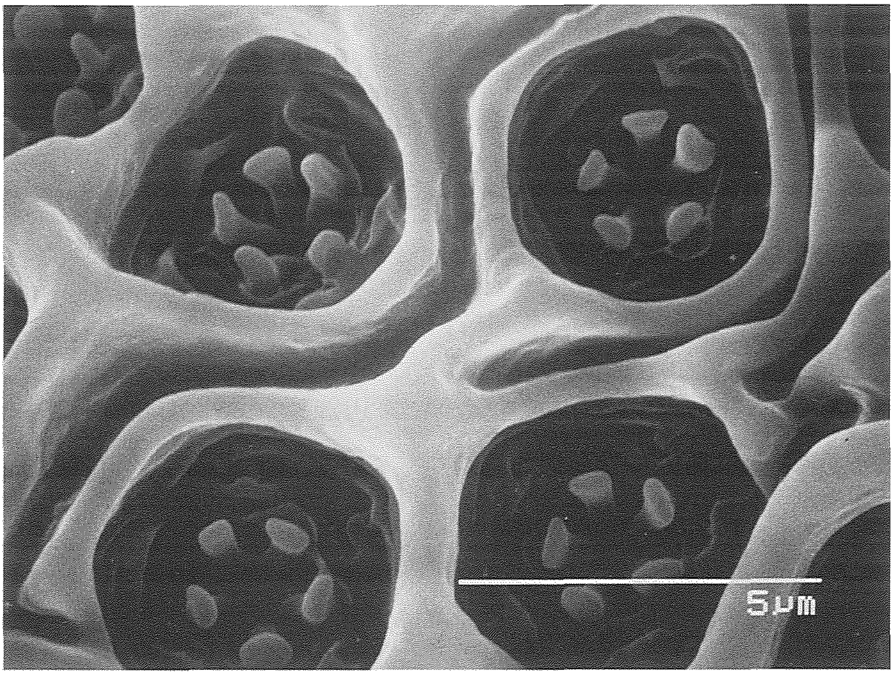

Fig. 23. *Natalaspis formosana*, adult female: perivulvar disc pores [93PL-135].

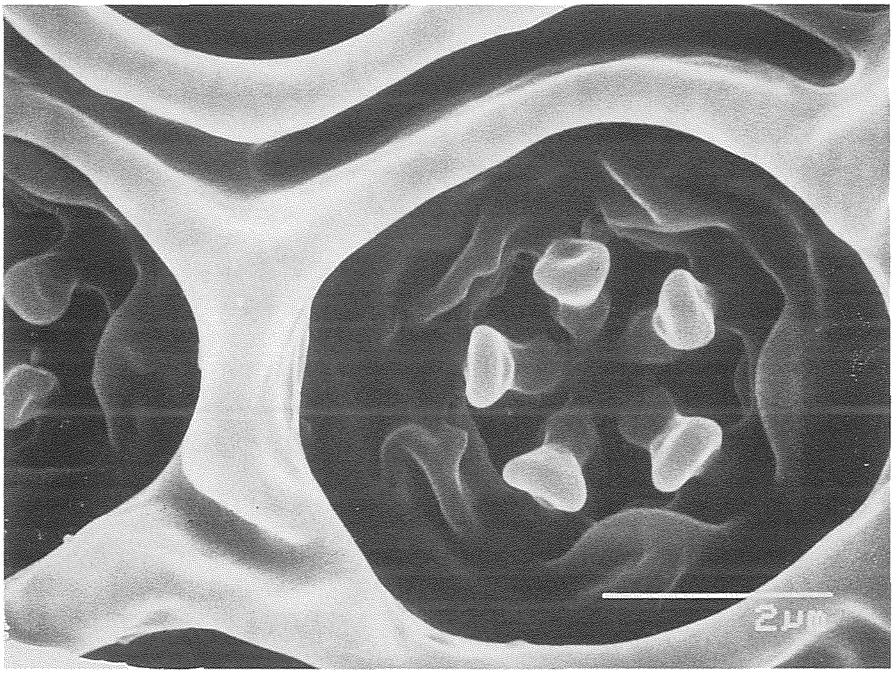

Fig. 24. *Natalaspis formosana*, adult female: perivulvar disc pore [88ML-227].

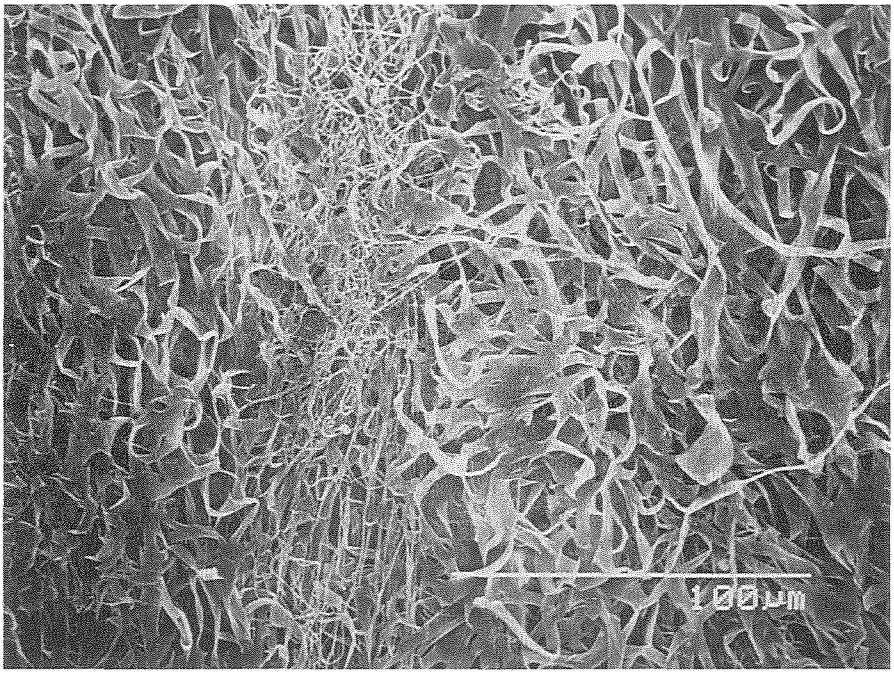

Fig. 25. *Natalaspis formosana*, test of female, dorsal surface [93PL-135].

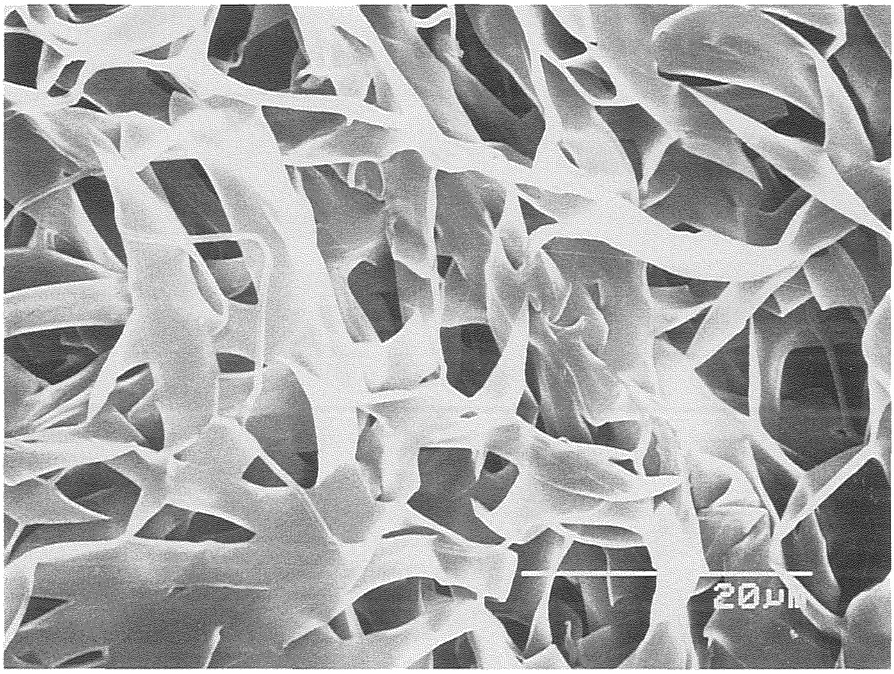

Fig. 26. Same as Fig. 25, magnified.

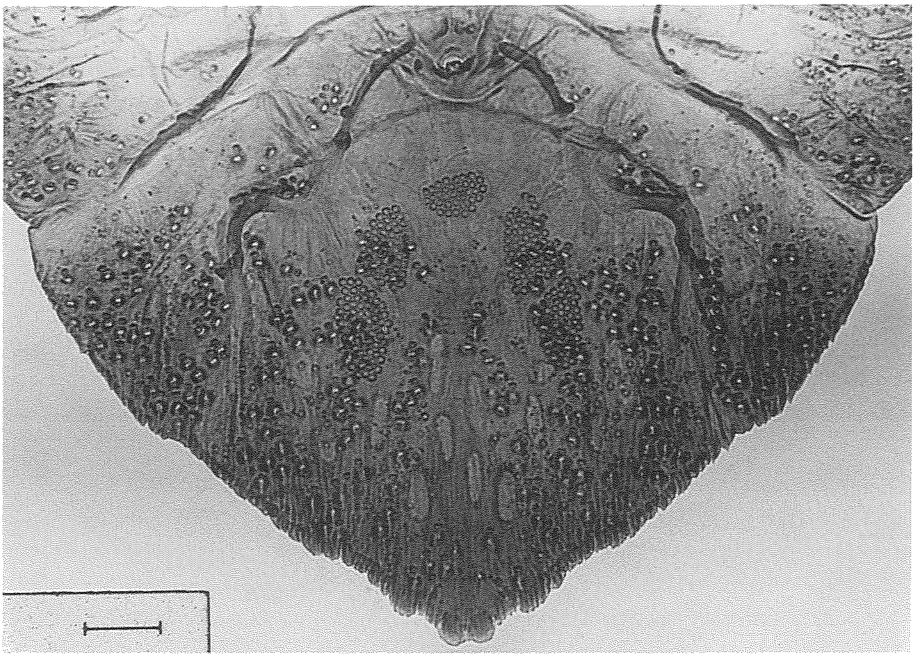

Fig. 27. *Natalaspis* sp., adult female: pygidium [86ML-247]. Scale: 50 μm.

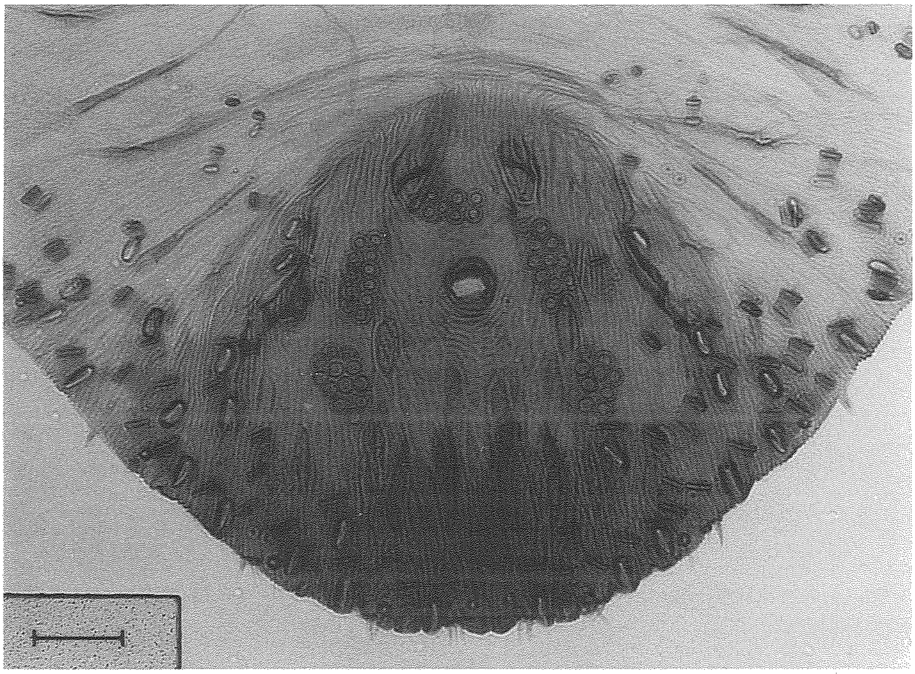

Fig. 28. *Amphisoma erectum*, adult female: pygidium. Scale: 25 μm.

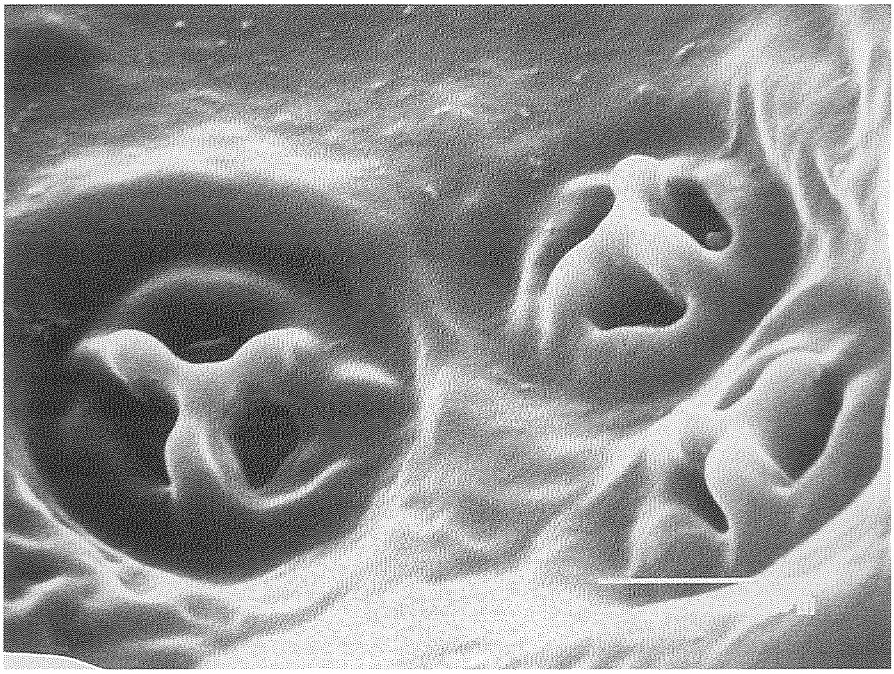

Fig. 29. *Amphisoma erectum*, adult female: anterior spiracular disc pores. ×15 K.

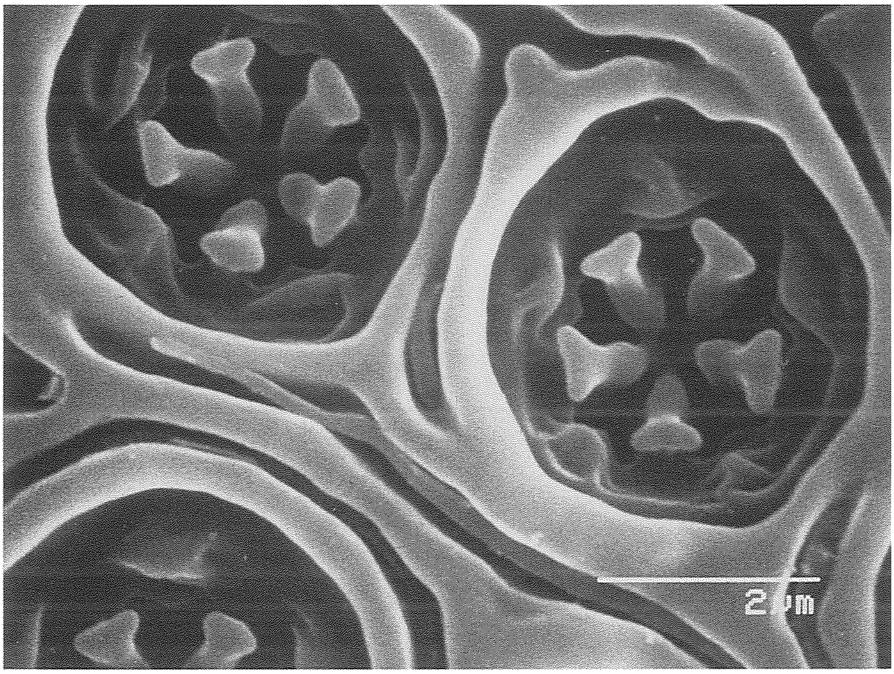

Fig. 30. *Amphisoma erectum*, adult female: perivulvar disc pores.

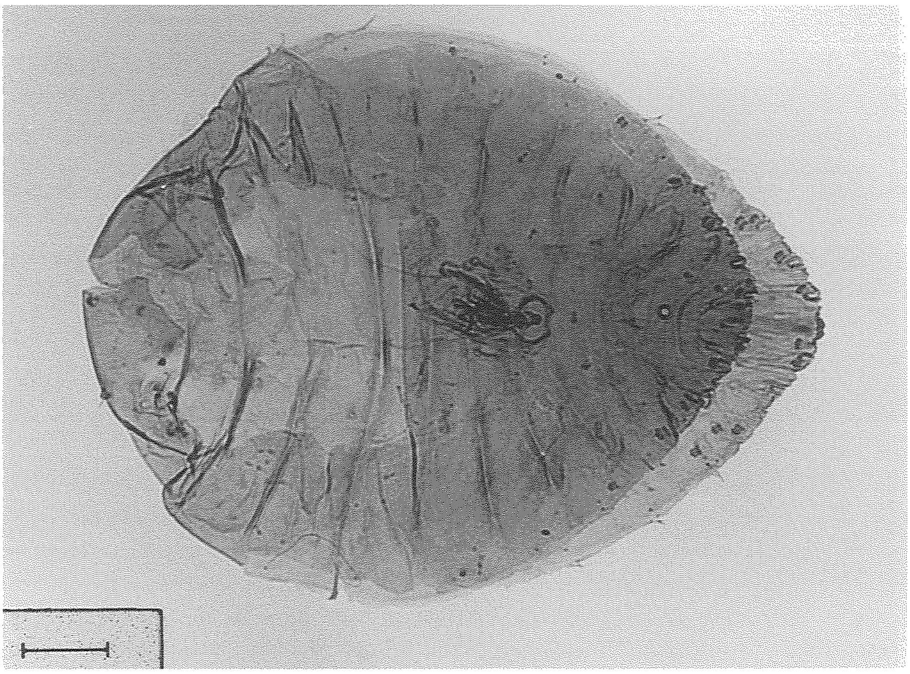

Fig. 31. *Amphisoma erectum*, exuvial cast of 2nd instar female. Scale : 50 μm.

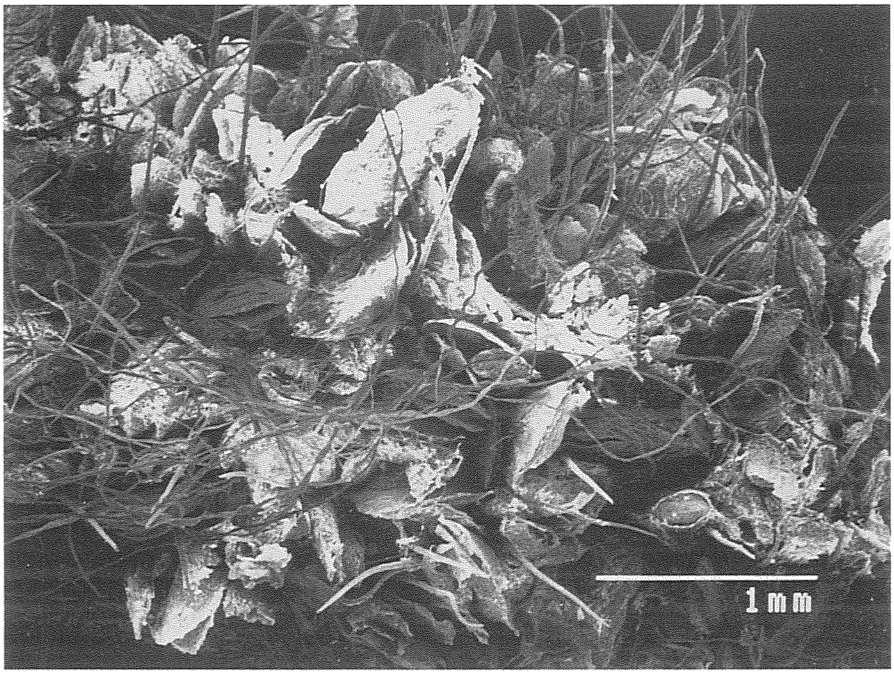

Fig. 32. *Amphisoma erectum*, tests *in situ*.

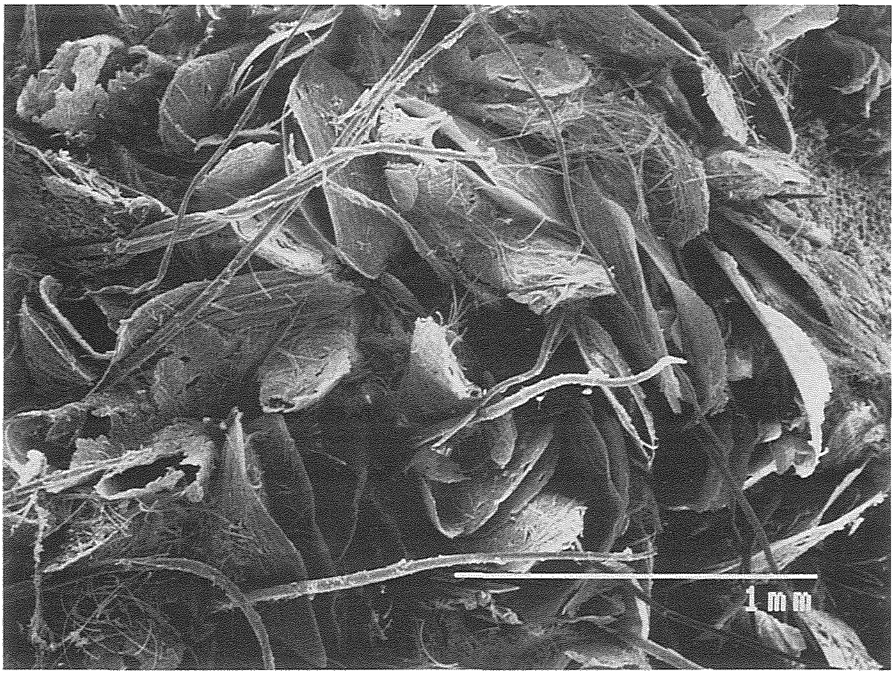

Fig. 33. *Amphisoma erectum*, another lot of tests.

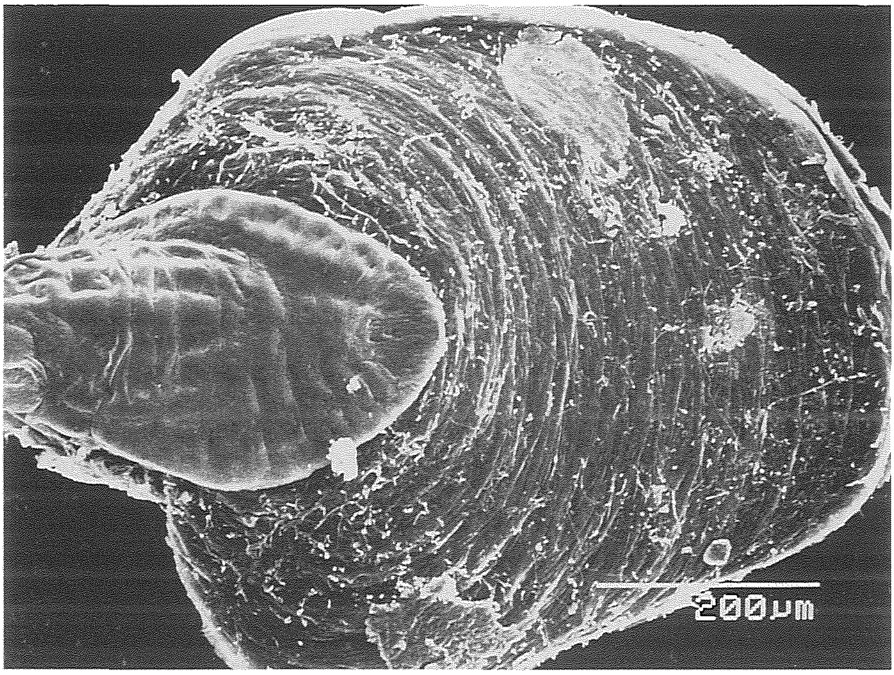

Fig. 34. *Amphisoma erectum*, test of female, dorsal surface.

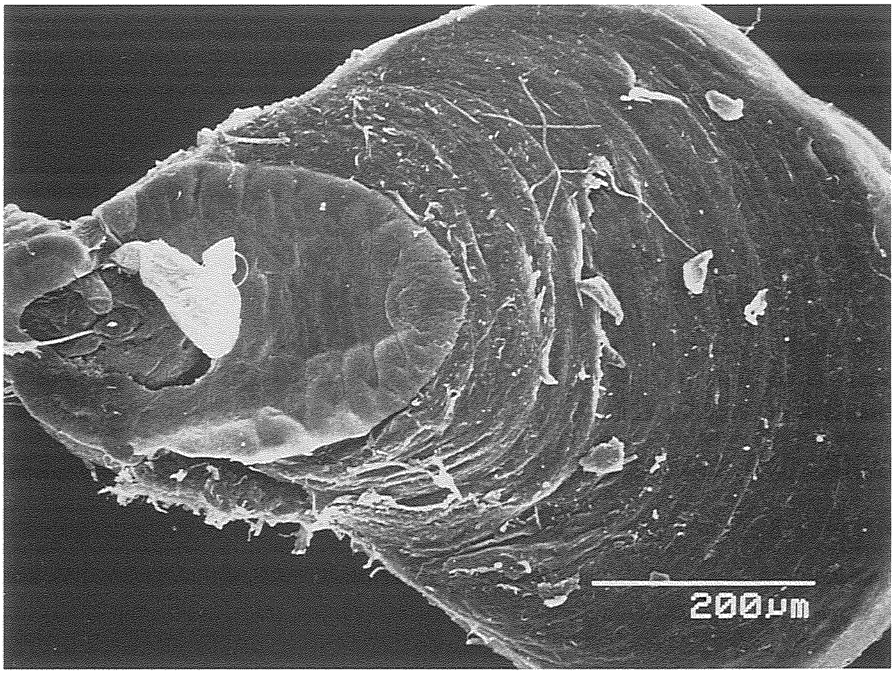

Fig. 35. *Amphisoma erectum*, test of female, ventral surface.

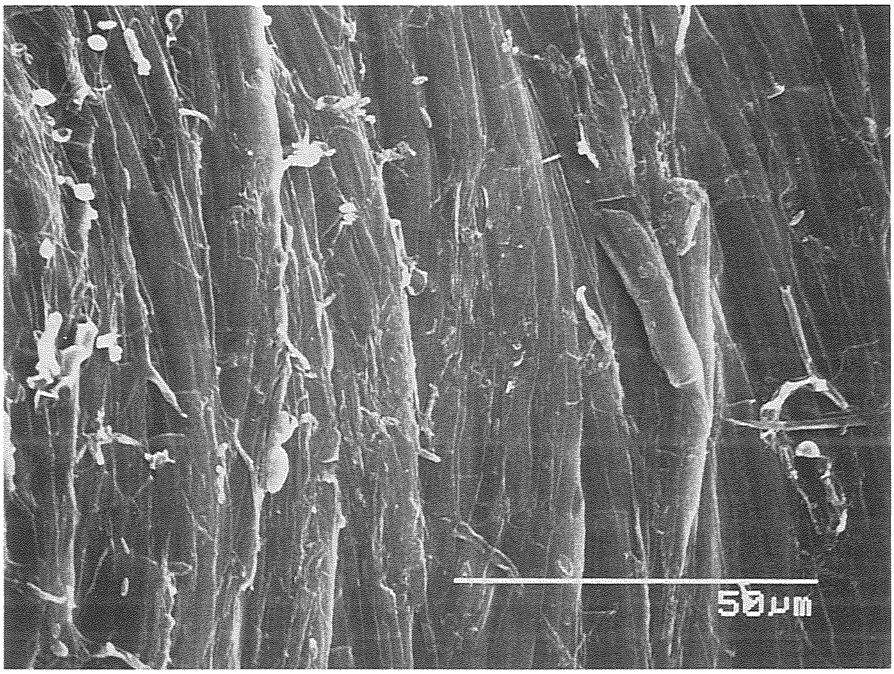

Fig. 36. *Amphisoma erectum*, test of female: dorsal surface, median part behind 2nd exuvial cast.

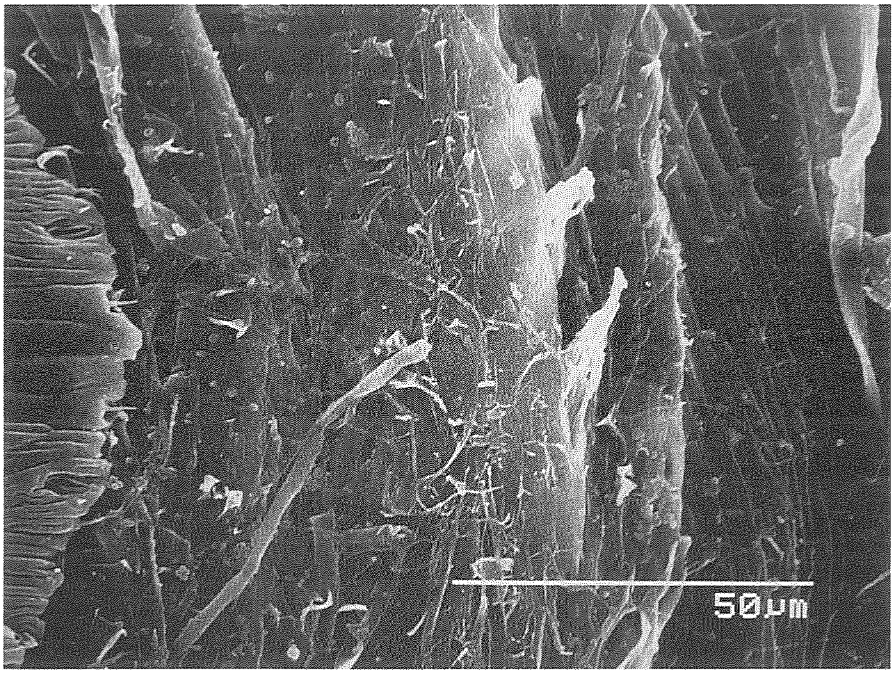

Fig. 37. *Amphisoma erectum*, test of female: ventral surface, median part behind 2nd exuvial cast.

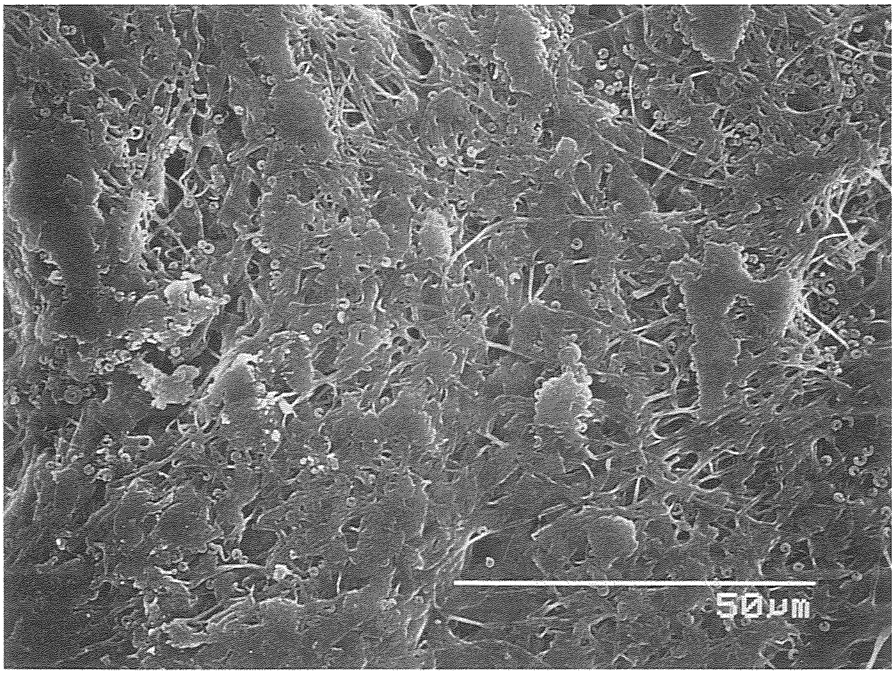

Fig. 38. *Amphisoma erectum*, test of female: inner surface of dorsal portion.

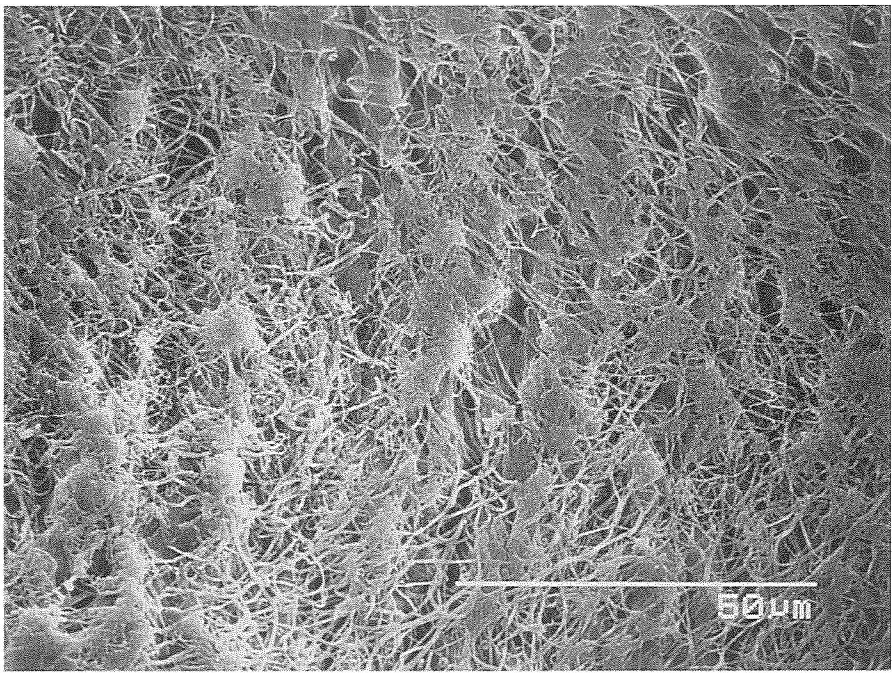

Fig. 39. *Amphisoma erectum*, test of female: inner surface of ventral portion.

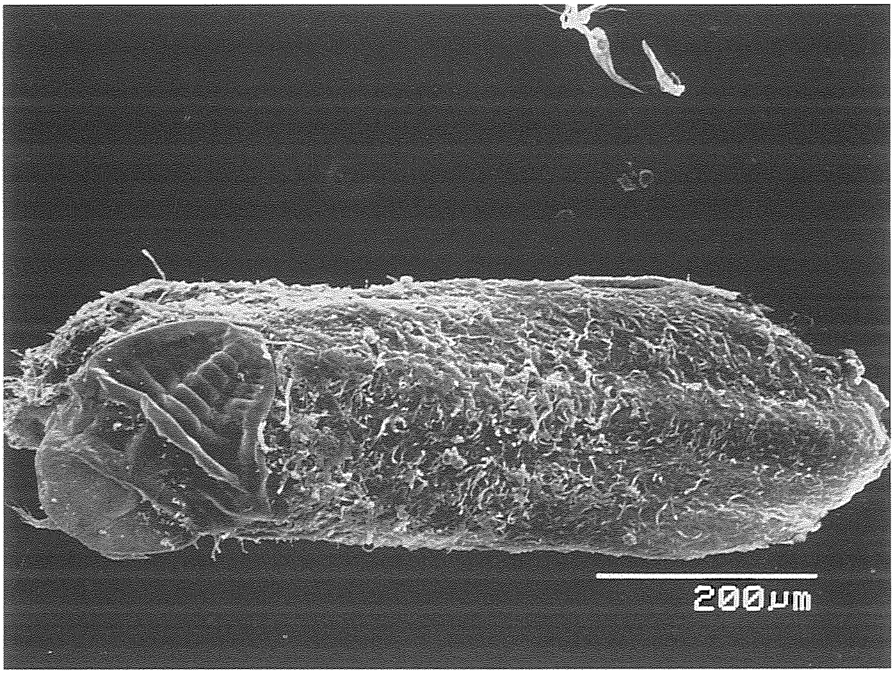

Fig. 40. *Amphisoma erectum*, test of male, dorsal surface.

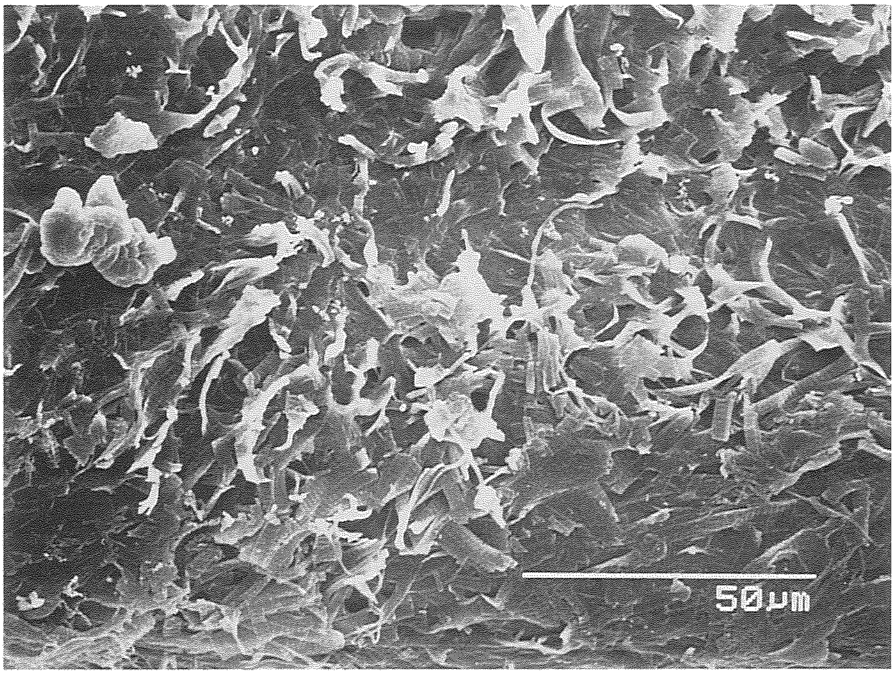

Fig. 41. *Amphisoma erectum*, test of male: dorsal surface [median carina along top margin].

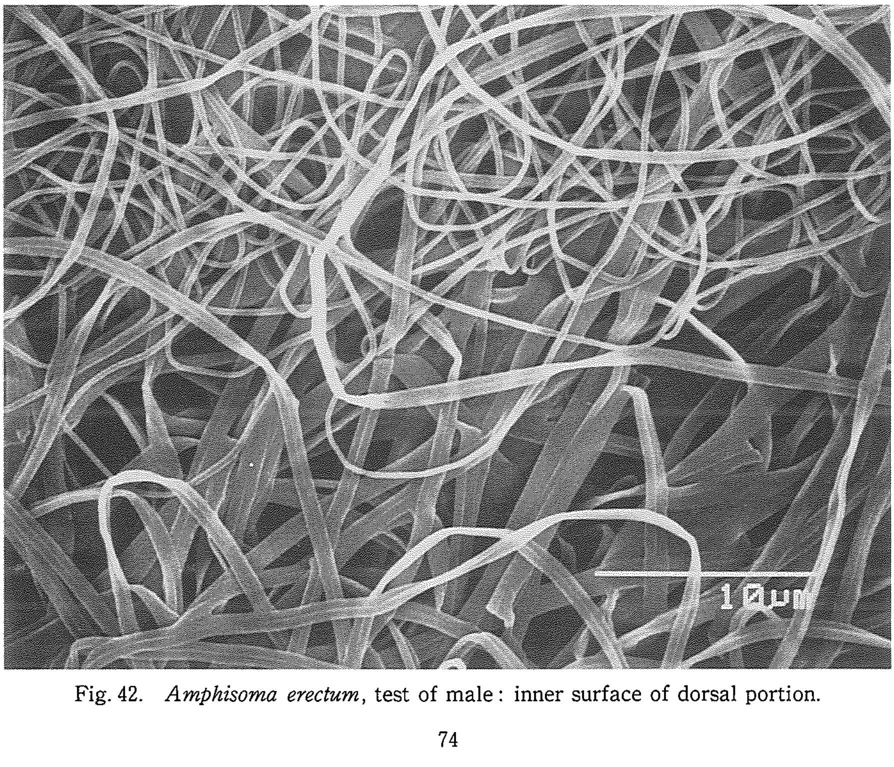

Fig. 42. *Amphisoma erectum*, test of male: inner surface of dorsal portion.

Fig. 43. *Galeomytilus obesus*, adult female: pygidium, dorsal surface.

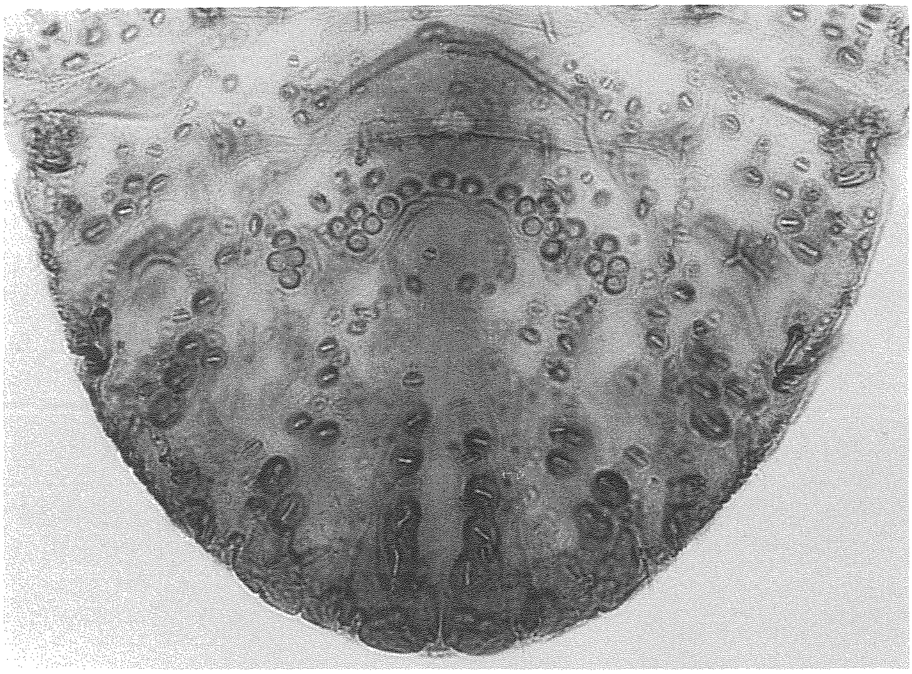

Fig. 44. Same as Fig. 43, ventral surface.

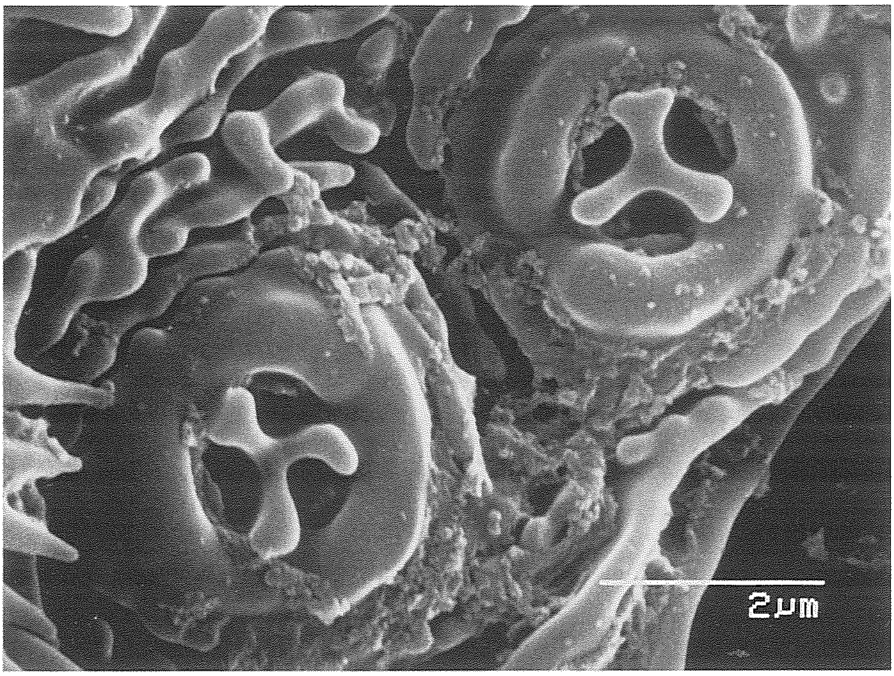

Fig. 45. *Galeomytilus obesus*, adult female: posterior spiracular disc pores.

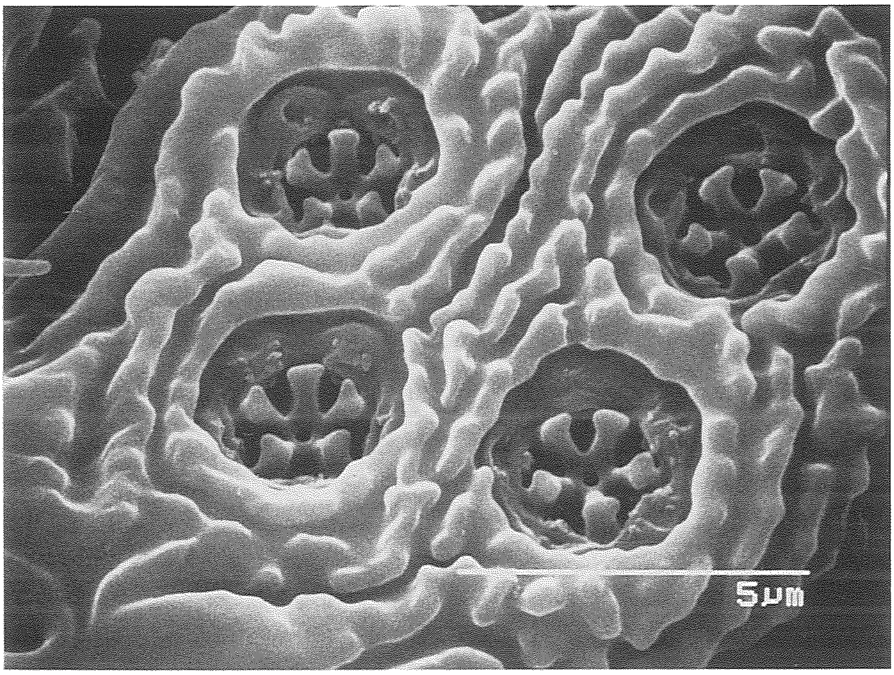

Fig. 46. *Galeomytilus obesus*, adult female: perivulvar disc pores.

Fig. 47. *Galeomytilus obesus*, exuvial cast of 2nd instar female, mounted laterally. Scale: 50 μm.

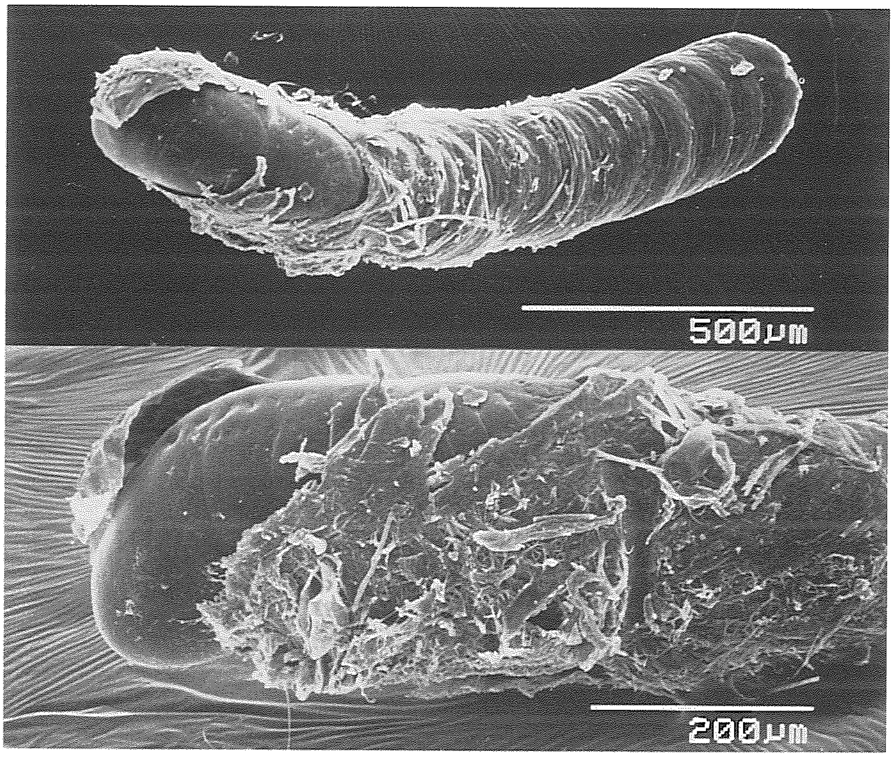

Fig. 48. *Galeomytilus obesus*, test of female: dorsal view [upper] and lateral view of 2nd exuvial cast [lower].

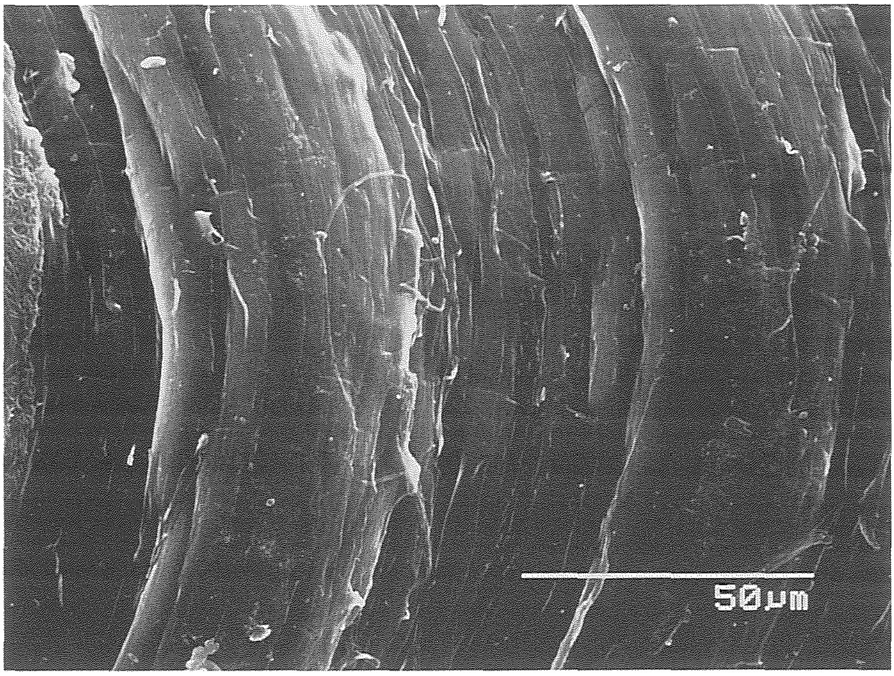

Fig. 49. *Galeomytilus obesus*, test of female : dorsal surface.

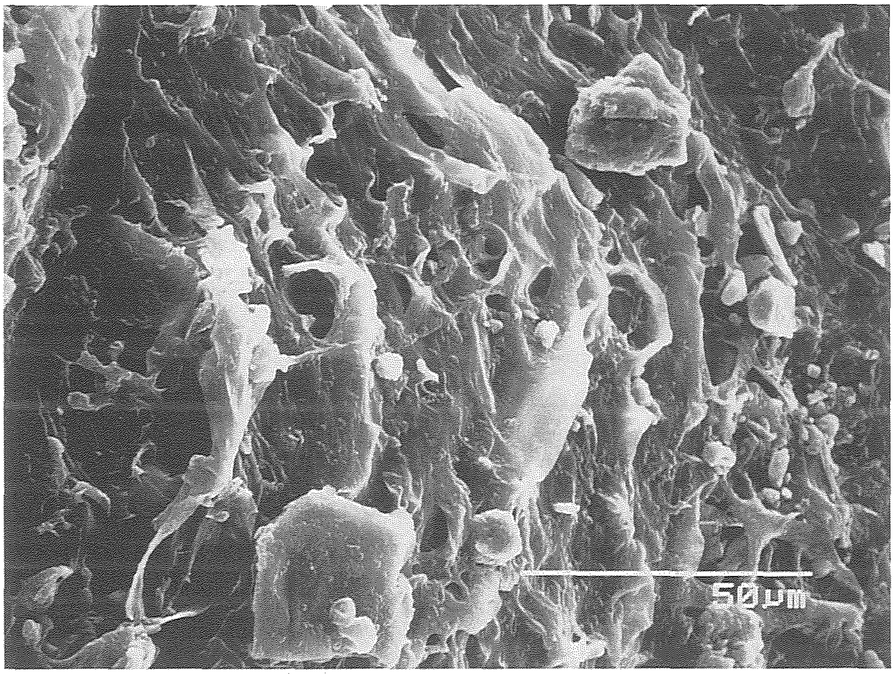

Fig. 50. *Galeomytilus obesus*, test of female : ventral surface.

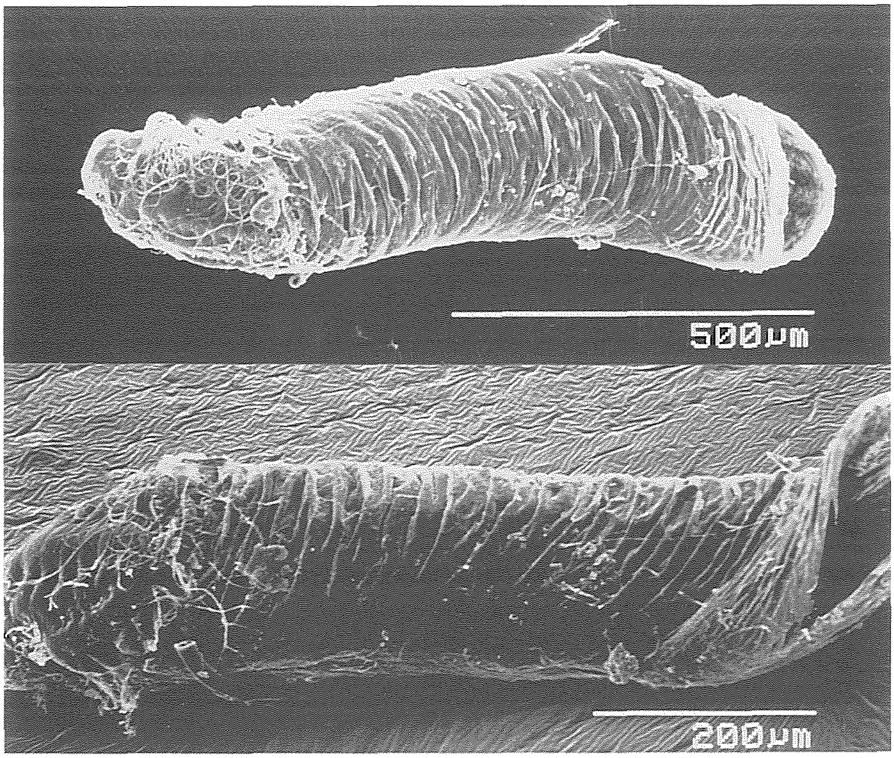

Fig. 51. *Galeomytilus obesus*, test of male : dorsal [upper] and lateral [lower] views.

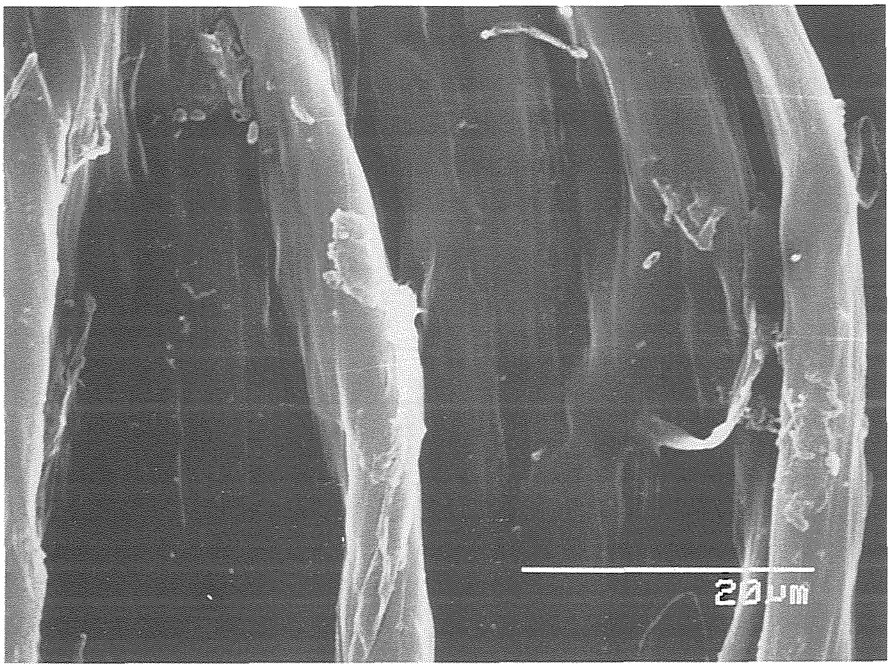

Fig. 52. *Galeomytilus obesus*, test of male : dorsal surface.