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**A CONTRIBUTION TO CONCHASPIDID SYSTEMATICS
(HOMOPTERA : COCCOIDEA)**

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Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods
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Four species of *Conchaspis*, *C. angraeci*, *C. vaccinii*, *C. buchaniae* (n. sp.) and *C. garciniae* (n. sp.), were collected in Peninsular Malaysia and studied by light microscopy and scanning electron microscopy. Only 2 larval instars are recognized in the female as well as in the male. *C. buchaniae*, *C. vaccinii* and *C. garciniae* are supposed to be closely related to each other; they differ in the size of the body (as represented by the length of the hind trochanter and femur combined) and in the number of the tubular ducts, among other features. Evolutionary changes are noticed in the ontogenetic development of the antennae. Observations on some other body parts are given; multilocular disc pores of *C. angraeci* and *C. garciniae* were examined at high magnification, and the moulding device to produce wax rings is analysed; the tubular ducts are ventropleural in position, and these and the '3-fissural disc pores' secrete ribbonlike wax filaments, which are impressed with longitudinal lines; fimbriate processes or pectinae, similar to those of *Fagisuga triloba*, occur at the abdominal apex in at least three of the species examined. Tests were observed by scanning electron microscopy; the test of *C. angraeci* is made of a substance excreted probably from the anus; in the other species the test is composed of the substance intermingled with fragments of wax filaments; the female tests of *C. vaccinii* and *C. garciniae* are composed of 3 strata or zones; the tests differ from diaspidid ones in using crushed wax filaments, which are mingled with the anal substance just like pieces of aggregate mixed with cement to make concrete. Preliminary considerations are given on the phylogenetic significance of the pectinae commonly occurring in *Conchaspis* and *Fagisuga* and on the evolutionary significance of the difference in the test structure between the Conchaspidae and the Diaspididae.

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INTRODUCTION

The Conchaspidae are a small family of scale insects, comprising 26 known species (25 species catalogued by Ben-Dov, 1981, plus another species described by Ben-Dov and Williams, 1984) classified in 3 genera (Ben-Dov, 1981 ; Williams, 1985). They are interesting especially because they form tests which are completely detached from the insect body and similar in appearance to those of the Diaspididae. They are characterized by distal segments of the abdomen fused into a pygidium in the adult female and larval instars, and most of them by having tubular ducts, which alone among the wax-secreting organs may be concerned with test formation. These features also connect them with the Diaspididae. Differences in other features, however, are remarkable. An early question to arise, therefore, is whether the similarities imply a close phylogenetic relationship between these families or are due to convergence. In fact, some authors supposed that the Conchaspidae are more closely related to the Diaspididae than to any other family of the Coccoidea, but others placed them elsewhere in the classification scheme of the Coccoidea and are not all in agreement (literature was reviewed by Mamet, 1954, Afifi, 1969, and Ben-Dov, 1990). Thus, we are still uncertain about the phylogenetic relationship of the family Conchaspidae (Miller and Kosztarab, 1979).

The question also arises why the Conchaspidae are so poorly represented in contrast to the flourishing Diaspididae in spite of the fact that they are comparable to the latter in forming good tests. In other words, why are the Diaspididae so successful but not the Conchaspidae?

In 1990 I collected some material of Conchaspidae from the east coast of Semenanjung Malaysia [Peninsular Malaysia]. A study of this material revealed that it contains *Conchaspis angraeci*, *C. vaccinii* and 2 undescribed species. Some body structures, secretions and tests were studied by scanning electron microscopy, providing new information to the questions indicated above.

The concept of *Conchaspis* proposed by Mamet (1954) is substantially valid with the inclusion of the East Asian species. I do not think, however, that he was accurate in all details of his observations. The other genera of the family, *Fagisuga* and *Paraconchaspis*, are represented each by a single species. *Fagisuga* was excluded from the family by Mamet (1954). A finding in the present study connects *Conchaspis* with it and suggests that it is a primitive form of the Conchaspidae.

PREPARATION OF MATERIAL

Material preserved in dried condition was used. Petioles or twigs with scale insects were put in humid atmosphere (with creosote in a small open vial) for some days. After the insect bodies within the tests absorbed moisture and became relaxed, the specimens were separated from the host plant.

For light microscopy insect specimens were 1) treated with 10% KOH for 24-48 hours at room temperature, 2) heated at 60°C in lactic acid with acid fuchsin for several hours or more and then 3) in a mixture of glacial acetic acid and methyl salicylate [acetosalicylate], 4) transferred to terpineol, and 5) mounted in Canada balsam (usually after having been washed on the slide by a drop of xylol). When specimens were not well clarified at the end of step 1), they were gently pressed between the tips of forceps in the fluid to make a puncture on the body wall. When clarifying proved still insufficient at step 3), specimens were heated again in lactic acid and then in acetosalicylate. Completed slides were dried at 60°C for a few days and then at 45°C for 1 week

or more.

For scanning electron microscopy moist insect specimens and tests were dehydrated in alcohol, critical point dried, and coated with gold. Some dehydrated insect specimens were treated with chloroform in an ultrasonic cleaner. Some dehydrated tests were cut across in alcohol by the use of a razor blade for the examination of the internal structure. Observations were made in Hitachi S-2100A.

SPECIES EXAMINED

Conchaspis angraeci

Collected at Hutan Simpan Beserah, Kuantan, Pahang, on the twigs, petioles and leaves of *Trigonostemon malaccanus* [Euphorbiaceae], July 25 [90ML-324] and Aug. 15 [90ML-511]. Adult females (over 100 specimens) and larvae were mounted from the twigs and mostly from 90ML-511.

Remarks. This species has been recorded from many localities and a long list of plants since it was described in 1893 by Cockerell from Jamaica and also by Newstead from Trinidad [under the name *Pseudinglisia rodrigueziae*]. However, the published records had been limited to Americas until Ben-Dov (1974, 1981) recorded the species from some localities of Africa and also from Western Australia. The above material is the first record of *C. angraeci* from Asia.

No specimens of the adult male, pupa and prepupa have been found in the material. The larvae and tests studied probably belong all to the female.

Figures. 1, 31 [multilocular disc pores]; 4 [antennae]; 14, 15 [pygidium]; 29 [minute spines]; 33, 34 [wax rings]; 43-45 [apex of abdomen]; 51 [anus]; 52-57 [test].

Conchaspis buchananiae, n. sp.

Collected at Bukit Bauk, Daerah Dungun, Terengganu, on the twigs and petioles of *Buchanania arborescens* [Anacardiaceae], July 17 [90ML-239]. Adult females (25 specimens), larvae, and a few specimens of each of the prepupa, pupa and adult male were mounted. Name-bearing specimen [holotype]: adult female.

Recognition characters (adult female). Body elongate, at maturity somewhat obovate, with cephalothorax slightly swollen; ca. 1 mm long and 0.6 mm wide at maximum. Prothoracic protuberances absent. Head with 5 long setae ventrally on each side; on dorsal surface without cicatrices; dorsal spots ('dorsal ocellar spots') membranous. Antennae with 3 sclerotized segments and another incompletely sclerotized one basally; terminal segment well sclerotized, with 2 fleshy setae and 3 much shorter, pointed setae subapically and 2 fleshy club-shaped setae subbasally; penultimate segment with 1 fleshy seta, which is larger than the club-shaped setae of the terminal segment and located within the sclerotized band of the segment. Claws without denticle on the plantar surface; hind trochanter+femur measuring 98-112 μ m in length. Anterior spiracle with 2 (rarely 1 or 3) and the posterior with 1-2 (usually 2) disc pores. Dermal invaginations occurring only on metathorax. Tubular ducts ventropleural; 1-5 on metathorax, 4-10 on 1st abdominal segment, 5-8 on the 2nd, 4-8 on the 3rd, and 3-6 on the 4th, total on one side of body 19-36; total on both sides 40-69. Submarginal dorsal bosses on 1st to 5th abdominal segments (1 on each of the segments). Multilocular disc pores with 11 loculi; 1-3 submarginal, 1-2 (usually 1) intermediate, and 1 (sometimes 0) submedian pores on 3rd abdominal

segment; 1-3 submarginal and 1-2 (rarely 0) intermediate pores on the 4th; rarely 1 pore present submedially on the 4th and submarginally on the 5th; total 4-9 on one side of body, 10-17 on both sides.

Remarks. This species is similar to *C. vaccinii*, *C. malesiana* and *C. garciniae* (n. sp.), but differs from all the latter three in lacking dermal invaginations on the mesothorax, in the fewer tubular ducts, and in the pointed setae occurring on the terminal antennal segment being all very short. It is also distinguishable from *C. malesiana* and *C. garciniae* in lacking cicatrices on the dorsal surface of the head.

Figures. 1 [multilocular disc pores]; 2, 8 [adult female]; 6 [antennae]; 9 [pupa]; 10, 11 [dorsal spots]; 87-89 [test].

Conchaspis garciniae, n. sp.

Collected at Hutan Simpan Beserah, Kuantan, Pahang, on the petioles of *Garcinia scortechinii* [Guttiferae], July 10 [90ML-167], July 12 [90ML-186], and July 24 [90ML-295]; on the petioles of *Garcinia nigrolineata*, July 12 [90ML-187]. Specimens of the adult female (57 specimens) and larval instars and some specimens of the prepupa, pupa and adult male were mounted. Name-bearing specimen [holotype]: adult female, from *G. scortechinii*.

Recognition characters (Adult female). Body elongate, at maturity somewhat obovate, with cephalothorax slightly swollen; ca. 1.9 mm long and 0.9 mm wide at maximum. Prothoracic protuberances developed, bearing eye. Head with 5 long setae ventrally on each side; with a pair of cicatrices dorsally; dorsal spots ('dorsal ocellar spots') membranous. Antennae with 3 sclerotized segments; terminal segment with 4 pointed and 4 fleshy setae subequal in length; a thicker fleshy seta occurring on the base of the sclerotized area of the terminal segment (or on the borders of the sclerotized area and the membranous area separating the terminal segment from the penultimate). Claws without denticle on the plantar surface; hind trochanter + femur measuring 156-192 μm in length. Anterior spiracle with 2-5 and the posterior with 1-6 (usually 2-4) 5-locular disc pores. Dermal invaginations occurring on meso- and metathorax. Tubular ducts ventropleural, numerous; their approximate numbers are as follows: 33-52 on metathorax, 23-48 on 1st abdominal segment, 20-41 on the 2nd, 9-31 on the 3rd, and 2-12 on the 4th; total on both sides of body, 230-306. Submarginal dorsal bosses on 1st to 5th abdominal segments (1 on each of these segments), tending to be rudimentary on the 5th. Multilocular disc pores with 11 loculi; 4-12 submarginal and 0-3 intermediate pores and sometimes 1 submedian on 3rd abdominal segment; 4-9 submarginal and sometimes 1 or 2 intermediate pores on the 4th; rarely 1 submarginal pore on the 5th; total on one side of body 8-22; total on both sides 18-38.

Remarks. This species is close to *C. malesiana*, which was described by Ben-Dov and Williams (1984) on the basis of 10 adult females collected at Bukit Timah, Singapura, on a plant of the family Apocynaceae. It is readily distinguishable from the latter in having much more numerous tubular ducts. These ducts are so numerous and crowded in the pleural region that it was often difficult to count them exactly. I have examined 2 adult females of *C. malesiana* from the original series of specimens and found another difference: the position of the thickest fleshy seta of the antenna. This seta originally belongs to the penultimate segment (see p.

11). In *C. garciniae* it occurs about the borders of the terminal and penultimate segments (or, more exactly, on the basal margin of the sclerotized area of the terminal antennal segment). In the 2 specimens of *C. malesiana* I could not find it at the expected position; a seta occurring well within the sclerotized area of the terminal segment is especially thick instead, and may be the expected one. Further, *C. malesiana* is distinctly smaller than *C. garciniae*, the hind trochanter and femur combined measuring 132–150 μm in length (in disagreement with the measurements given in the original description).*

Figures. 1, 32 [multilocular disc pores]; 3 [adult female]; 5, 18 [antennae]; 7, 37–39 [tubular ducts and wax filaments]; 7, 13, 40–42 [3-fissural disc pores and wax filaments]; 16, 17, 46, 49 [pygidium]; 19–22 [dorsal spots]; 23 [cicatrix]; 24 [dermal invagination]; 25 [submarginal dorsal boss]; 26, 27 [dermal slits]; 28 [crenulae]; 30 [minute spines]; 35, 36 [spiracular disc pores]; 47, 48, 50 [apex of abdomen]; 58–79 [tests].

Conchaspis vaccinii

Collected at Bukit Bauk, Daerah Dungun, Terengganu, on *Garcinia opaca* [Guttiferae], July 17 [90ML-238]; at Hutan Lipur Telok Cempedak, Kuantan, Pahang, on *Garcinia andamanica*, July 25 [90ML-311]; and at Desaru, Johor, on *Payena lucida* [Sapotaceae], Aug. 19 [90ML-545]. Adult females (53 specimens), larvae, 1 prepupa and 1 adult male were mounted.

Remarks. This species was originally described by Khoo (1978) on the basis of specimens collected at Gunong Bunga Buah, Selangor, Semenanjung Malaysia, on *Vaccinium malaccense* [Ericaceae]. There has been no further record.

The 3 localities where I collected the specimens are ca. 100 km, 280 km and 375 km apart from each other. However, no significant difference was found in the numbers of the tubular ducts and disc pores among the local forms.

The specimens examined well agree with the original description except for the tubular ducts, which do not exactly cover the ranges given in the original description. In the adult females from the east coast the tubular ducts are counted as follows: 15–33 on the metathorax, 13–32 on the 1st abdominal segment, 9–23 on the 2nd, 6–13 on the 3rd, and 1–8 on the 4th, total on one side of the body 50–111; total on both sides 101–209.**

Figures. 1, 12 [multilocular disc pores]; 6 [antennae]; 80–86 [test].

In this paper *C. buchanae*, *C. garciniae* and *C. vaccinii* are called the

* In revising this manuscript Dr D.J. Williams informed me as follows: 'You are correct in criticising the measurements given for *C. malesiana*. In the type specimens available the antennae are 120 μm long, the trochanter+femur 150–160 μm long and the hind tibia+tarsus 100–110 μm long. . . . Furthermore, in the holotype one antenna has the thickest fleshy seta on the penultimate segment but this seta on the other antenna is at the base of the apical segment. In most of the paratypes the seta is well within the apical segment.'

** In revising this manuscript Dr Khoo Soo Ghee informed me as follows: 'I think the number of tubular ducts is more or less similar to the range given in the original description. Perhaps I was vague in stating the number of tubular ducts of abdominal segments 2 and 4. They should be L17 & R17 instead of only 17, and L7 & R7 instead of only 7 for the respective segments. Also in my paper I mentioned the multilocular pores on abdominal segments 2 and 3 which should be segments 3 and 4.'

Malaysian species, and these three and *C. malesiana* the East Asian species. *C. angraeci* is probably native to tropical or subtropical America, and may be a recent introduction in Malaysia.

Depositories of the slide-mounted specimens. The main part of the specimens examined, including the name-bearing specimens [holotypes] of the 2 new species, are deposited in the Entomology Division, Forest Research Institute of Malaysia, Kepong, Selangor, Malaysia, and the other part, comprising half the specimens, in the Entomological Institute, Faculty of Agriculture, Hokkaidô University, Sapporo, Japan.

Pest status. *C. angraeci* has been recorded from diverse plants including many kinds of orchids (Ben-Dov, 1981). *C. garciniae* and *C. vaccinii*, being associated with wild species of *Garcinia*, may be potential pests of mangosteen (*G. mangostana*) and other fruit trees of the genus.

INSTARS

Mamet (1954) recognized 3 larval instars in the female and 2 in the male in some species of *Conchaspis*. According to him, however, the 3rd instar female is very similar to the 2nd instar female. He described all the instars of *C. vayssierei*. D'Ascoli and Kosztarab (1969) also recognized 3 female larval instars in *C. lata*: the 2nd and 3rd instars were separated by slight differences. Khoo (1978) described the 1st instar larva and the 'intermediate stage female' of *C. vaccinii*. He did not differentiate between the 2nd and 3rd instars.

In the course of the present study I examined many specimens of larvae. I could recognize only 2 larval forms or stages in each species. One of them is undoubtedly the 1st instar, being smaller and having 6-segmented antennae. The other may represent the 2nd or 3rd instar or both. I follow Khoo in calling it 'intermediate stage'.

However, I doubt whether the species examined have 3 larval instars in the female. I have observed 65 intermediate stage larvae of *C. garciniae* and 52 of *C. vaccinii*. These specimens may be sufficient to represent both the 2nd and 3rd instars (if the 3rd really occurs) and the male and female, but I have failed to recognize the presence of 2 instars as well as the occurrence of any distinct sexual difference in the specimens. The features I have examined in this connection include the length of the hind trochanter and femur combined (as an indication of the body size) and the number of the tubular ducts (on each of the metathorax and 1st to 4th abdominal segments). The length of the hind trochanter and femur measures about 86-98 μm in *C. garciniae* and 78-90 μm in *C. vaccinii*, with no conclusive indication of the presence of more than 1 instar (needless to say, it is unlikely that succeeding larval instars are indistinguishable in size). The tubular ducts are rather numerous in the intermediate stage larvae of these species. They are somewhat variable in number, but are unimodal in frequency (Table 1).

Nine mounted larvae of *C. buchananiae* and *C. garciniae* have been found to contain a developing or almost completed body of the succeeding instar, thus showing the succession from the 1st instar to the intermediate stage and that from the intermediate stage to the adult female or prepupa. Having examined them, I am much inclined to believe that these species have only 2 larval instars in the

Table 1. Number of tubular ducts in the intermediate stage of the Malaysian species, frequency distribution (% in parentheses).

Segment	Number	<i>C. buchananiae</i>	<i>C. vaccinii</i>	<i>C. garciniae</i>
Metathorax	0	3 (7.9)		
	1	35 (92.1)		
	2			
	3			
	4		4 (4.0)	
	5		24 (23.7)	7 (5.7)
	6		37 (36.6)	32 (26.0)
	7		23 (22.8)	47 (38.2)
	8		9 (8.9)	26 (21.1)
	9		4 (4.0)	11 (9.0)
Abd I	1	1 (2.6)		
	2	35 (92.1)		
	3	2 (5.3)	1 (1.0)	
	4		10 (9.7)	
	5		30 (29.1)	12 (9.2)
	6		42 (40.8)	40 (30.5)
	7		19 (18.4)	46 (35.1)
	8		1 (1.0)	25 (19.1)
		9		
Abd II	1	1 (2.8)		
	2	31 (86.1)		
	3	4 (11.1)	2 (1.9)	
	4		25 (24.1)	2 (1.5)
	5		49 (47.1)	30 (22.7)
	6		23 (22.1)	63 (47.7)
	7		5 (4.8)	34 (25.8)
	8			2 (1.5)
		9		
Abd III	2	36 (94.7)	3 (2.9)	
	3	2 (5.3)	29 (27.9)	3 (2.3)
	4		58 (55.8)	38 (29.0)
	5		13 (12.5)	64 (48.9)
	6		1 (0.9)	24 (18.3)
				2 (1.5)
		7		
Abd IV	1	3 (7.9)	5 (4.8)	28 (21.4)
	2	35 (92.1)	91 (87.5)	93 (71.0)
	3		8 (7.7)	10 (7.6)
Total on one side both sides		8-11 17-21	16-29 31-57	21-34 46-65

female as well as in the male. Among them 1 intermediate stage larva with an almost completed body of the adult female and 4 with a developing prepupa, all belonging to *C. garciniae*, suggest that the male is a little larger than the female (in the length of the body and also in the length of the hind trochanter and femur combined), but the specimens are too few to generalize the observation. Further, they do not indicate the presence of any distinct sexual difference in the antennae, the number of tubular ducts, and other features.

Mamet (1954) refers to 'the first stage female' and 'the third stage female' of *C. angraeci*. In the specimens of this species from the Malay Peninsula I have recognized only 2 larval forms, which may probably be the 1st and 2nd instars. Further, in describing the larvae of *C. vayssierei*, Mamet (1954) does not give any measurements for the body size.

D'Ascoli and Kosztarab (1969), in describing 3 female instars for *C. lata*, give measurements for the body and some body parts. However, their description does not convincingly show that the 'second instar female' and the 'third instar female' are not age groups nor sexual forms within the same instar.

Some species of *Conchaspis* may really have 3 female larval instars whereas others 2. But it is doubtful if a genus can be heterogeneous in the number of larval instars. It may be premature to make a decision, but here I would like to form a tentative conclusion, based on my own observations: the female has a total of 3 instars and the male 5 in *Conchaspis* (Table 2).

BODY SIZE AND WAX-SECRETING PORES

Table 3 shows the length of the hind trochanter and femur combined (as an indication of the body size), the total number of the tubular ducts, and the total number of the multilocular pores in the adult females of *C. angraeci* and the East Asian species. The presence or absence of the dorsal cicatrices on the head and also of the mesothoracic dermal invaginations are added for tabulating main recognition characters. The Malaysian species appear closely related phylogenetically, yet remarkably differ in the body size (as represented by the length of the hind trochanter and femur combined) and in the total number of the tubular ducts. *C. malesiana* also belongs to this species group. It agrees with *C. garciniae* in having dorsal cicatrices on the head, but falls within the range of *C. vaccinii* in the body size and also in the total number of the multilocular pores. These 4 species are successively larger and with more tubular ducts in the order *C. buchanae* < {*C. vaccinii*, *C. malesiana*} < *C. garciniae*. They overlap in the total number of the multilocular pores; however, the means differ significantly and are successively larger in the order mentioned. The smallest *C. buchanae* also differs from the others by lacking dermal invaginations on the mesothoracic ventrum.

Table 2. Instars in *Conchaspis*.

Instar	I	II	III	IV	V
Female	larva	larva	adult		
Male	larva	larva	prepupa	pupa	adult

Table 3. Some characters in the adult females of *C. angraeci* and the East Asian species.

	<i>C. angraeci</i>	<i>C. buchanae</i>	<i>C. vaccinii</i>	<i>C. malesiana</i>	<i>C. garciniae</i>
Length of hind trochanter + femur (μm)	81-95	98-112	130-164	132, 138 148, 150	156-192
(Sample size)	(30)	(25)	(30)	(2)	(30)
Total number of tubular ducts	0	40-69	101-209	111	ca. 230-306
(Sample size)		(25)	(52)	(2)	
Total number of multilocular disc pores	17-32	10-17	12-32	16, 19	18-38
Mean \pm 2 S.E.	25.1 \pm 0.6	13.7 \pm 0.7	20.6 \pm 1.2	—	27.8 \pm 1.2
(Sample size)	(90)	(25)	(53)	(2)	(54)
Cicatrices on head	—	—	—	+	+
Derm invaginations on mesothorax	—	—	+	+	+

The East Asian species are very similar in other external characters, and may appear to be mere fragments from a continuous series of variations. But this impression is false. The multilocular pores increase from *C. buchanae* through *C. vaccinii* to *C. garciniae* in terms of the total number, but, while the submarginal pores increase, the intermediate and submedian pores may decrease (Fig. 1). Each of these species seems to have a unique pattern in the occurrence of the multilocular pores, supporting the view that they are good species.

The body size and the number of the tubular ducts are outstanding features to characterize and distinguish the Malaysian species (and also to separate *C. garciniae* from *C. malesiana*). The association of these features must have a biological significance. It is reasonable to assume that a larger species forms a larger test and needs more wax (secreted by the tubular ducts) to form the test. Preliminary measurements of tests support this assumption. For a meaningful comparison, however, it is necessary to know the amount of wax to be consumed in test formation, but this is out of the scope of the present work.

The total number of multilocular pores may be correlated to some degree with the number of eggs to be deposited, and the latter with the body size. (Needless to say, the correlation is expected within the limits of closely related species.) This assumption is also to be ascertained.

LM AND SEM OBSERVATIONS

In this section some parts of the body are dealt with on the basis of light microscopy [LM_y] and scanning electron microscopy [SEM_y]. Needless to say, SEM_y is superior to LM_y in supplying 3-dimensional images in a much broader range of magnification. However, LM_y and SEM_y have different roles, and LM_y is essential in examining patterns of dermal sclerotization. In the present work SEM_y was applied to *C. angraeci* and *C. garciniae*, which may represent different species

groups.

Figs. 2-17 are drawings or photographs made by LMy and Figs. 18-89 are photographs by SEMy.

Antennae

LMy and SEMy give somewhat different appearances of the antennae (Fig. 18 against Fig. 5Aa offers an example). In the present study, however, useful information has been obtained by LMy with an oil immersion objective, and the characters given below are based on LMy. Above all, LMy shows even a delicate pattern of dermal sclerotization, which is unrecognizable by SEMy.

In the 1st instar the antennae are slender and 6-segmented, showing 6 sclerotized bands (Figs. 4A and 5A). The Malaysian species agree with each other and differ from *C. angraeci* in that the bands are annulate or reticulate-annulate; the setae occurring on the terminal segment are somewhat different in state among these species (in *C. garciniae* these setae are all short and mostly fleshy as shown in Fig. 5A, but in the other species some of the setae are slender and pointed). However, *C. angraeci* and all the Malaysian species agree in the following characters: 1st segment less sclerotized than the succeeding segments, with 2 slender setae; the 2nd also with 2 setae and, on the dorsal side, a rounded low tubercle (sensillum?); the 3rd with no seta; the 4th with 1 slender seta on the dorsal side; the 5th with 1 fleshy seta on the ventral side.

In the intermediate stage larva and the adult female the antennae show 5, 4 or even only 3 sclerotized bands and, therefore, may be described as 5-, 4- or 3-segmented. But the setae and tubercle observed on the basal 5 segments in the 1st instar find the corresponding setae and tubercle in these later stages, so that ontogenetic changes of antennal segments are traceable. The following changes are indicated: 1) in *C. angraeci* and *C. buchanaiana* the setae occurring on the 1st segment of the 1st instar find the corresponding ones on the stippled derm near the base of the antenna in the intermediate stage and the adult female, that is, the original 1st segment is incorporated into the head in the later stages; 2) in *C. garciniae* and *C. vaccinii* the 1st and 2nd segments are incorporated into the head; and 3) in all of the species examined the original 3rd and 4th segments are united to form an apparent segment in the adult female (in the intermediate stage the 3rd and 4th segments are still recognizable, and in *C. angraeci* they are quite distinct) (Figs. 4-6).

In the intermediate stage and the adult female the fleshy seta occurring on the penultimate segment (ontogenetically, 5th segment) is especially thickened and more or less spatulate. In the adult females examined of *C. malesiana* this seta is not found at the expected position, while there is on the terminal segment an especially robust seta instead; this seta is interpreted to be the expected one dislocated from the penultimate segment. In *C. vaccinii* and *C. garciniae* the seta is dislocated to the distal border of the penultimate segment (Figs. 5Ca and 6Ba).

In *C. angraeci* the antennae of the intermediate stage and the adult female are rather slender and not so much different from those of the 1st instar as in the Malaysian species, in which the antennae are more or less plump in the later stages. In *C. garciniae* the antennae of the later stages are especially modified in shape in comparison with those of the 1st instar.

Thus, the species examined represent several evolutionary stages in the ontogenetic development of the antennae. Evolutionary trends are observed in the incorporation of the basal 1 or 2 segments into the head, in the fusion of the 3rd and 4th segments, in the dislocation of the spatulate seta, and in the modification of the shape. Obviously *C. angraeci* is primitive in comparison with the other species examined. *C. buchanae* shares with *C. angraeci* the character that only the 1st segment is incorporated into the head in the later stages, in which, however, *C. buchanae* differs from *C. angraeci* in the sclerotized band of the 2nd segment being incomplete on the dorsal side (Fig. 6A).

Dermal spots with radiating creases

The Conchaspidae are uniquely characterized by having the structures known under the name 'eye spots' or 'dorsal ocellar spots' (Mamet, 1954), which are a pair of dermal spots of a considerable size lying on the dorsal surface of the head in the larval stages and the adult female. In the species examined they are wholly membranous, and therefore may not always be easy to observe in LMy. They appear to be round and flat spots (Figs. 10 and 11), each with numerous creases radiating from a longitudinal area within. In SEMy the longitudinal area is an invagination (Figs. 19 and 21), which shows nothing particular on the bottom (Fig. 20).

A pair of similar spots are present on the dorsal surface of the thorax submedially between the pro- and mesothorax, and also between the meso- and metathorax, with the invagination running transversely along the segmental borders (Fig. 22).

A pair of much smaller spots having rather irregular creases may also be seen submedially on the dorsal surface of the 1st abdominal segment, and also of the 2nd, just posteriorly to the anterior margin of the segment. They are clearly visible by LMy in the adult female of *C. buchanae* (Fig. 2).

All these spots, especially the cephalic and thoracic ones, agree in having numerous radiating creases. This suggests a common function for them, if they have any function. Especially the cephalic ones, the so-called 'ocellar spots', occur in all the described conchaspids. Therefore, they must have a function essential to the members of the family. To go further is a matter of speculation, for my study covers only a small part of the family and, above all, includes no species with a sclerotized centre in the cephalic spot. However, I suspect that all these dorsal spots are eversible, and that they have a definite role in test formation.

Other dermal structures

In describing *C. malesiana* Ben-Dov and Williams (1984) state that it is characterized by 'having dorsal cicatrices lateral to the ocellar spots; these cicatrices being present also in the second female instar'. *C. garciniae* is also provided with them in the first instar (Fig. 5Ab), the intermediate stage larva, and the adult female. The cicatrix is a small, elongate, sclerotized structure and appears to be divided into 2 parts (see figures in Ben-Dov and Williams, 1984). In SEMy, however, it is not divided but simply constricted, and irregularly scattered with many stubs (Fig. 23). So far as I am aware, this structure has not been mentioned in other conchaspids. It is definitely absent in *C. angraeci*, *C. buchanae* and *C. vaccinii*.

The 'dermal invaginations of the thorax' (Mamet, 1954) are a pair of rounded and depressed structures occurring on the ventral surface of the metathorax mesocaudad of the coxae. They also occur in the corresponding position on the mesothorax in several species (*C. madagascariensis*, *C. vaccinii*, *C. malesiana* and *C. garciniae*). So far as known, they are limited to the adult female. In LMy they are well sclerotized. Fig. 24 shows a metathoracic one of *C. garciniae* in SEMy. It is stippled but somewhat differently from the surrounding derm; otherwise there is nothing particular. The universal occurrence of this structure in the genus is noteworthy, but no idea as to its possible function has been suggested from my observations.

There are other invaginations occurring on the ventral surface of the supposed 7th segment. These structures have not been mentioned by authors but shown by Khoo (1978) and Ben-Dov and Williams (1984) in their drawings of *C. vaccinii* (adult female and larvae) and *C. malesiana* (adult female). I would like to call them 'dermal slits'. In LMy the dermal slits may appear to be short and simple sclerotized lines laid transverse to the body axis (Fig. 17), but in SEMy they are obviously invaginated (Figs. 26 and 27). In the adult females of *C. vaccinii*, *C. malesiana* and *C. garciniae* a pair of slits are situated caudad of the vulva at some distance from the latter and superimposed on the sclerotized plates of the 7th abdominal segment. The adult females of *C. buchanae* and *C. angraeci* have no dermal slits. On the other hand, the 1st instar and intermediate stage larvae of the Malaysian species (including *C. buchanae*) have 3 slits, the median one being situated somewhat posteriorly. These slits as compared with those of the adult female are dislocated anteriorly, being situated near the anterior end of the 7th abdominal sternite. In the larval stages of *C. angraeci* there are only 2 slits, the median one being lacking, and in the intermediate stage larva the slits are rudimentary, being very poorly developed in SEMy and hardly recognizable in LMy.

The presence or absence of the dermal slits and their number are summarized in Table 4.

The 'abdominal tubercles' (Mamet, 1954) or 'submarginal dorsal bosses' (in this paper) are simple tubercles both in LMy and in SEMy (Fig. 25). They have been found in all of the 1st instar, intermediate stage and adult female of *C. angraeci* and the Malaysian species, occurring on the 1st to 5th abdominal segments.

Another dermal feature is crenulae or spiny processes, which occur on the 3rd to 6th, especially 4th and 5th, abdominal segments, dorsally along the lateral margin (Fig. 28) and ventrally along the posterior margin in the lateral region. These crenulae are present in *C. malesiana*, *C. vaccinii* and *C. garciniae*, but absent in *C. angraeci* and *C. buchanae*. I have observed them also in the intermediate stage larvae of *C. vaccinii* and *C. garciniae*.

Table 4. Number of dermal slits in *C. angraeci* and the East Asian species.

	<i>C. angraeci</i>	<i>C. buchanae</i>	<i>C. vaccinii</i>	<i>C. malesiana</i>	<i>C. garciniae</i>
First instar	2	3	3	no information	3
Intermediate stage	2 (rudimentary)	3	3	no information	3
Adult female	0	0	2	2	2

Minute spines, recognizable only by SEMy, are scattered on the 4th to 6th abdominal sternites in *C. angraeci* (Fig. 29). Still minuter ones are observed in *C. garciniae*; in this species they occur also on the 7th sternite lateroposteriorly to the dermal slits (Figs. 26 and 30).

Wax-secreting pores

Generally in the Conchaspidae the adult female is provided with 3 types of external secretory organs: 5-locular disc pores associated with the spiracles, multilocular disc pores occurring on the ventrum, and tubular ducts. The intermediate stage larva may also have the tubular ducts, and the 1st instar larva another kind of disc pore, besides the 5-locular spiracular disc pores. These organs are supposed to secrete waxy substances, which, however, have not been analysed chemically.

Mamet (1954) gives an excellent description of the multilocular disc pores, and, at the same time, shows limitations of LMy in observing them. In LMy the pore consists of a thick, well-sclerotized rim, a series of 11 clear spots arranged in a circle within the rim, another series of 11 spots in an inner circle, and a rather broad central area, the corresponding spots in the outer and inner series being situated opposite in spokelike clear areas radiating from the central area (Fig. 12).

Multilocular disc pores of *C. angraeci* (Fig. 31) and *C. garciniae* (Fig. 32) were examined by SEMy. The whole disc pore is sunken under the level of the dermal surface; no structure corresponding to the sclerotized rim is visible; the clear spots in the outer series are excavations of the wall just under the dermal surface; the spots in the inner series are wax-secreting openings, arranged on another story more sunken than the excavations; and the central area is further sunken, with a round mound or core. In *C. garciniae* the core is surrounded by an unfixed number of pin-holes.

The multilocular disc pores produce wax cylinders, which are moulded into rings probably as follows: a cylinder of wax secreted by an opening on the lower (inner) story is depressed on the side faced to the circumference of the pore and, therefore, grows excurved; the tip of the growing cylinder is led into the corresponding excavation on the upper (outer) story and stops there; the cylinder, being pushed by its newly secreted part, grows more and more curved until it forms a ring (Figs. 33 and 34). Fig. 34 shows several jointed cylinders, which may have failed to complete rings. The joint suggests a stop in wax secretion. It seems that the secretion normally stops each time it has supplied a definite amount of wax to make a ring. The role of the mounded core is unknown; it may support growing cylinders.

The multilocular disc pores of *Conchaspis* are unique in structure, and their moulding device for producing wax rings must also be peculiar to the genus (or to the family). They are 'abducent' (for this term, see Takagi, 1990b) in secreting wax cylinders, which, however, do not go out of the pore but are led to the excavations on the wall. I would like to apply the term 'retroduction' to this manner of conducting wax cylinders.

The spiracular disc pores are inset in a well-defined, sclerotized area just anterior to the spiracle (Fig. 35). They are 5-locular, and the septa separating the locules are simple (Fig. 36), with no process as in the 5-locular perivulvar disc pores of diaspids.

In the Malaysian species the tubular ducts occur in the adult female and the intermediate stage larva and on the metathorax and the basal 4 abdominal segments. They are ventropleural as pointed out by Khoo (1978) for *C. vaccinii*. He states that 'in unmounted specimens, long glassy filaments can be seen arising from this region'. I observed the same by SEMy (Fig. 38). The tubular ducts may partly open dorsally in the pleural region, but otherwise they are always on the ventral side.

The tubular duct bears a 3-pronged structure near the orifice as described by Khoo (1978); the orifice is so poorly rimmed that it is not always visible distinctly, while the inner end of the duct is surrounded by a well-marked fold (Fig. 7A). In SEMy (Fig. 37), however, the orifice is well rimmed, elliptical and laid transverse to body axis; it opens backward, showing the median prong in the form of an elevated stripe on the posterior wall and dentations on the anterior margin. It produces a ribbonlike filament of wax, which appears slightly undulate on the surface owing to longitudinal linear impressions (Fig. 39). These impressions apparently correspond to the dentations of the orifice.

The 1st instar larvae of the Malaysian species are provided not with ducts but with disc pores, which are dorsopleural and occur singly on the 1st to 3rd abdominal segments. Khoo (1978) described and figured them for *C. vaccinii*. In LMy the pore is surrounded by a thick rim, and the area inside the rim is completely divided into 3 transparent parts by 3 sclerotized bars connected together at the centre of the pore (Figs. 7B and 13); it is difficult to understand the true nature of this tripartite structure. In SEMy it is a flat tubercle and has 3 clefts or fissures running from the margin to the centre, where they meet together (Figs. 40 and 41); it produces from each of the fissures a ribbonlike filament of wax (Fig. 42), which is similar to the filament secreted by the tubular duct in having linear impressions. I would like to propose the term '3-fissural disc pore' for this type of secretory organ.

Authors referred to 'dorsal tubular ducts' and figured tubular ducts on the dorsal side of the body in their descriptions of *Conchaspis* species. Further, the ducts I observed do not agree with the general description of the ducts presented by Mamet (1954), and little resemble the figures (broad tubes with both ends truncate) he depicted for many species. Furthermore, the occurrence of 3-fissural disc pores in the 1st instar has been reported only by Khoo (1978). According to Mamet (1954) the 1st instar larvae of some *Conchaspis* species he examined are provided with 'dorsal tubular pores'. He showed short tubular ducts in his figure of the 1st instar of *C. vayssierei*. The 1st instar larva of *C. lata* is also provided with 'dorsal tubular pores', which are truncate on both ends (D'Ascoli and Kosztarab, 1969).

The Malaysian species do not appear to be closely related to *C. angraeci*, the name-bearing species [type-species], which has no tubular ducts nor 3-fissural disc pores. However, they agree with the latter in the general characters of the features common to all these species. It seems that *Conchaspis* is a considerably homogeneous group, the members being uniform in the general structure of the body. Therefore, I do not think that the disagreements between authors' observations and mine are real. Ben-Dov and Williams (1984) in their description of *C. malesiana* stated that the tubular ducts are 'placed marginally on dorsum' and figured them on the dorsal side. Actually, in this species, too, the tubular ducts are ventropleural as in its close relative *C. garciniae*.

It is natural to presuppose that any ducts or pores responsible for the formation

of a dorsal test should be dorsal in position. Apparently Mamet (1954) and other authors erroneously understood the structure of the tubular ducts, and this may also have led them to take the ducts to be dorsal. The orifice of the duct is, as stated above, very poorly rimmed and may be overlooked in LMy. The 3-fissural disc pores, too, may be mistaken for short ducts when they are viewed laterally.

Pygidium

The 7th and succeeding sternites of the abdomen are fused to form a pygidium (or pseudopygidium in some authors); in the larvae the 6th sternite, and in the adult female the 5th also, is fused with the pygidium in the median region; these sternites assume a strongly longitudinal position so that the 4th sternite is attenuated medially. On the dorsal side the 6th and succeeding segments take part in the pygidium. The pygidium has some sclerotized plates, which are combined to form a pattern peculiar to the genus. These plates may differ among species in their details (compare Figs. 14 and 15 with Figs. 16 and 17), and may be worthy of careful comparison especially when establishing species groups.

Structures really worthy of future study have been discovered by SEM observations at the apex of the pygidium. They are fimbriate processes, which are similar to those structures known under the name 'pectinae', 'fimbriate plates' or 'plates' in diaspidids. They may be called 'pectinae' in this paper. *C. angraeci* have 3 pectinae, 1 median and 2 laterals, which are broad and well fimbriate in all of the adult female, the intermediate stage and the 1st instar (Figs. 43-45). The pectinae and the setae around them are situated on the ventral margin of the anus (Fig. 51), which is situated at the apex of the abdomen.

C. garciniae is provided with the lateral pair alone. These pectinae are well developed in the first instar (Fig. 50) as in *C. angraeci*, but are small and slender in the adult female (Figs. 47 and 48) (the intermediate stage has not been examined for the pectinae). When the pygidium is viewed directly from above, the pectinae are, while clearly visible in the 1st instar (Fig. 49), hardly visible in the adult female, being confounded with the setae occurring nearby (Fig. 46).

I have examined no specimens of *C. buchanae* and *C. vaccinii* by SEM. However, I have observed a pair of broad, well-fimbriate pectinae in *C. buchanae* by LMy. (In *C. angraeci*, too, the 3 pectinae are recognizable by LMy. Nevertheless, they have been overlooked by authors.) It has been difficult to confirm by LMy the presence of pectinae in *C. vaccinii*, but the same has been the case with *C. garciniae*.

The pectinae are well represented in *C. angraeci*, while reduced in *C. garciniae*. In the state of the antennae *C. angraeci* is deemed to be primitive in comparison with *C. garciniae*; the former, then, may represent a comparatively primitive state of the pectinae.

TESTS IN SEMY

The tests of the Conchaspidae are very similar to those of the Diaspididae in external appearance, differing from the latter in retaining no exuvial cast. However, the tubular ducts open on the ventral surface of the body in the Conchaspidae whereas they are primarily on the dorsal surface in the Diaspididae. Further, some

conchaspids including *C. angraeci* have no tubular ducts and yet form good tests. These facts suggest some peculiarity in the tests of the Conchaspidae.

C. angraeci

Fig. 56 shows part in a cross section of the dorsal portion of a completed female test. Internally the test appears to be made of the same material throughout, which is laid in a number of thin layers. However, there has been found on the body no organs which may produce this material. I supposed, therefore, that the material of the test came from the anus, and submitted a small amount of tests to Prof. Seiya Chiba, a biochemist, for a preliminary chemical analysis. Shortly after, I received from him a letter, which reads as follows :

'Ten mg of the sample was dissolved in 2 ml of 10N NaOH solution by heating at 55°C. The solution showed a faint brown color and remarkable viscousness. Ten μ l aliquots of the solution, corresponding to 50 μ g of the sample, were pipetted out and transferred into test tubes for the determination of sugar content by phenol-sulfuric acid method.* Sugar content was estimated as D-mannose. The sample contained carbohydrate in about 60%. These findings suggest that the substance from the test of *Conchaspis angraeci* may be a kind of peptidoglycan.

* M. Dubois, R. Gilles, J.K. Hamilton, P.A. Robers and F. Smith, *Anal. Chem.*, 28, 350 (1956).'

The result of his analysis does not contradict my supposition. Further, when preparing material I found some adult females dead with the abdomen kept bent up and the anus opened round (Fig. 51). The insect may assume this posture when it forms the dorsal portion of the test, thus applying the anus, which is situated at the apex of the abdomen, to the inner surface of the test under formation. It seems that the abdomen when bent up makes the anus open round.

The dorsal portion of the test is rugged externally (Fig. 55), but internally it is composed of layers tightly appressed together, and on the inner surface it is even and smooth. Therefore, it is postulated that the test had been pressed from the inside (that is, by the insect) throughout its formation. On the other hand, the ventral portion, which is formed within the margin of the dorsal portion, is very coarse in texture (Fig. 57), thus probably showing the state of the material placed without being pressed.

Many 1st instar larvae were found naked on the twigs of the host plant. However, contrary to Mamet's (1954) statement, the formation of the test starts in the 1st instar (Figs. 52 and 53). The test has strong ridges radiating from the top as noticed by authors (e.g., Newstead, 1902) (Figs. 53 and 54); the formation of these ridges begins in a very early stage of the test (Fig. 52). However, in the completed test the inner surface of the dorsal portion shows no trace of depressions corresponding to the ridges; in cross sections the test is thickened dorsally where the ridges run across.

C. garciniae

In the adult female numerous tubular ducts occur in the ventropleural region of the metathorax and basal 4 abdominal segments. They open backward (Fig. 37) so that the wax filaments secreted by them mostly extend onto the ventral side of the abdominal apex (Fig. 38). The test is composed of the supposed anal substance

inlaid with wax filaments, which are broken into short and long fragments. Apparently by bending the abdomen up the insect applies the ventral side of the abdomen onto the inner surface of the dorsal portion of the test under formation, thus supplying wax filaments (being crushed into fragments) and the anal substance to the test. The intermediate stage larva has also many ducts ventropleurally and may behave the same. The 1st instar larva is provided with 3-fissural pores dorsopleurally on the abdomen, and may not necessarily bend the abdomen in order to supply wax filaments secreted by the pores. Still it may bend up the abdomen when supplying the anal substance to the dorsal portion of the test.

The completed test is very thick dorsally, where are recognized 3 strata or zones (Figs. 64-69), all composed of the anal substance intermingled with fragments of wax filaments. Each of the outer- and innermost zones (Figs. 67 and 69) is narrow and tight, with wax filaments, flattened and ribbonlike as already stated, laid all parallel to the zone. While the outer surface of the test is rugged (Figs. 59-61), the inner surface (the bottom of the innermost zone) is smooth (Fig. 63). Pressing from the inside is postulated for the formation of these zones. The intermediate zone (Fig. 68), a large space, is a coarse assemblage of irregular lumps of the anal substance and fragments of wax filaments; however, it shows a rather regular growing pattern at lower magnification (Figs. 64 and 65).

A great part if not all of the outermost zone may be formed during the larval stage. The earliest part of the zone is composed almost of the anal substance alone (Fig. 72), but soon abundant wax filaments are incorporated into the formation of the test (Fig. 73). The intermediate zone, at least for the greater part, and the innermost zone are undoubtedly referable to the adult female. The test is attached to the plant with a coarse mixture of the anal substance and wax filaments (Figs. 70 and 71).

The female test is variable in shape. On *Garcinia scortechinii* it is highly conical, clasping the petiole between its extended lower parts (Figs. 58, 62, 64 and 66). This type was described by Khoo (1978) for *C. vaccinii*. It may be called 'cypraeiform test' [after the familiar cowrie, *Cypraea*, Gastropoda]. On *Garcinia nigrolineata* the test is variable in height, with no extended lower parts to clasp the petiole. In fact, the petioles of *G. nigrolineata* are thicker than those of *G. scortechinii*, and may be too thick to be clasped by the test formed by *C. garciniae*. This 'patelliform' [shaped like a limpet shell] test has a rather well-developed ventral portion within the margin of the dorsal portion, instead (Fig. 74). Internally the patelliform test of *C. garciniae* is the same as the cypraeiform one in having the 3 zones. Both types show no ridges radiating from the top. The test of *C. angraeci* is patelliform, but it is composed of the anal substance alone and remarkably ridged on the dorsal surface.

The male test of *C. garciniae* also occurs on the petiole. It is much smaller than the female one and elongate (Fig. 75), with a complete ventral portion, thus forming a puparium [a pupa container] (Figs. 78). Internally the dorsal portion is composed of a single zone (Fig. 79), which is the same in texture as the outer- and innermost zones of the female. It is rugged on the outer surface (Fig. 76), but smooth on the inner surface (Fig. 77). In this sex, too, pressing from the inside is postulated throughout the formation of the dorsal portion.

C. vaccinii

Female tests from *Payena lucida* were observed. They are cypraeiform (Figs. 80 and 81), showing 3 zones internally (Figs. 81-86), though the intermediate zone appears different in the growing pattern at low magnification (Figs. 81 and 82) from that of *C. garciniae* (Figs. 64 and 65).

C. buchanae

The female test is patelliform and variable in height, with the ventral portion developed within the margin of the dorsal portion (Fig. 87). *C. buchanae* differs from *C. garciniae* and *C. vaccinii* in having only a single zone in the completed female test (Figs. 88 and 89). This zone, however, is the same in texture as the outer- and innermost zones in the female tests of the latter 2 species.

CONCLUDING DISCUSSION

Now I return to the questions I mentioned in Introduction, though I have no definite answers yet. My study of the family Conchaspidae is substantially limited to *C. angraeci* and the 3 Malaysian species, only one seventh of the Conchaspidae now known. But some pieces of information newly obtained may be worthy of consideration in connection with the questions.

Where should the Conchaspidae be placed ?

First of all, the discovery of the pectinae in *Conchaspis* has a twofold meaning : it connects *Conchaspis* with *Fagisuga* and, at the same time, supports the view that *Fagisuga* belongs to the Conchaspidae. Not only that, the examination of the pectinae gives a reason for considering *Fagisuga* as a primitive conchaspid. Based on the association with the state of the antennae the occurrence of 3 pectinae (as represented by *C. angraeci*) is assumed to be primitive in comparison with the occurrence of 2 pectinae (*C. garciniae*). According to the figures presented by Lindinger (1909) and Williams (1985) *Fagisuga triloba* is provided with 3 well-developed pectinae and, laterally to them, another pair of rudimentary ones. Other noteworthy characters of *Fagisuga* are the dorsal position of the anus and the less specialized sternites composing the pygidium (based on the figure presented by Williams, 1985); these characters may support the view that *Fagisuga* is primitive in comparison with *Conchaspis*.

If the view above is correct, research on the phylogenetic position of the Conchaspidae may be more promising by examining *Fagisuga*. Our present knowledge on the morphology of *Fagisuga*, however, is limited to the adult female and to recognition characters. *F. triloba*, being associated mainly with *Nothofagus*, inhabits Patagonia in spite of the fact that the family is mainly tropical or subtropical in distribution. Williams (1983) states that '*Fagisuga triloba* may have adapted to *Nothofagus* from the more tropical areas'. However, he also states that 'Present-day distribution suggests that many families of Coccoidea may be Gondwanic in origin'. If *Fagisuga* really represents a primitive form of the Conchaspidae, the possibility may not be excluded that it is a survivor from the ancestral stock which originated in temperate Gondwana.

The pectinae of these conchaspids are similar to those ['plates'] of diaspidids

(especially *Megacanthaspis*, *Thysanaspis*, etc.), and may be taken as another feature indicating a close connection between the Conchaspidae and the Diaspididae. However, recent discoveries support the view that very primitive diaspidids are simple-structured forms, from which advanced forms with pectinae and other pygidial appendages evolved (Takagi, Tho and Khoo, 1990). According to this view, the diaspidid pectinae first appeared *within* the Diaspididae, and, therefore, are independent in origin from the pectinae of the Conchaspidae (unless these are supposed to have been derived from an advanced diaspidid with pectinae — a very improbable assumption).

The 3-fissural disc pores of the 1st instar are also worthy of mention here. They agree with the tubular ducts of the intermediate stage larva and the adult female in occurring in the pleural region of the body. Functionally these pores also agree with the tubular ducts in producing ribbonlike wax filaments marked with longitudinal lines. Do these agreements indicate that the conchaspidid tubular duct evolved from the 3-fissural disc pore? However, because these wax-secreting organs appear too much different in structure, I would like to leave the problem to future study.*

In my limited knowledge no disc pores occurring in other families of the Coccoidea exactly agree with the 3-fissural pore. The 3-ocular disc pore of the Pseudococcidae, studied by SEMy by Foldi (1983), is somewhat similar, and may have some relation, to the 3-fissural pore. But we must take into consideration the fact that SEMy has still been applied to a limited number of coccoids. The conchaspidid tubular duct itself may find no counterpart in other families, appearing peculiar in its details. It may have nothing to do with the diaspidid tubular ducts, which have generally been supposed to have evolved from such a geminate disc pore as found in the asterolecaniid family group.

The pygidium of the Conchaspidae as represented by *Conchaspis* is very peculiar, and probably has developed in association with the manner of test formation described above. Fusion of distal segments of the abdomen is seen not only in the Conchaspidae and Diaspididae but also in other families of the Coccoidea sporadically (e.g., *Idiococcus* in the Pseudococcidae).

Similar features may sometimes (or often?) have evolved independently in different groups of the Coccoidea. Parallelism and convergence, and even atavism, may not be rare in organic evolution in general. Phylogenetic study based on morphology may fail unless the origin and evolution of features under discussion are clarified. The similarities of the Conchaspidae to the Diaspididae seem superficial, but we are still not on secure grounds to connect the Conchaspidae with any other family.

* As regards this problem Dr Khoo Soo Ghee wrote to me as follows: 'I wonder if you would agree that the tubular duct and 3-fissural disc pore are homologous structures and they probably represent different stages in the ontogenetic development of the tubular duct. The change in position could [be] due to the distension of the dorsum to accommodate the swelling of the body of the intermediate instar and adult female. The tubular duct could have arisen through the fusion of the plates on either side of each fissure, beginning from the rim towards the centre and eventually resulting in a shallow tube with an oval or circular external opening. As regards the internal tripartite structure the straightening of two arms together with a reduction of the third would result in a slit-like structure with a kink on one edge representing the vestigial arm.'

Infrageneric or infrafamilial relationship is not unrelated to the study of the phylogenetic position of the family. Comparisons of the antennae and also of the pectinae eventually have connected *Fagisuga* with *Conchaspis* and indicated the primitiveness of the former. Detailed study on the antennae may be especially useful in finding phylogenetic relationships of the *Conchaspis* species, which are, otherwise, considerably uniform.

The adult males of the 3 Malaysian species have been examined in connection with the phylogenetic position of the Conchaspidae, but I can add nothing to the study of the *C. lata* adult male made by Affi (1969). In fact, the adult males of all these species are very similar and more uniform than the adult females.

Why are the Conchaspidae so poorly represented ?

The 2nd question is also difficult to answer. Evolutionary explanations are often *ad hoc* ones and, thus, adaptation tends to be tautology. In the present study, however, a decided difference has been found in the structure of the test between the families Conchaspidae and Diaspididae, and the difference may have at least some concern with the question.

In the Diaspididae the main material for test formation is filamentous wax secreted by the tubular ducts. In a very primitive form, *Uluccoccus*, the test is simply a fluffy mass of wax filaments (which are cylindrical, being secreted from the ducts of the geminate-pore type). In advanced diaspidids the test takes a definite shape, with the framework composed of flattened, ribbonlike wax filaments (secreted from the 1- or 2-barred ducts), which are agglutinated together by a substance excreted from the anus (Foldi, 1982). Highly evolved female tests are quite thin and broad, being formed by rotative movements of the insect (Takagi, 1990a).

In the Conchaspidae, too, the test is composed of ribbonlike wax filaments and a substance from the anus. But here the wax filaments are crushed into fragments to be mingled with the anal substance just like pieces of aggregate mixed with cement to make concrete. This mixture, conchaspidid concrete, makes the test hard enough to resist stress between the finger and the thumb. In the species lacking tubular ducts (and 3-fissural disc pores in the 1st instar) the anal substance is the only material that forms the test.

The tests of the Conchaspidae are all alike in external appearance (Mamet, 1954); the female ones are more or less conical, with or without a pair of lower extensions. They cannot take other shapes probably because they are made from the amorphous anal substance (mixed with fragments of wax filaments in many species). On the other hand, advanced diaspidids form the framework of the test from long filaments of wax and use the anal substance to agglutinate them together; this manner, when combined with the insect's movements, may produce a wide variety of tests. Thus, the difference in the manner of test formation may have taken part in the causation of a great difference in evolutionary diversification between these families.

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ADDENDUM : NOTES ON THE USAGE OF THE TERM 'LOCULI'

Recently, after the completion of this manuscript, I have read the following paper, which is a valuable contribution to the knowledge of the coccoid wax-secreting organs and their secretions.

Foldi, I. 1991. The wax glands in scale insects : Comparative ultrastructure, secretion, function and evolution (Homoptera : Coccoidea). Annales de la Société Entomologique de France, N.S. 27 : 163-188.

In this paper the author gives short explanations to the multilocular disc pores (p. 167), tubular ducts (p. 168), and wax filaments (p. 176) of the Conchaspidae, and presents SEM photographs of the multilocular disc pore (Fig. 24) and wax filaments (Fig. 36) of *Conchaspis* sp.

Foldi states : 'the multilocular pores are "flowerlike" with 2 circles of loculi', while 'Each loculus is the site of secretion emission'. In my observation the multilocular disc pores of *Conchaspis* has wax-secreting openings only in the inner circle. The spots in the outer circle are simple excavations on the surrounding wall of the pore, and are not loculi according to Foldi's definition of the term.

I would like to take this opportunity to point out that the term 'loculi' has been used loosely in coccoid morphology. This term has been applied to clear spots visible within a wax-secreting pore in LM. Such clear spots have been supposed to be secreting openings with no direct evidence.

In SEM, however, the clear spots in a diaspidid disc pore are compartments defined by the septa and the surrounding wall, with the secreting apertures opened on the surrounding wall (Takagi, 1990b). They may rightly be called loculi, because *loculus* literally means a small compartment or chamber.

It has long been supposed that the pseudococcid 3-locular disc pore is partitioned by 3 curved walls. Foldi (1983 ; 1991) presents a SEM photograph of the 3-locular disc pore of *Planococcus citri*. This photograph shows that the supposed partitioning walls are, in reality, wax-secreting openings. Thus the parts which have been called loculi are the surface of the disc pore divided by the openings. In this case the application of the term may be changed to the real openings, but even with this

change the part designated under the term in the Pseudococcidae does not exactly correspond to that in the Diaspididae.

The term has generally been used in coccoid taxonomy, but the examples above show that sometimes it has been applied to different structures. The usage of the term is to be criticised on the basis of increasing SEM observations.

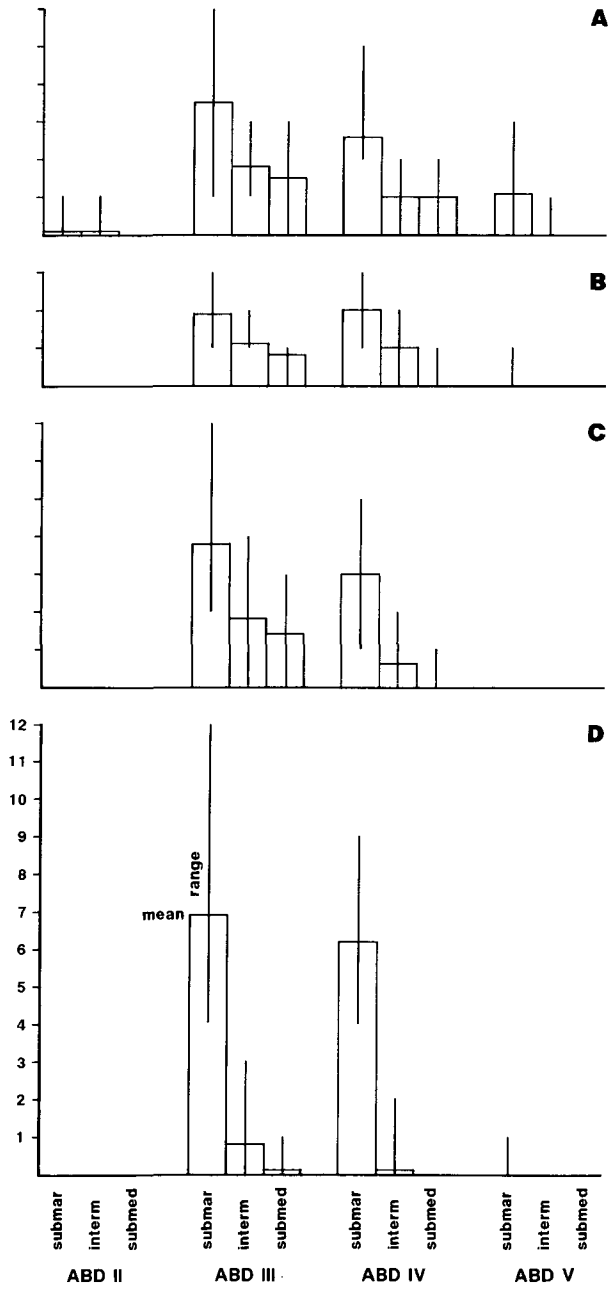


Fig.1. Number of multilocular disc pores in each of the submarginal, intermediate and submedian groups on the 2nd to 5th abdominal segments in *C. angraeci* (A), *C. buchanae* (B), *C. vaccinii* (C) and *C. garciniae* (D).

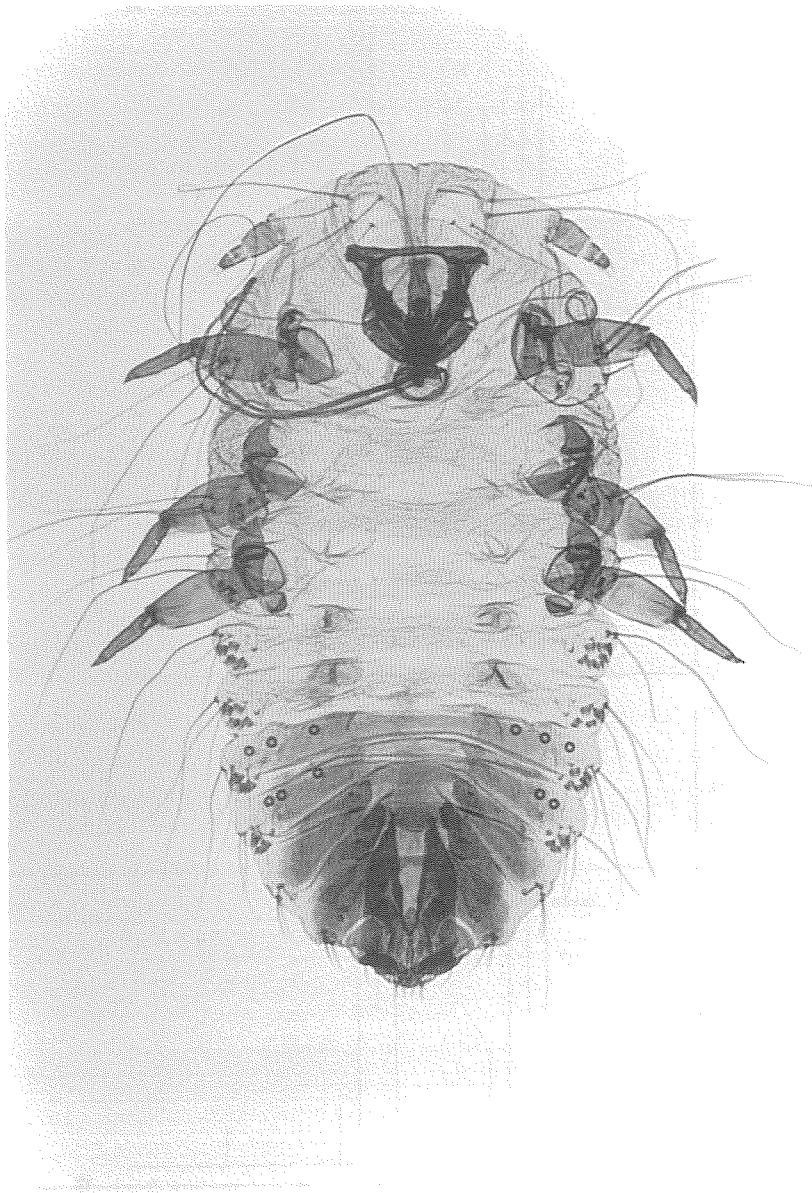


Fig. 2. *C. buchanae*, adult female.

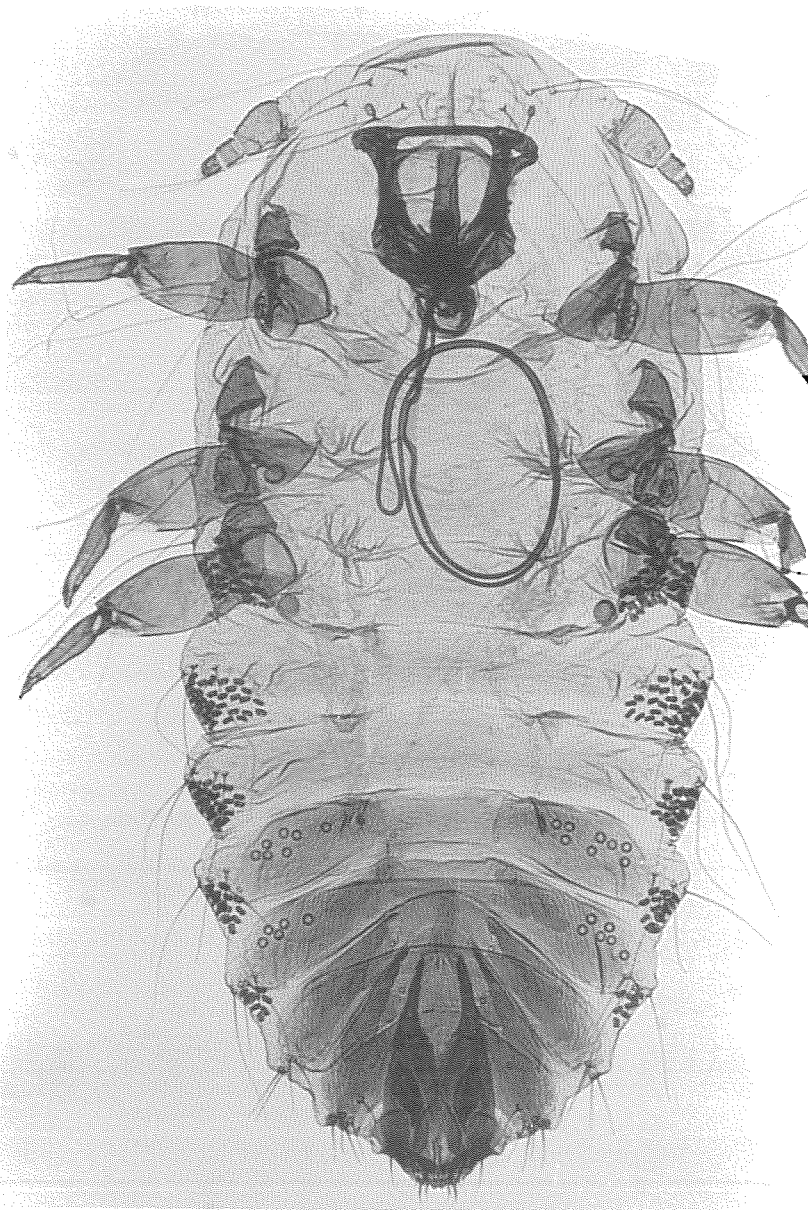


Fig. 3. *C. garciniae*, adult female [80ML-187].

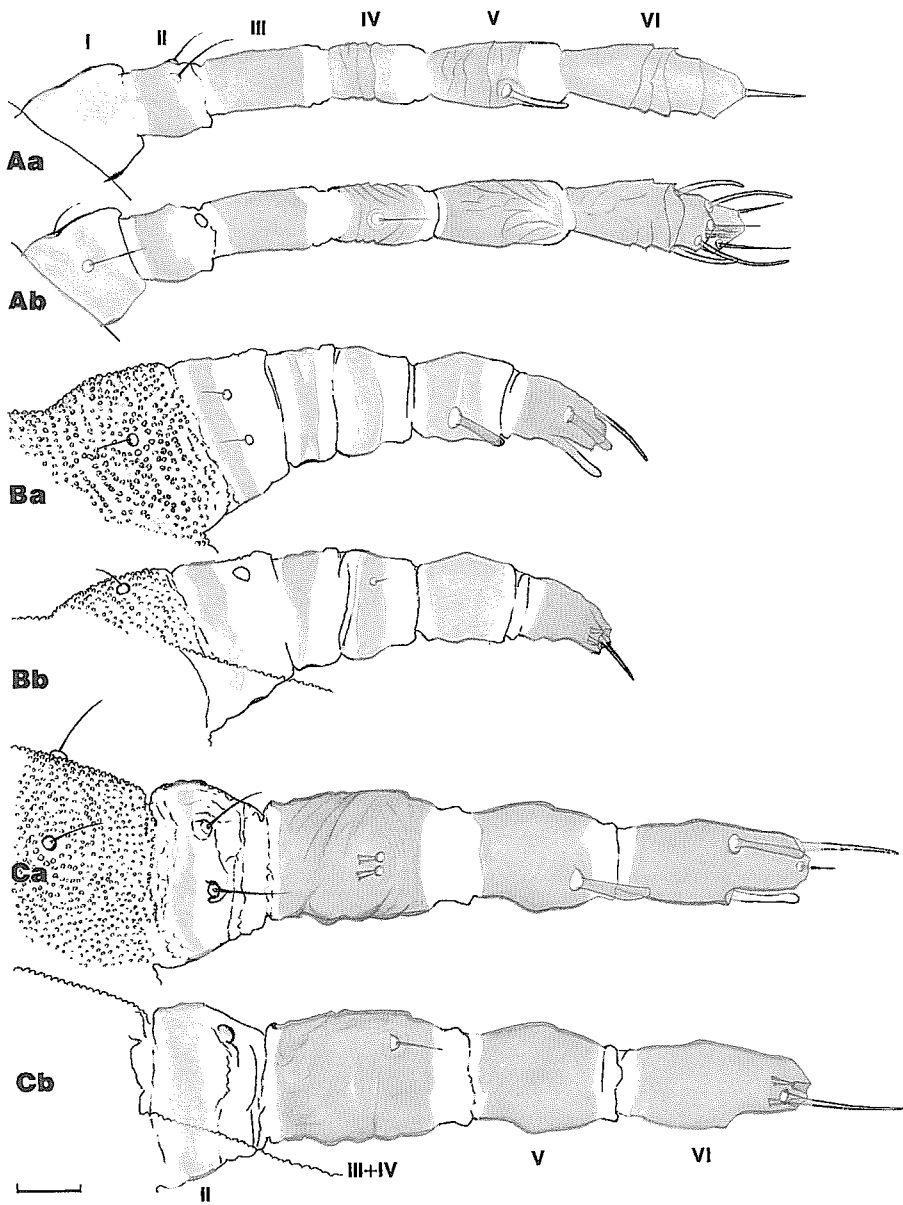


Fig. 4. Antennae of the 1st instar (A), intermediate stage (B) and adult female (C) of *C. angraeci* in ventral (a) and dorsal (b) views. Scale: 10 μ m.

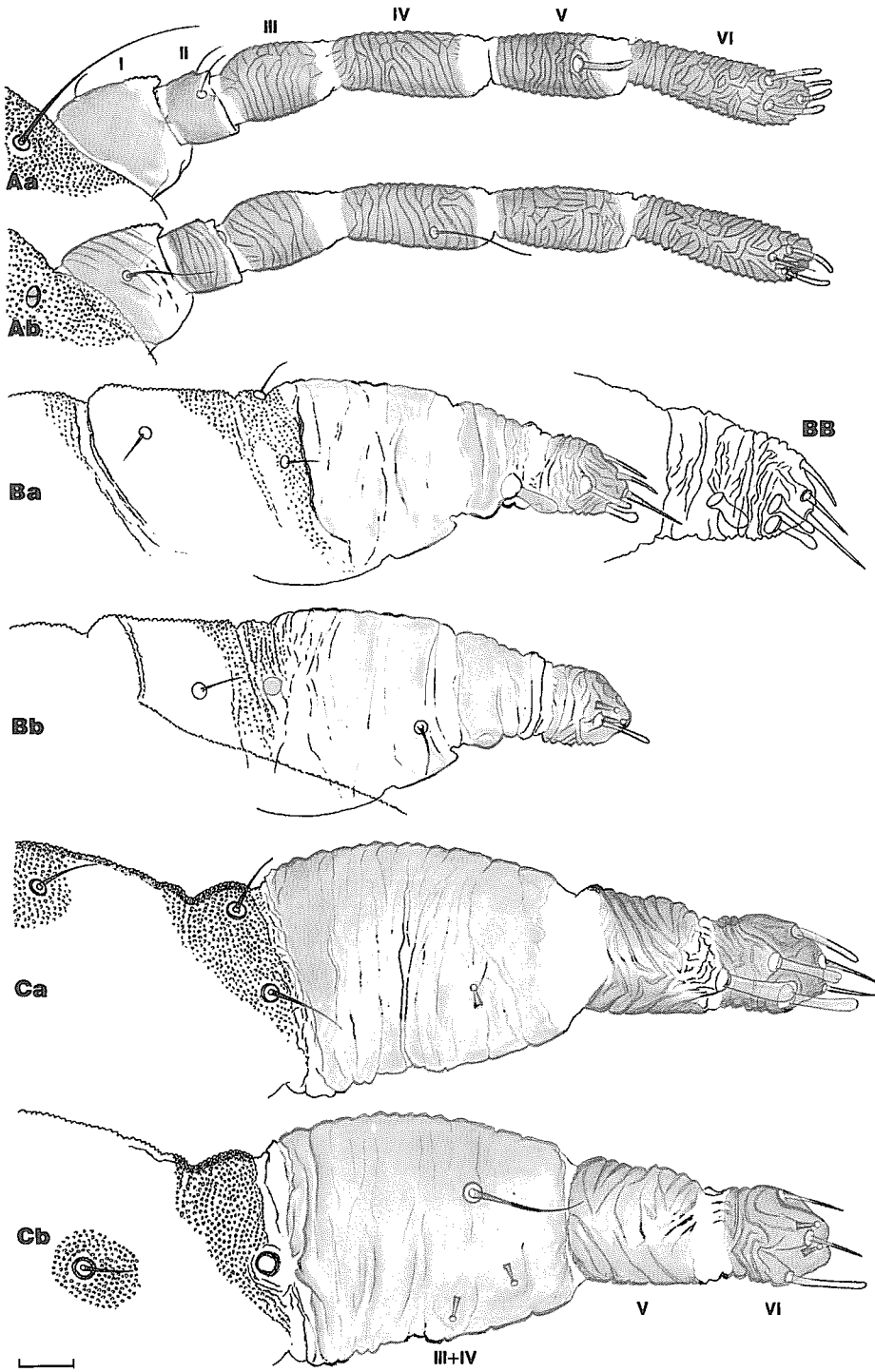


Fig. 5. Antennae of the 1st instar (A) [80ML-295], intermediate stage (B, BB) [80ML-186] and adult female (C) [80ML-167] of *C. garciniae* in ventral (a) and dorsal (b) views. Scale: 10 μ m.

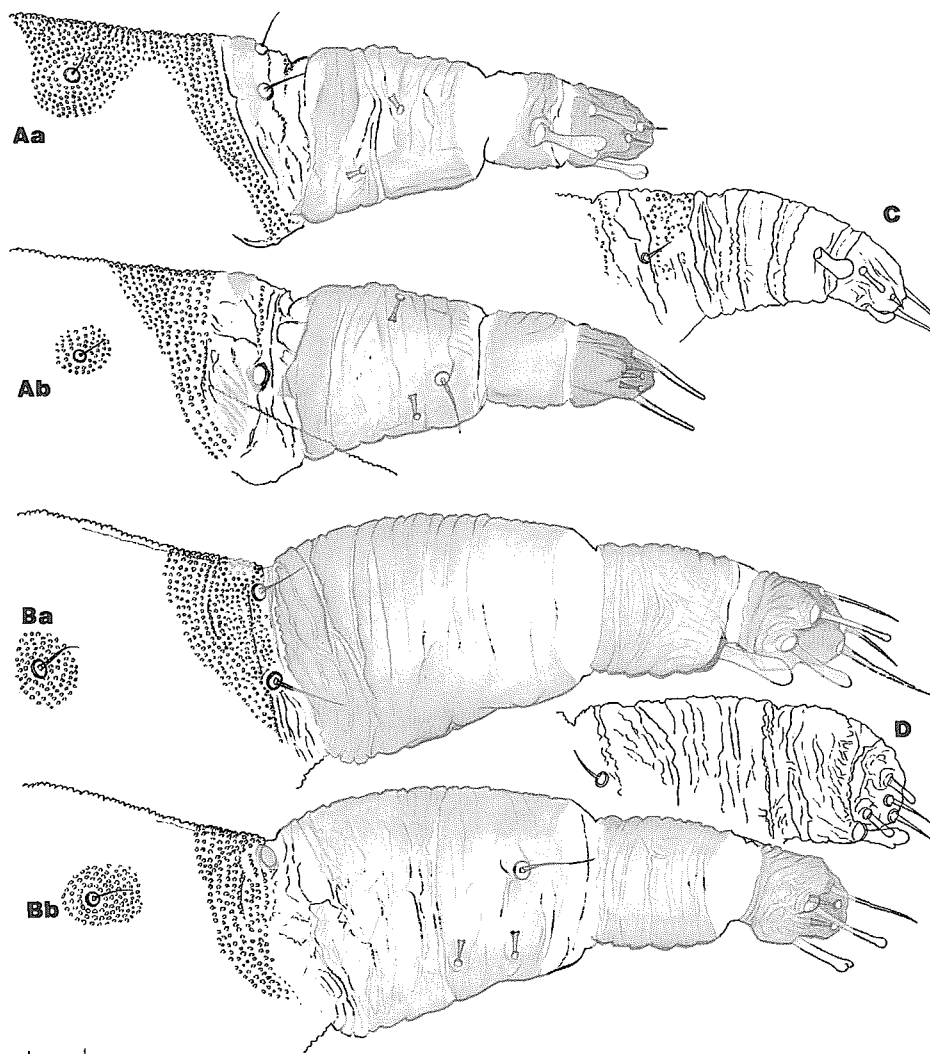


Fig. 6. Antennae of the adult female of *C. buchanaiae* (A) and *C. vaccinii* (B) [80ML-311] in ventral (a) and dorsal (b) views; Antennae of the intermediate stage of *C. buchanaiae* (C) and *C. vaccinii* (D) [90ML-238] in ventral view. Scale: 10 μ m.

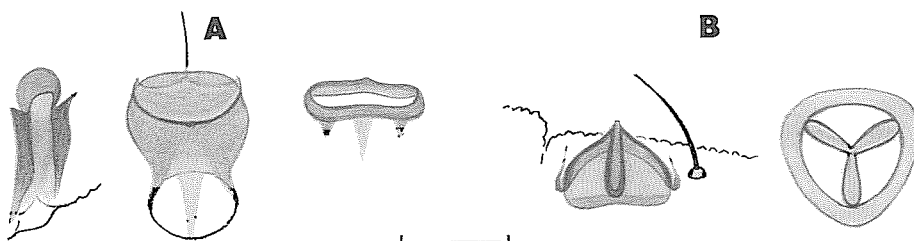


Fig. 7. *C. garciniae*, tubular ducts of the adult female (A) and 3-fissural disc pores of the 1st instar (B) in different views [90ML-295; 90ML-186 (B, right one)]. Scale: 10 μ m.

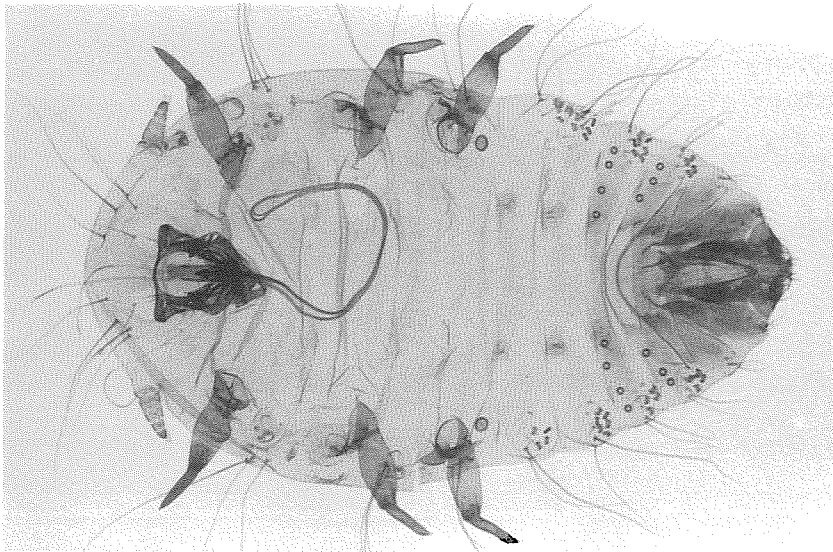


Fig. 8. *C. buchananiae*, adult female, full-grown.

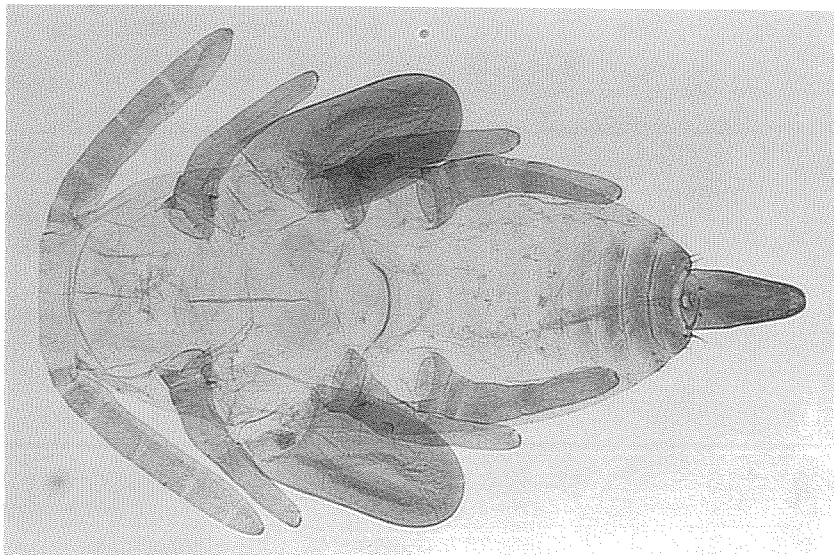


Fig. 9. *C. buchananiae*, pupa.

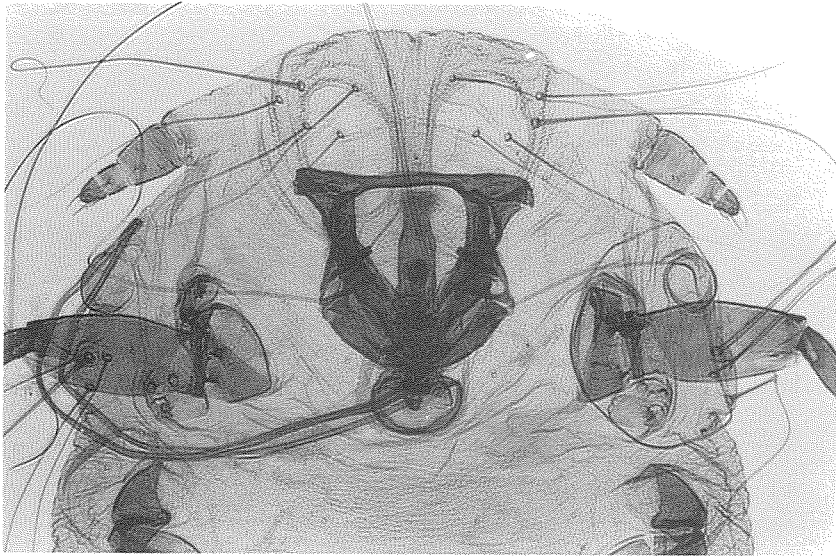


Fig. 10. *C. buchanaiae*, adult female : head, showing dorsal spots.

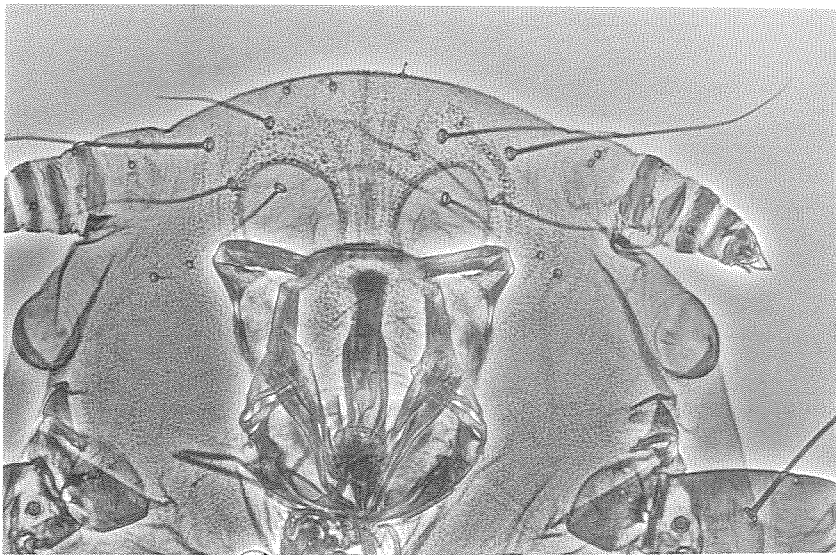


Fig. 11. *C. buchanaiae*, intermediate stage : head, showing dorsal spots.

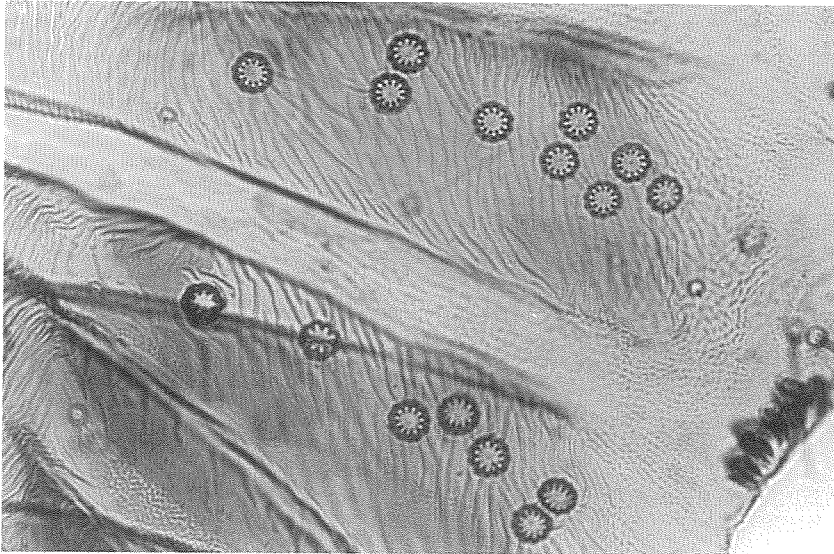


Fig. 12. *C. vaccinii*, adult female : multilocular disc pores in the submarginal, intermediate and submedian groups on the 3rd and 4th abdominal segments [90ML-545].

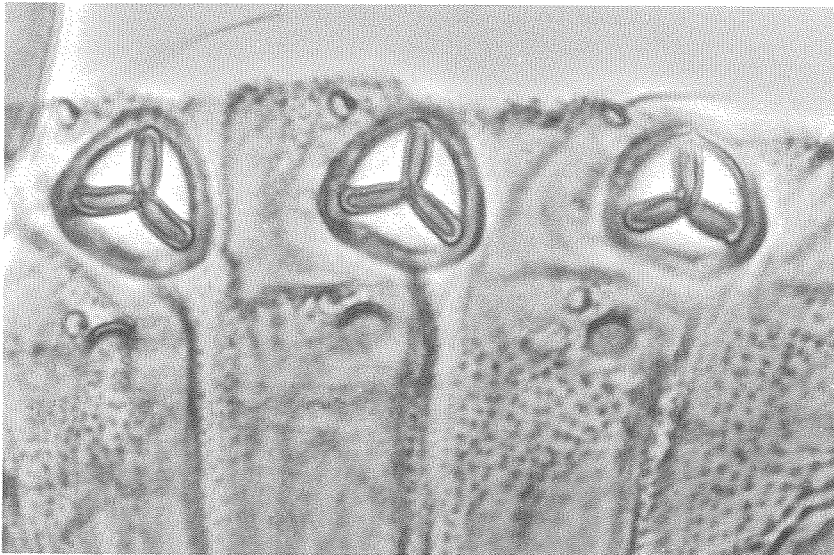


Fig. 13. *C. garciniae*, 1st instar : 3-fissural disc pores [90ML-186].

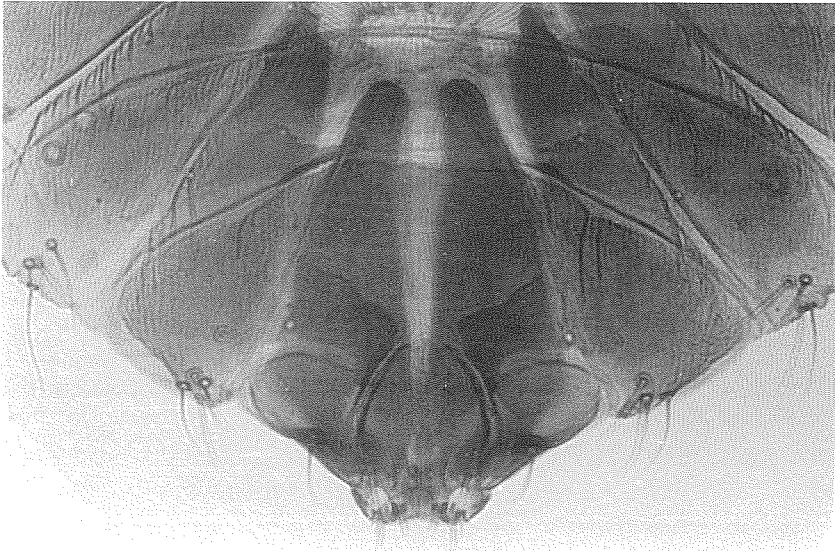


Fig. 14. *C. angraeci*, adult female : pygidium in dorsal view.

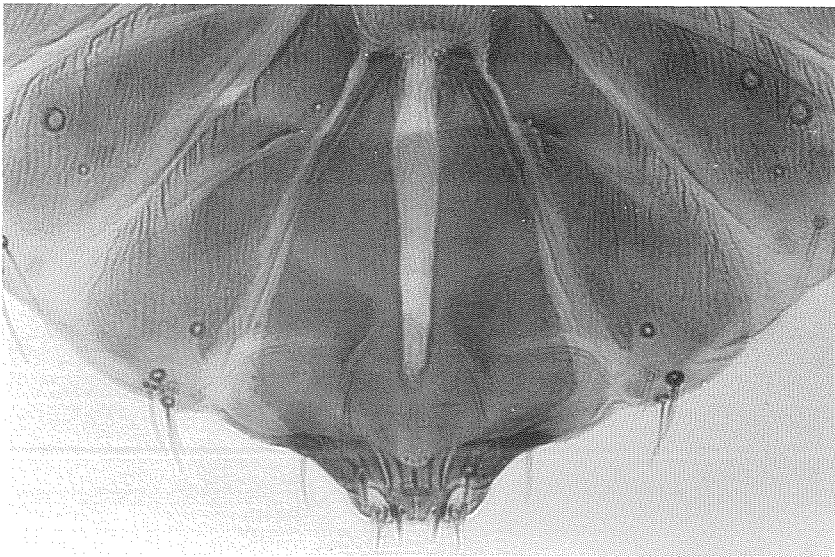


Fig. 15. *C. angraeci*, adult female : pygidium in ventral view.

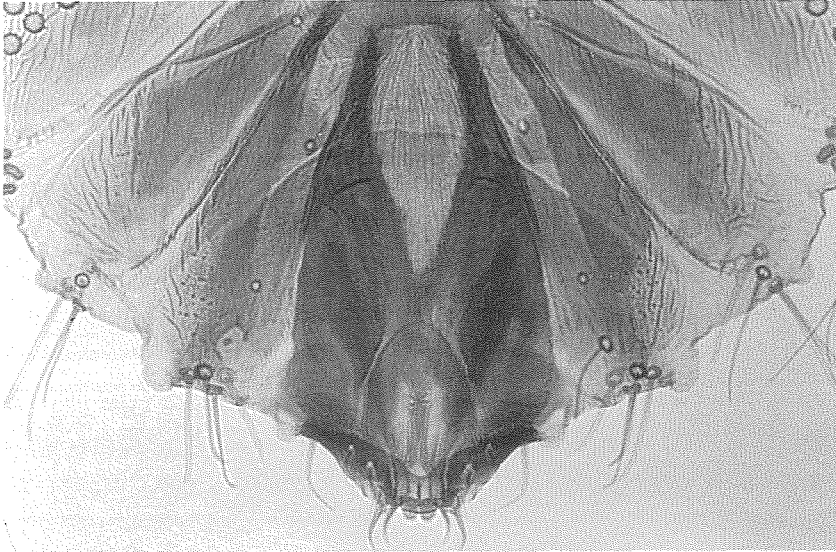


Fig. 16. *C. garciniae*, adult female : pygidium in dorsal view [90ML-167].



Fig. 17. *C. garciniae*, adult female : pygidium in ventral view [90ML-167].

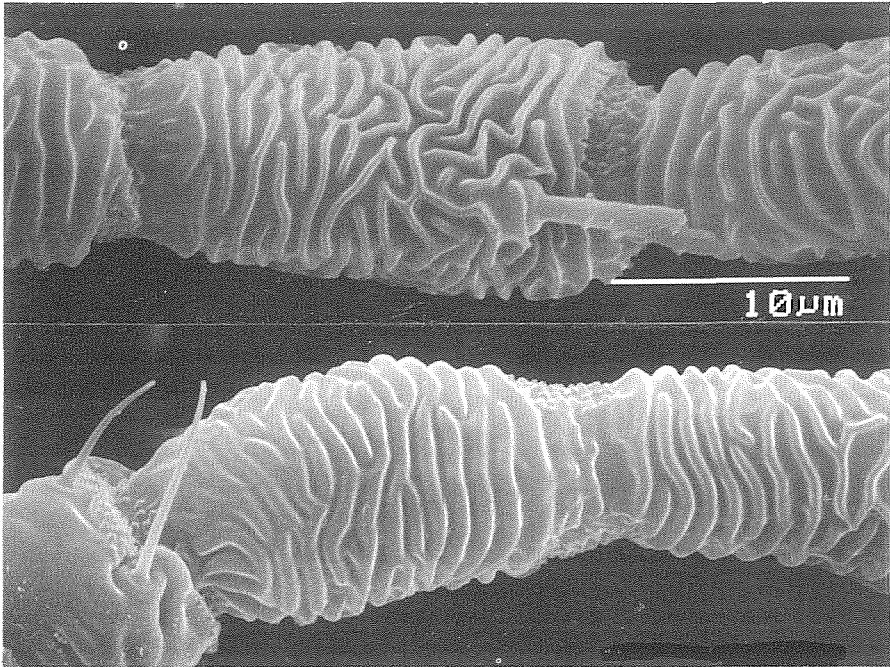


Fig. 18. *C. garciniae*, 1st instar : antennal segments in ventral view [90ML-186].

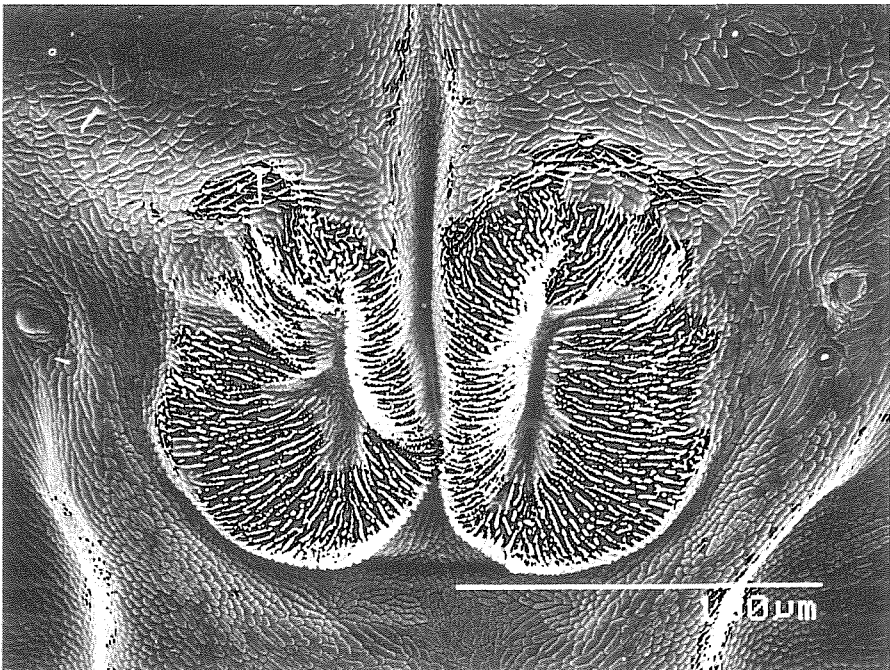


Fig. 19. *C. garciniae*, adult female : dorsal spots of head [90ML-186].

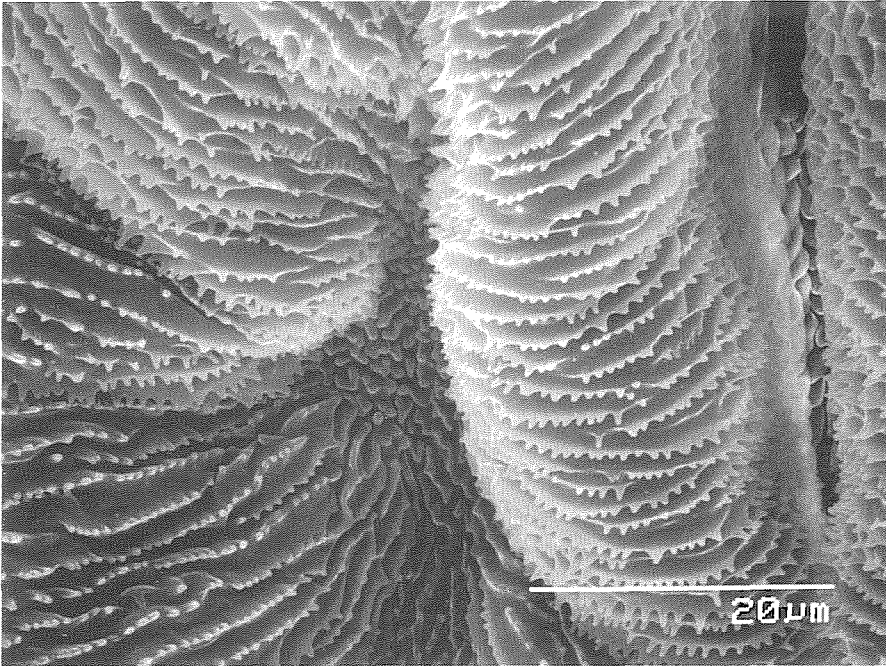


Fig. 20. *C. garciniae*, adult female : part of Fig. 19, showing the left one of the dorsal spots.

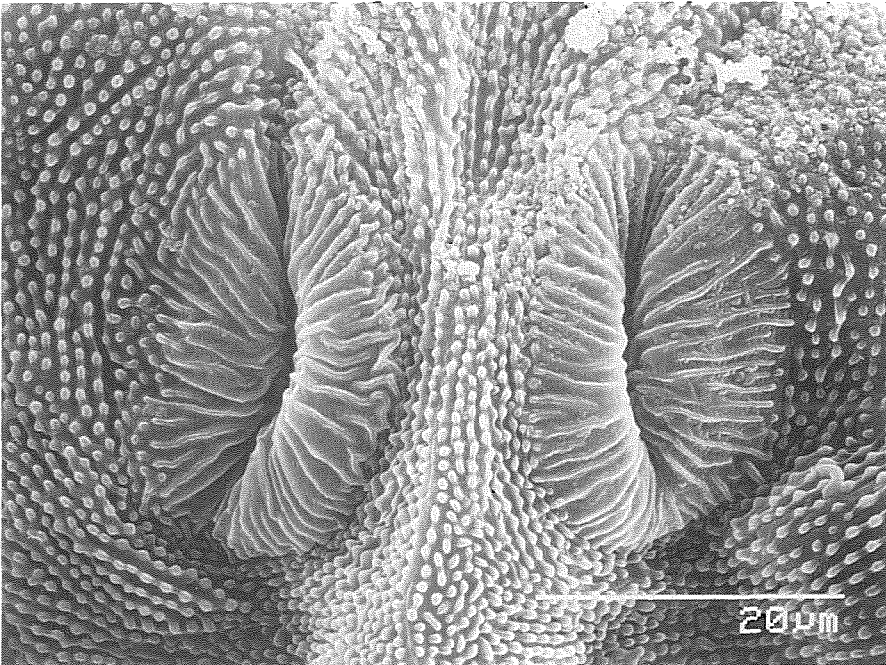


Fig. 21. *C. garciniae*, 1st instar : dorsal spots of head [90ML-186].

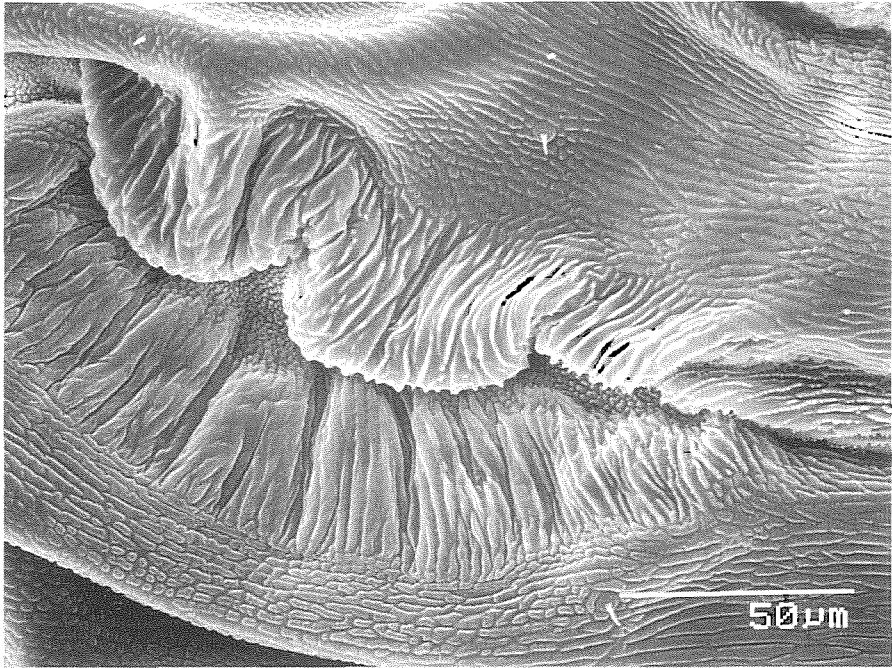


Fig. 22. *C. garciniae*, adult female : dorsal spot between the meso- and metathorax on the left side of the body [90ML-186].

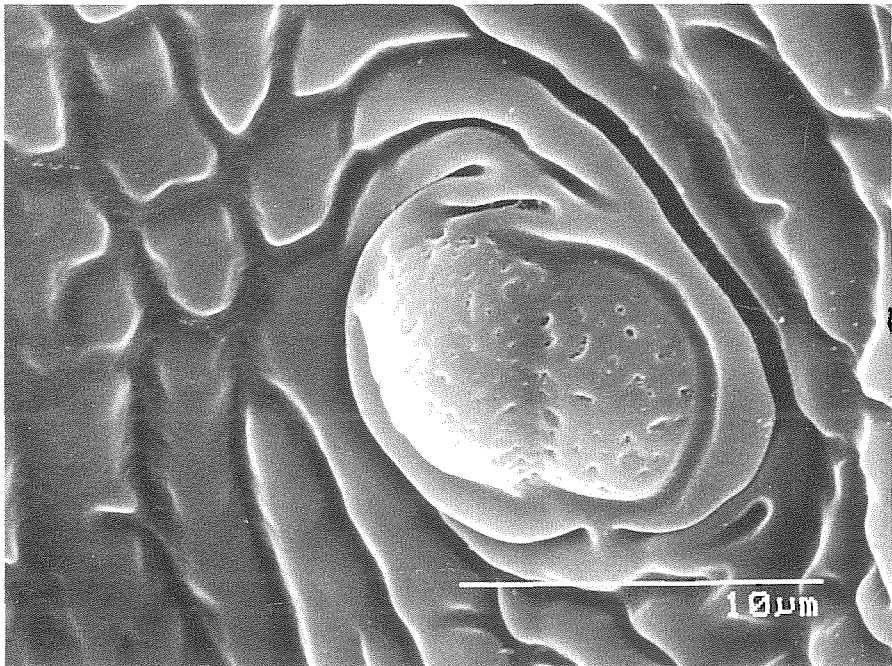


Fig. 23. *C. garciniae*, adult female : cicatrix on the head on the left side of the body [90ML-186].

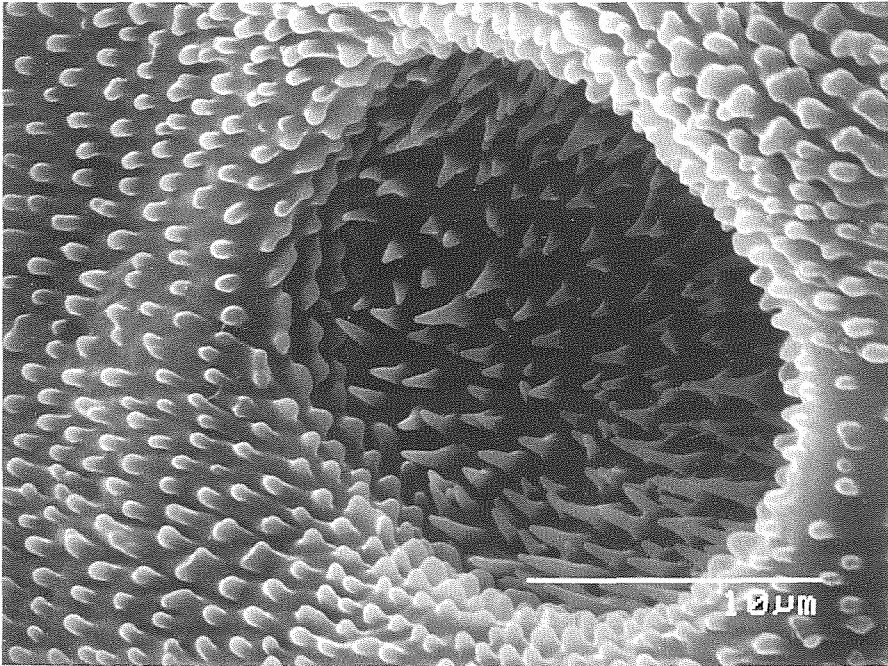


Fig. 24. *C. garciniae*, adult female: dermal invagination near the left mesocoxa [90ML-186].

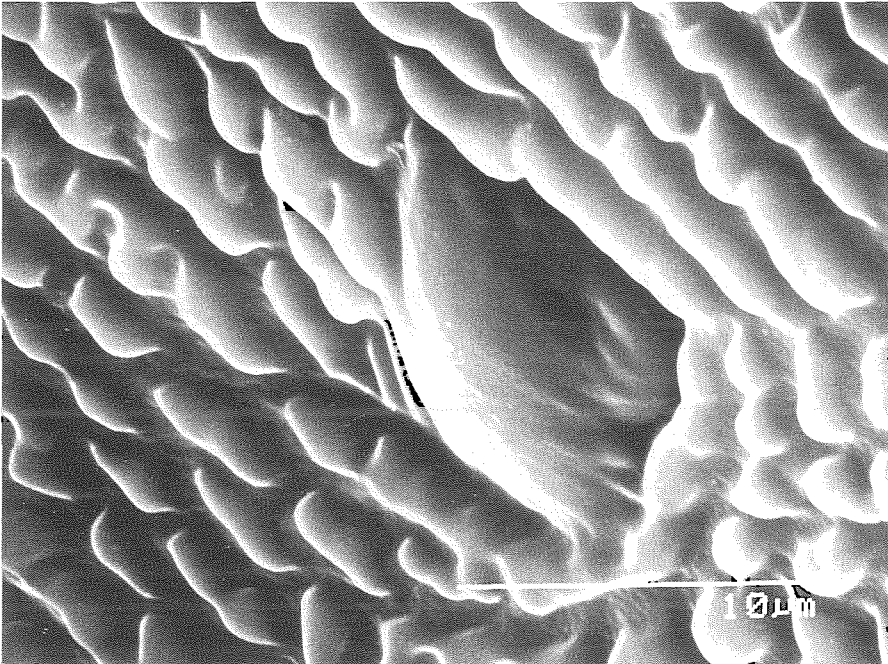


Fig. 25. *C. garciniae*, adult female: submarginal dorsal boss [90ML-186].

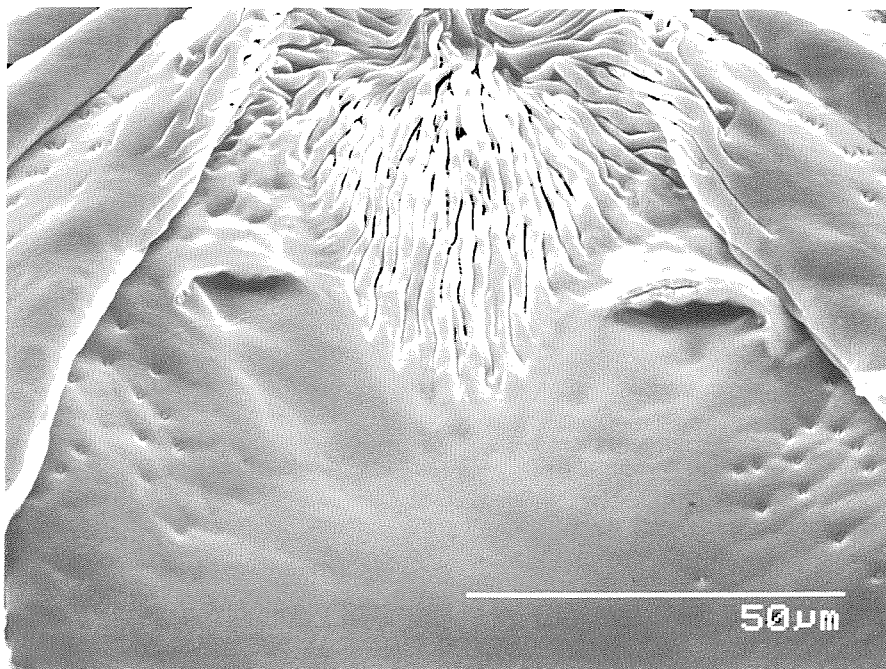


Fig. 26. *C. garciniae*, adult female : dermal slits [90ML-186].

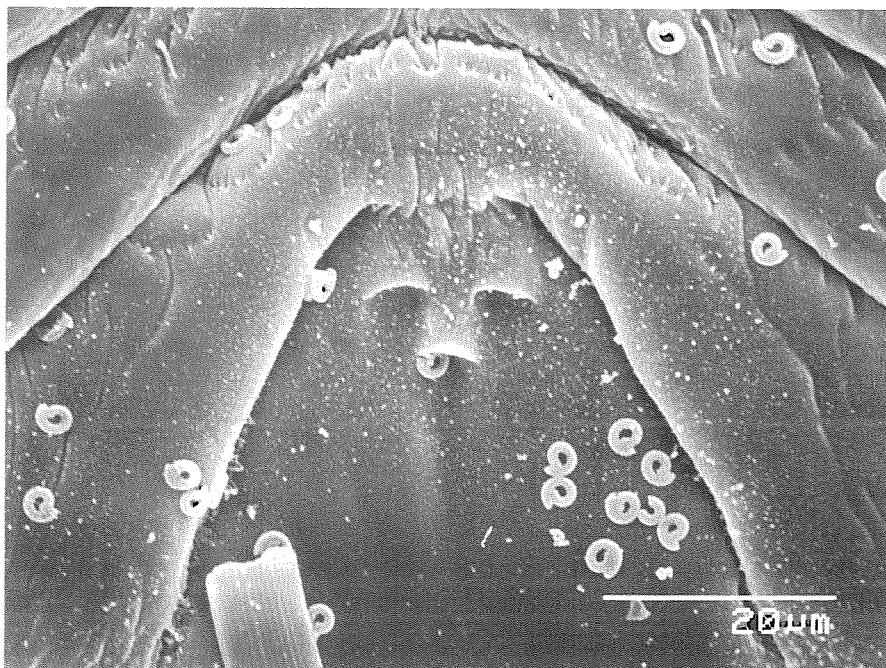


Fig. 27. *C. garciniae*, 1st instar : dermal slits [90ML-186]. (A wax ring is getting into the median slit, thus indicating that the slit is invaginated.)

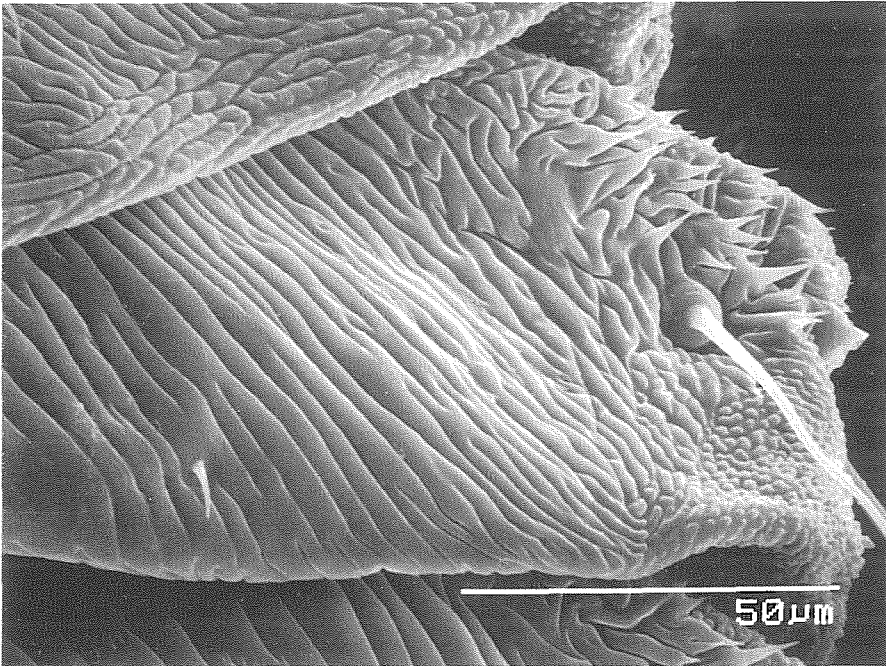


Fig. 28. *C. garciniae*, adult female: dorsal surface of the 5th abdominal segment with crenulae marginally [90ML-186].

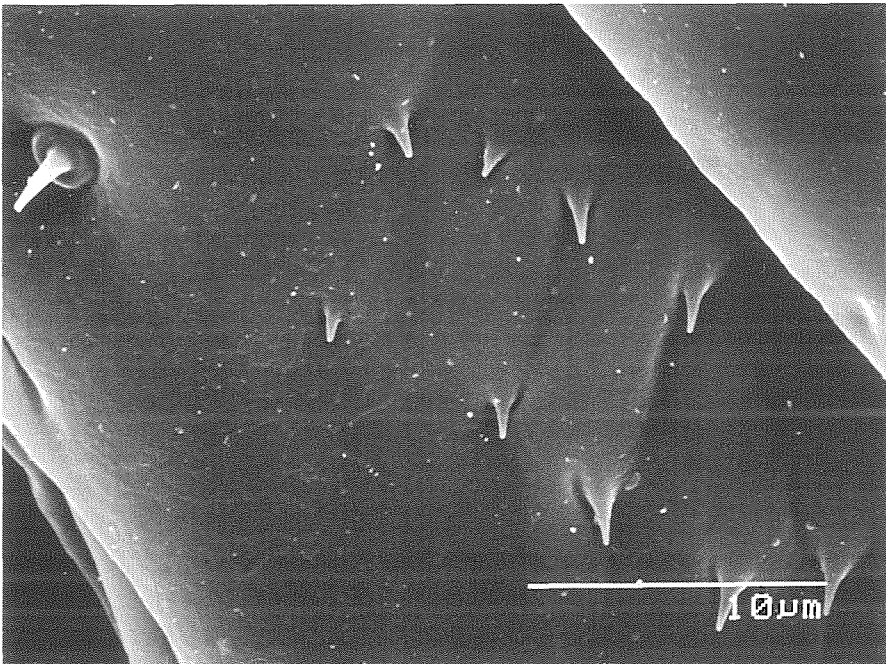


Fig. 29. *C. angraeci*, adult female: minute spines on the ventral surface of the 6th abdominal segment.

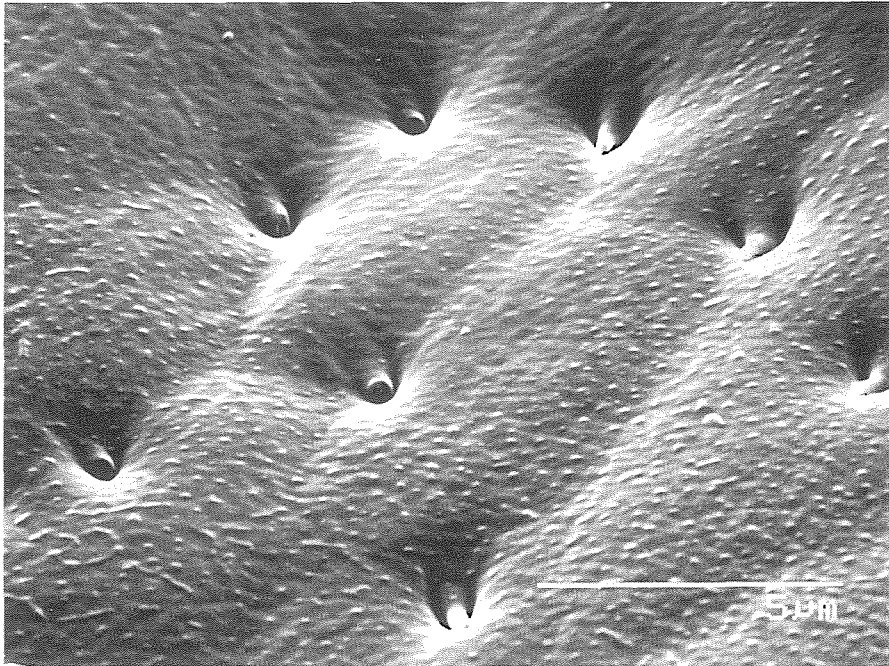


Fig. 30. *C. garciniae*, adult female: minute spines on the ventral surface of the 7th abdominal segment [90ML-186].

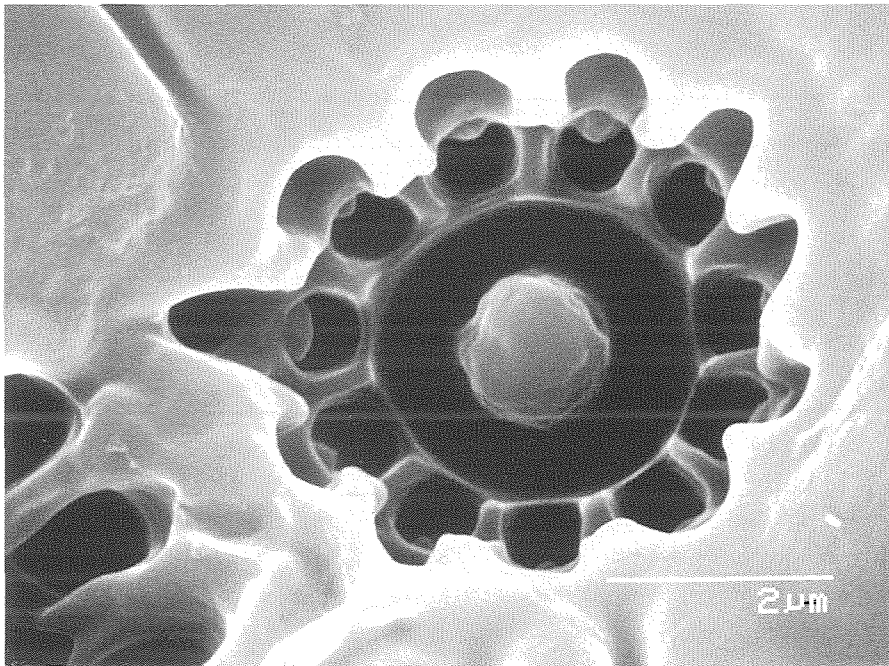


Fig. 31. *C. angraeci*: multilocular disc pore.

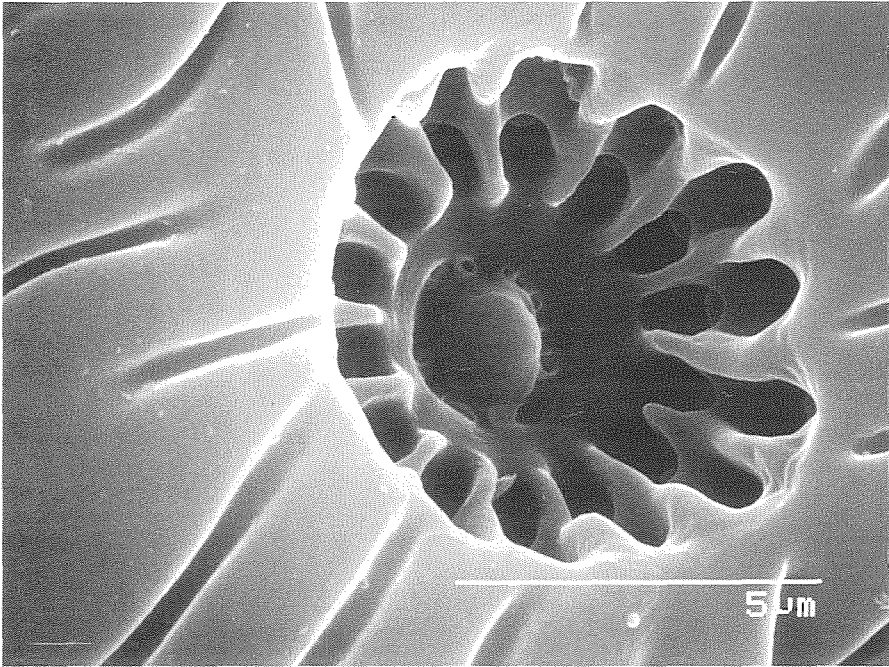


Fig. 32. *C. garciniae*: multilocular disc pore [90ML-186].

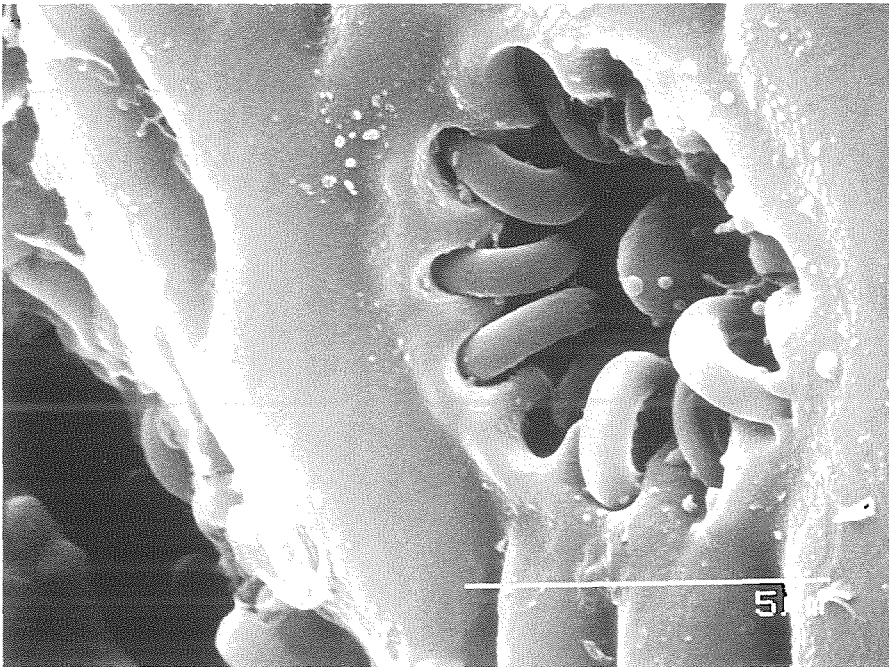


Fig. 33. *C. angraeci*: multilocular disc pore with growing wax rings.

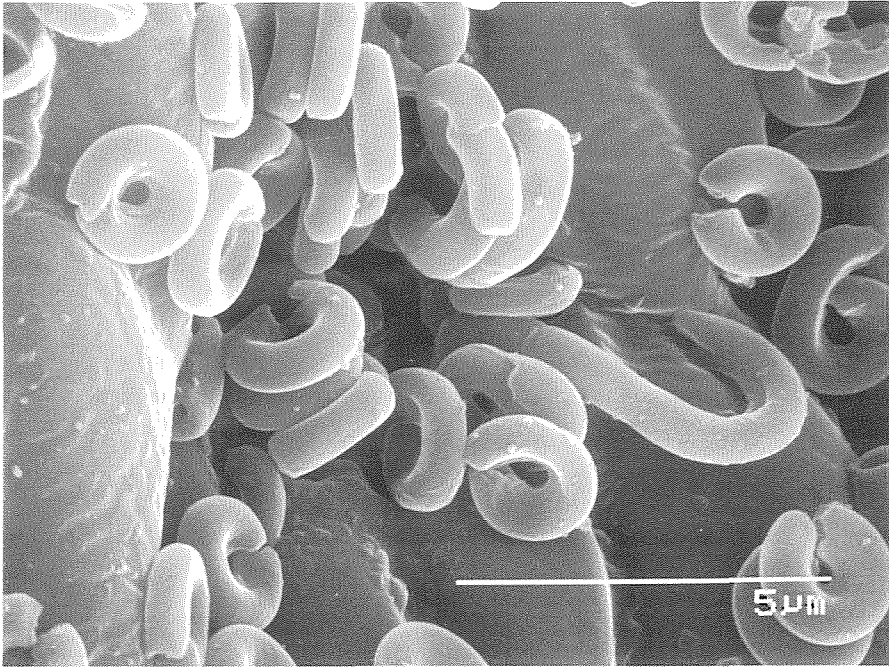


Fig. 34. *C. angraeci*: wax rings coming out of a multilocular disc pore.

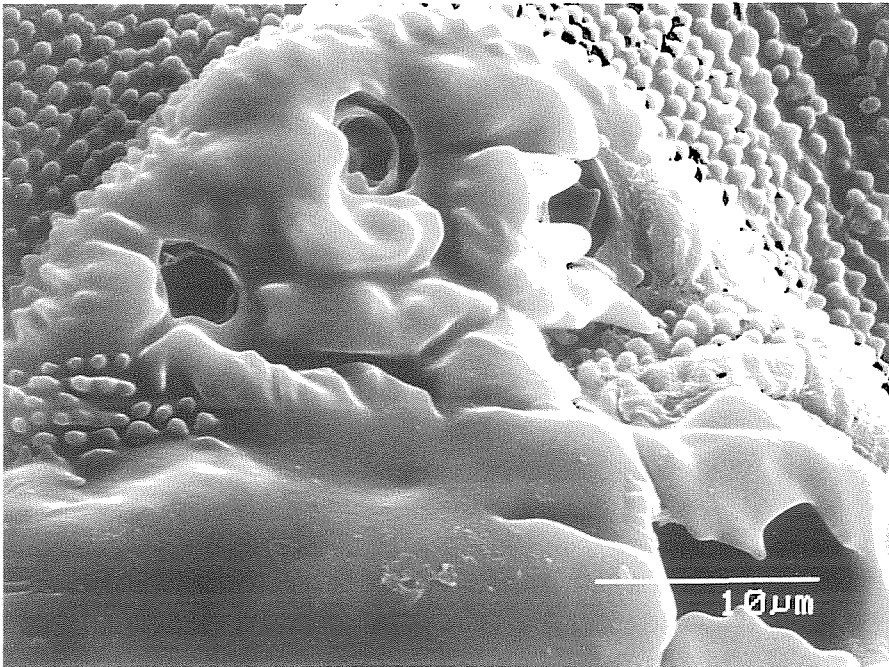


Fig. 35. *C. garciniae*, adult female: spiracular disc pores [90ML-186].

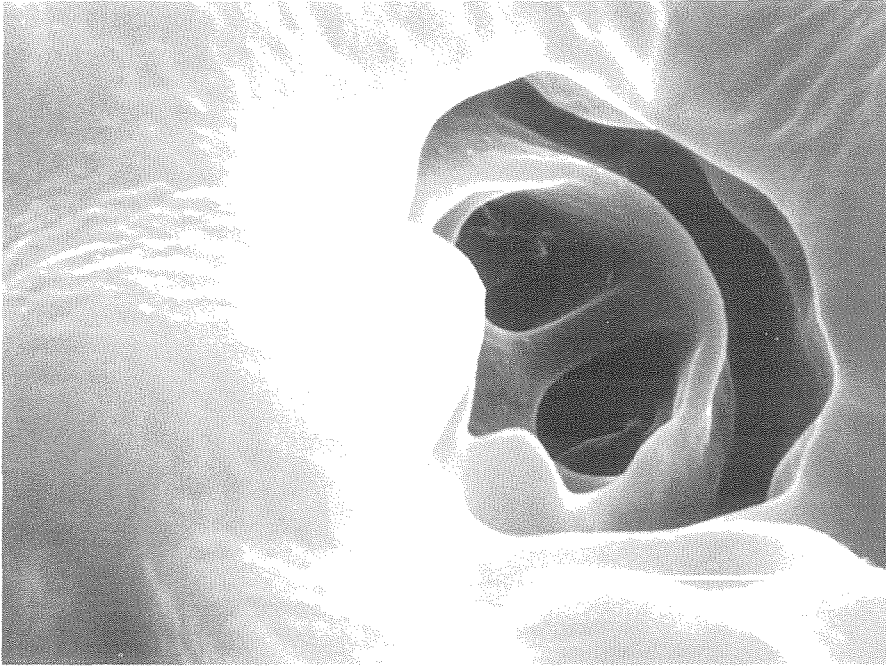


Fig. 36. *C. garciniae*, adult female: spiracular disc pore [90ML-186].

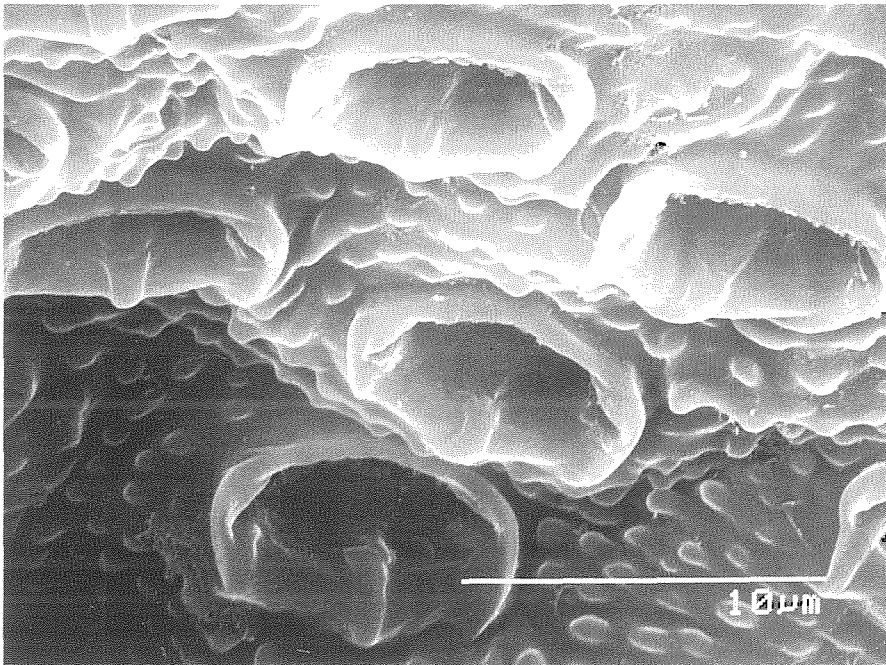


Fig. 37. *C. garciniae*, adult female: orifices of tubular ducts [90ML-186].

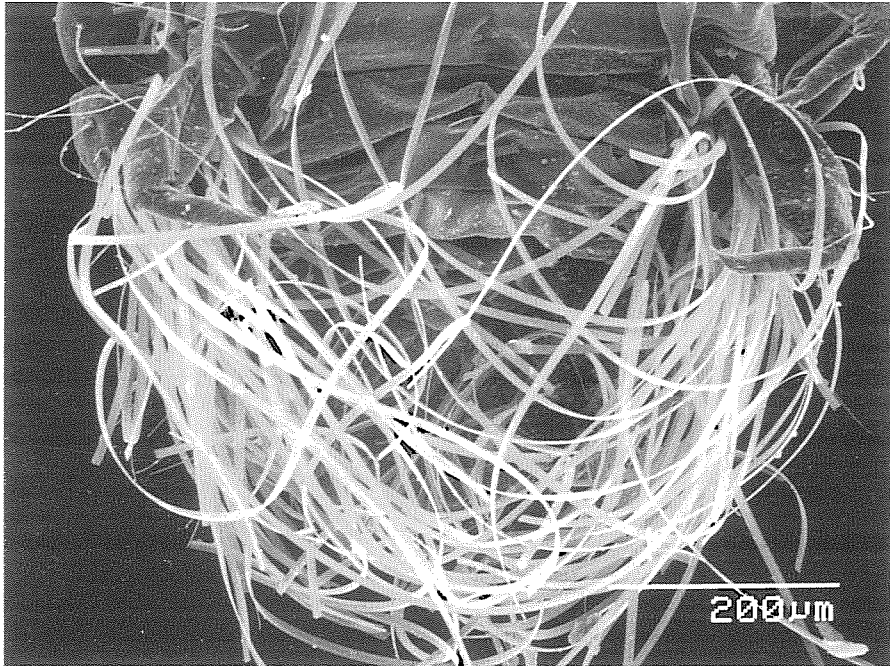


Fig. 38. *C. garciniae*, adult female : ventral side of abdomen with wax filaments [90ML-186].

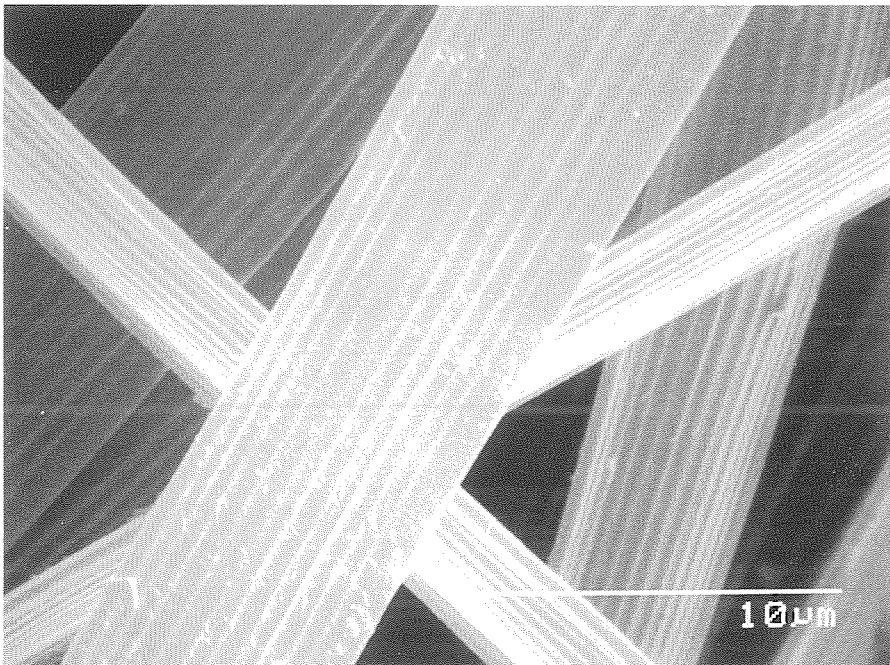


Fig. 39. *C. garciniae*, adult female : wax filaments.

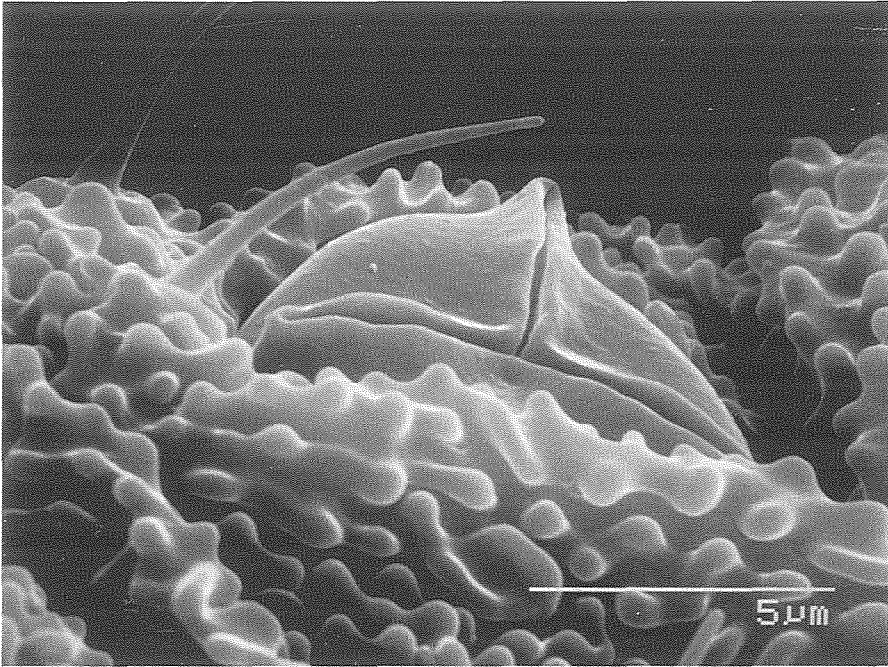


Fig. 40. *C. garciniae* : 3-fissural disc pore [90ML-186].

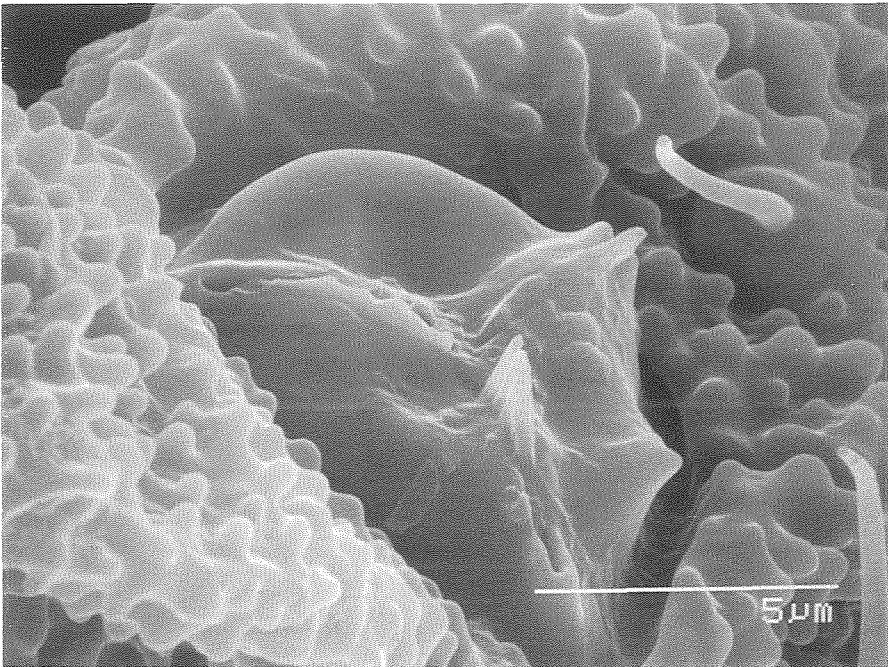


Fig. 41. *C. garciniae* : 3-fissural disc pore [90ML-186].

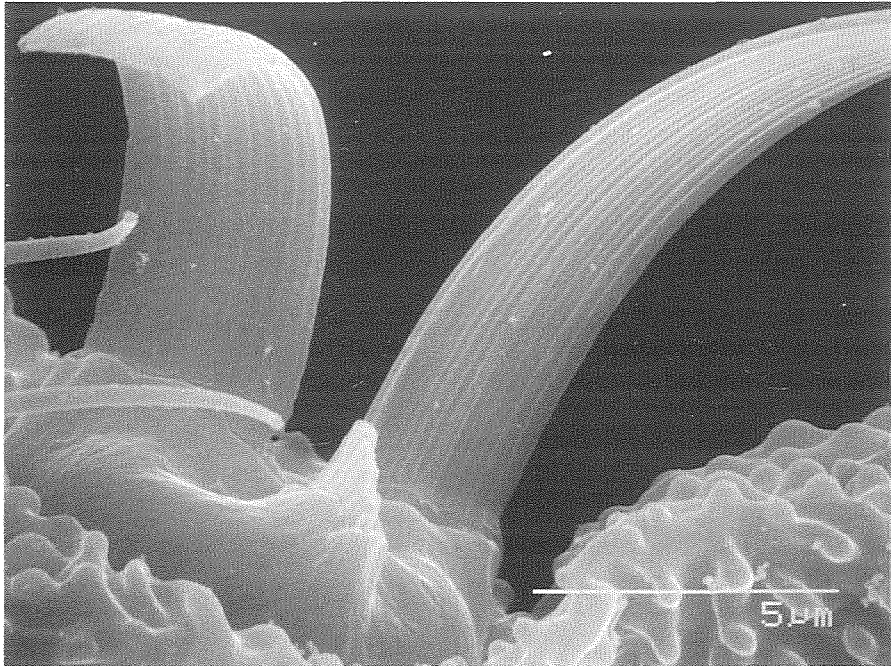


Fig. 42. *C. garciniae*: 3-fissural disc pore secreting wax filaments [90ML-186].

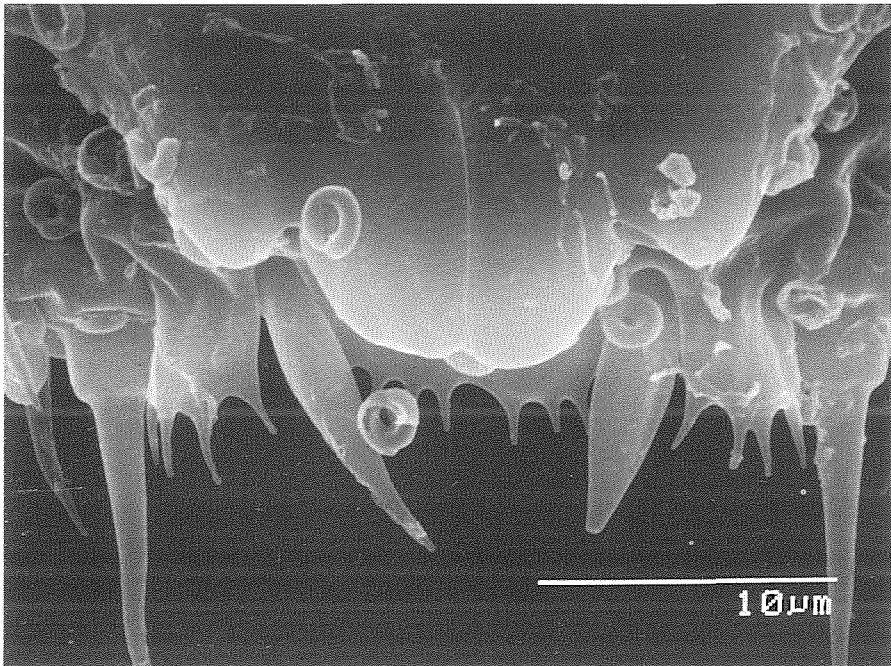


Fig. 43. *C. angraeci*, adult female: apex of abdomen in ventral view, showing pectinae.

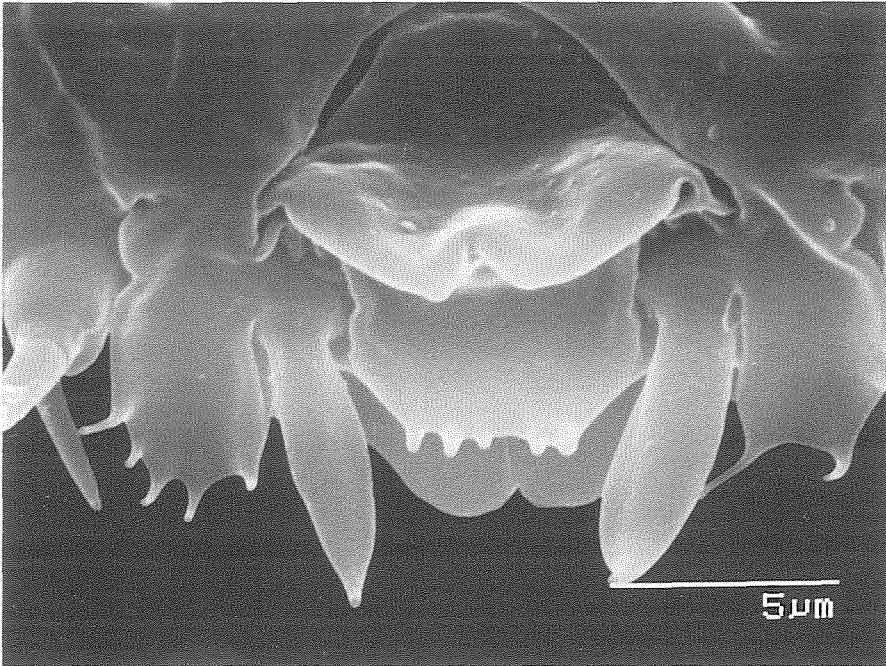


Fig. 44. *C. angraeci*, intermediate stage: apex of abdomen in dorsal view, showing pectinae.

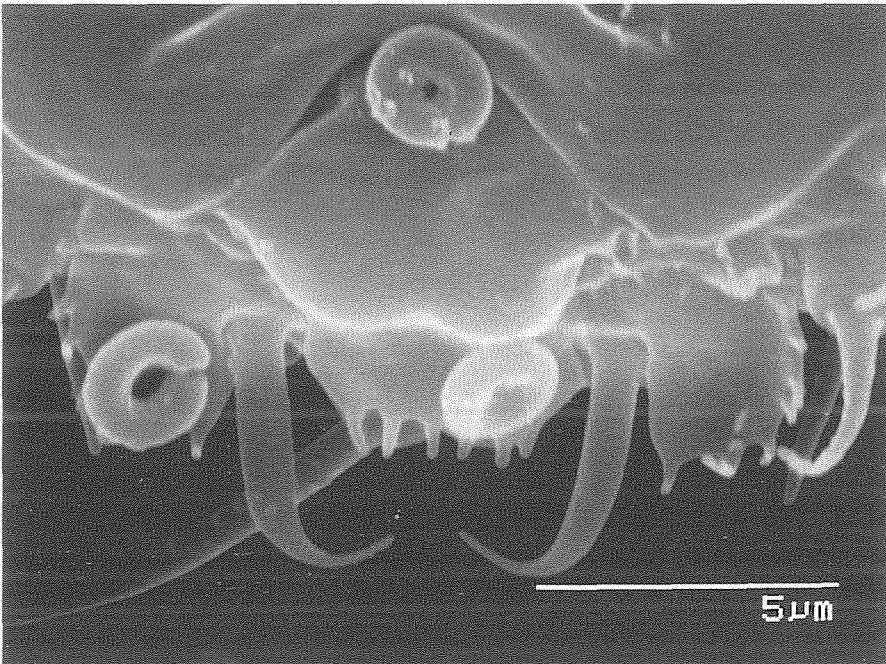


Fig. 45. *C. angraeci*, 1st instar: apex of abdomen in dorsal view, showing pectinae.

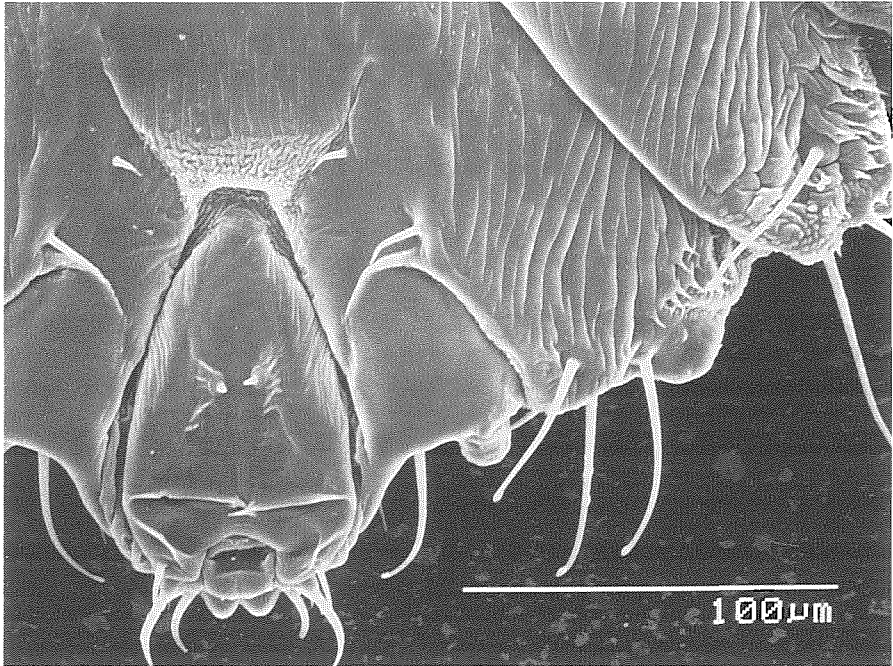


Fig. 46. *C. garciniae*, adult female: pygidium in dorsal view [90ML-186].

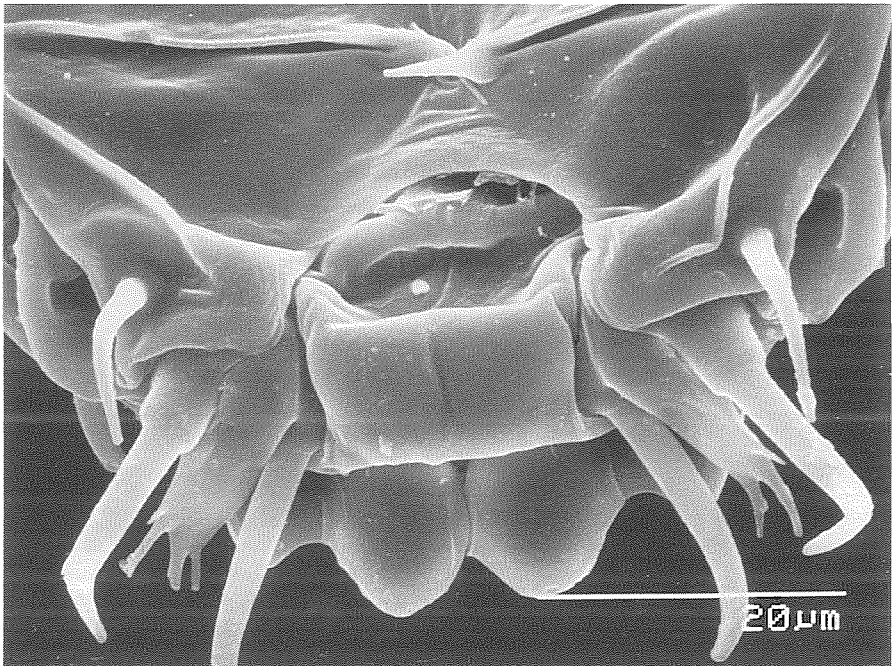


Fig. 47. *C. garciniae*, adult female: apex of abdomen viewed posterodorsally, showing pectinae [90ML-186].

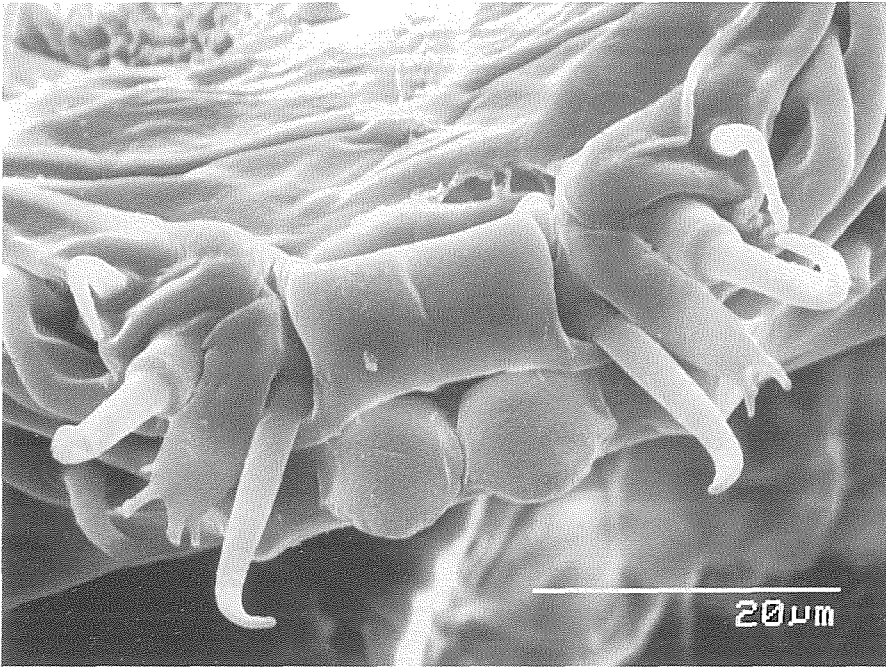


Fig. 48. *C. garciniae*, adult female : same as Fig. 47, viewed more posteriorly.

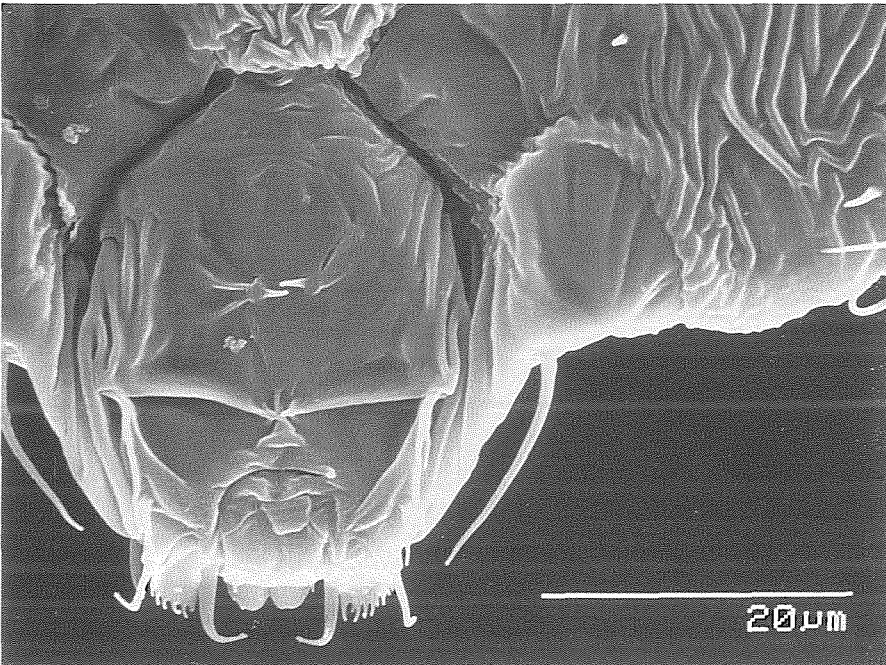


Fig. 49. *C. garciniae*, 1st instar : pygidium in dorsal view [90ML-186].

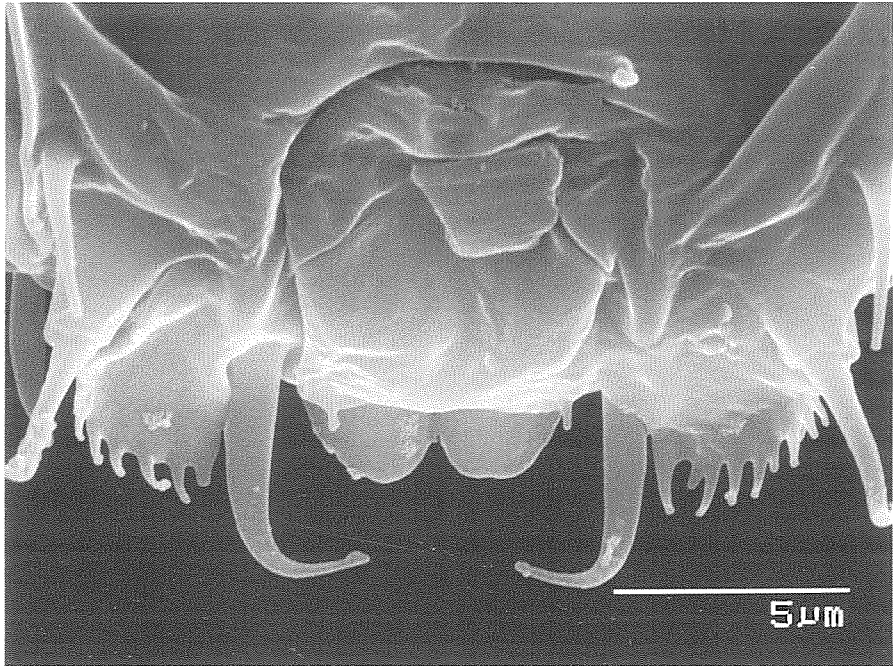


Fig. 50. *C. garciniae*, 1st instar : apex of abdomen in dorsal view, showing pectinae [90ML-186].

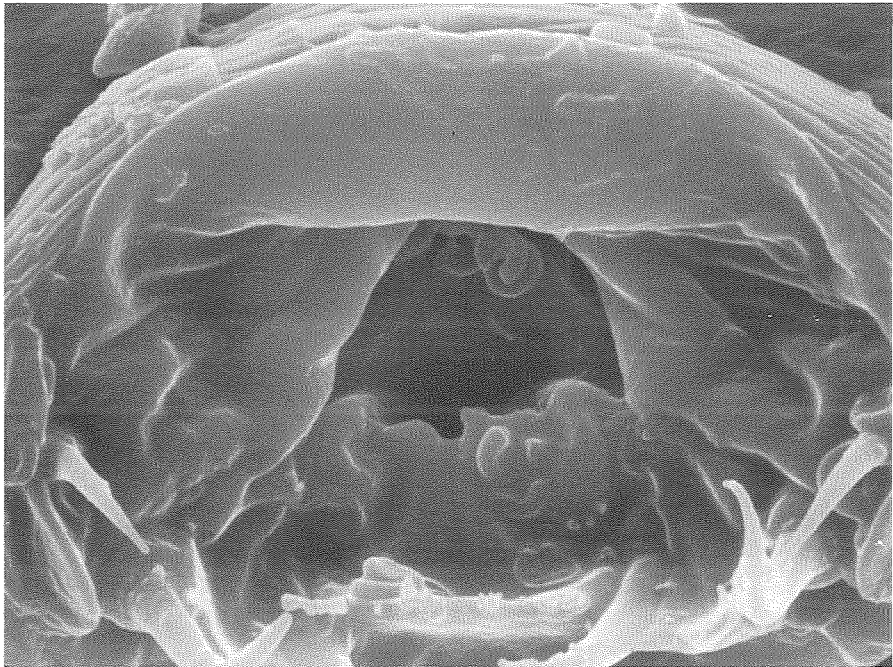


Fig. 51. *C. angraeci*, adult female : anus opened. ×4K.

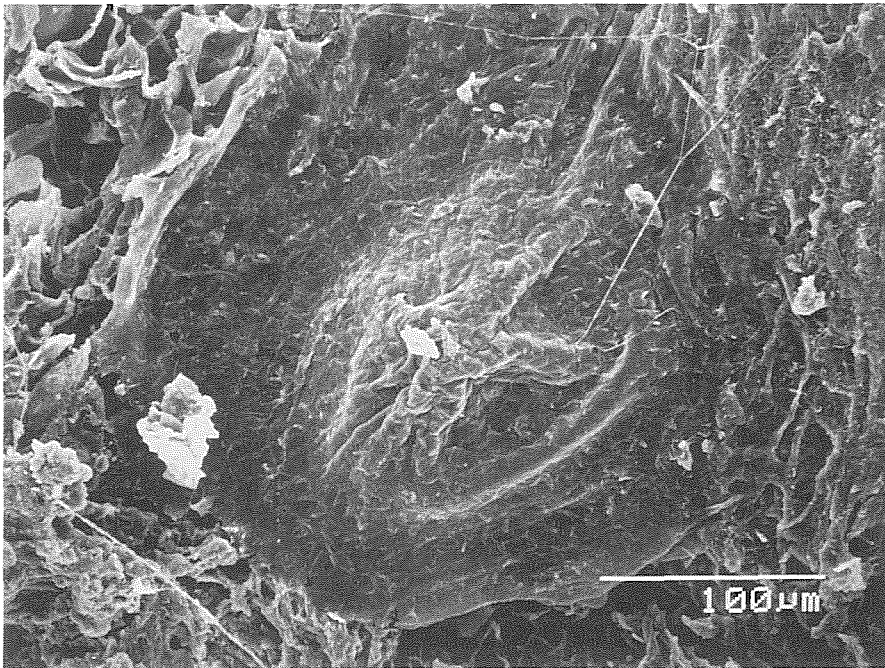


Fig. 52. *C. angraeci*, test in a very early stage. (The insect below the test was later examined and proved to belong to the 1st instar.)

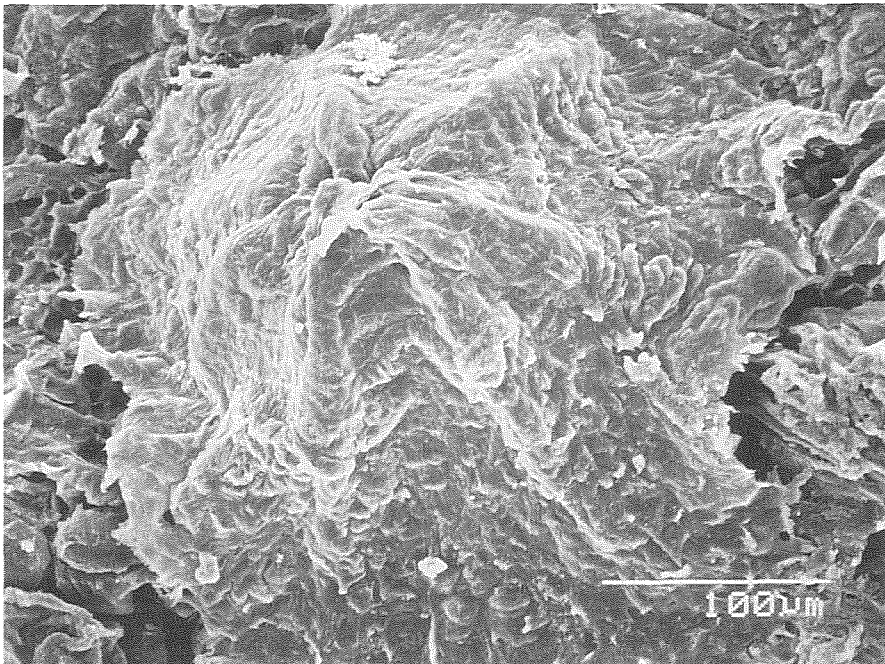


Fig. 53. *C. angraeci*, test under formation by a 1st instar larva (which was later examined for confirming the instar).

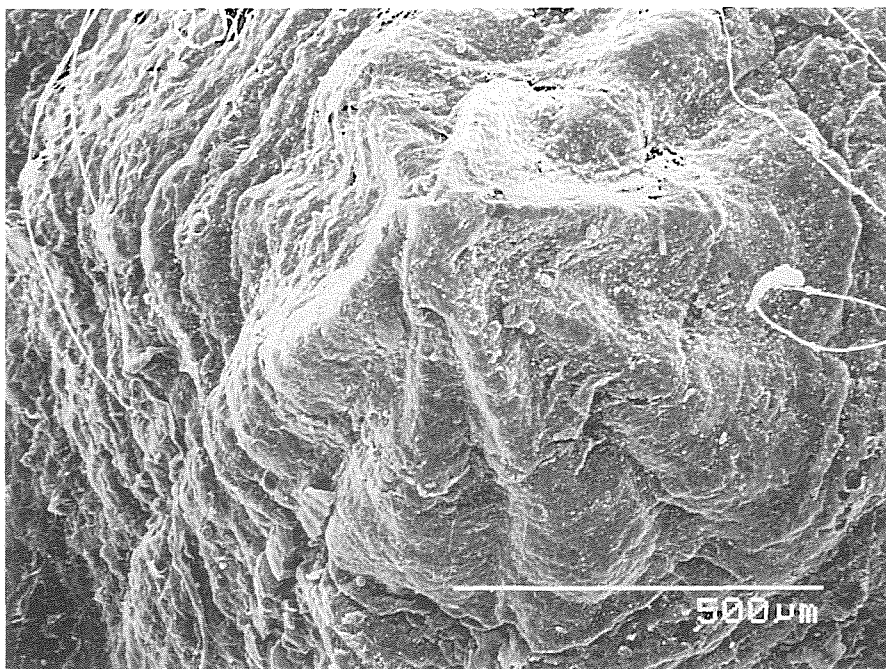


Fig. 54. *C. angraeci*, female test completed.

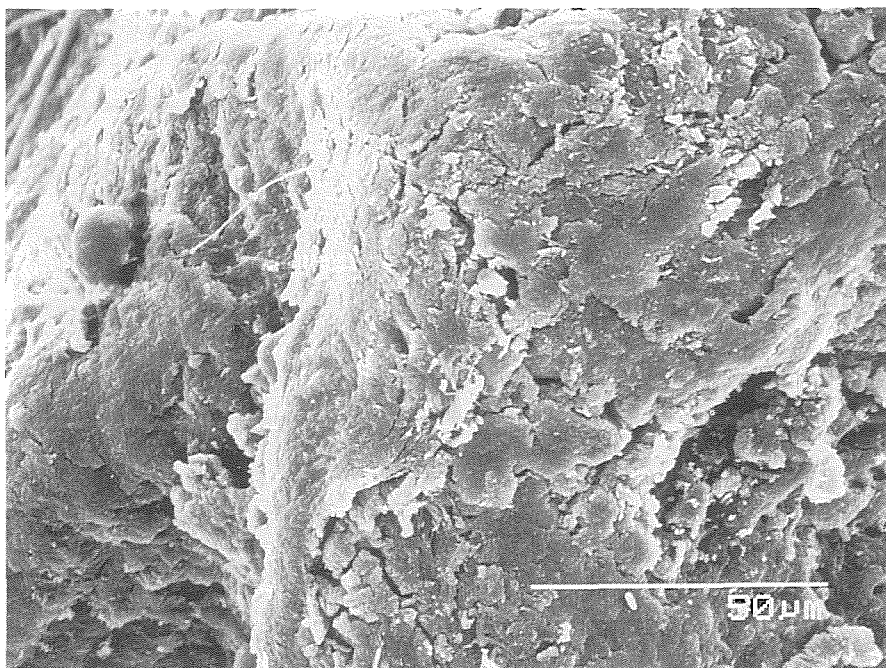


Fig. 55. *C. angraeci*, female test : part of Fig. 54, showing the dorsal surface.

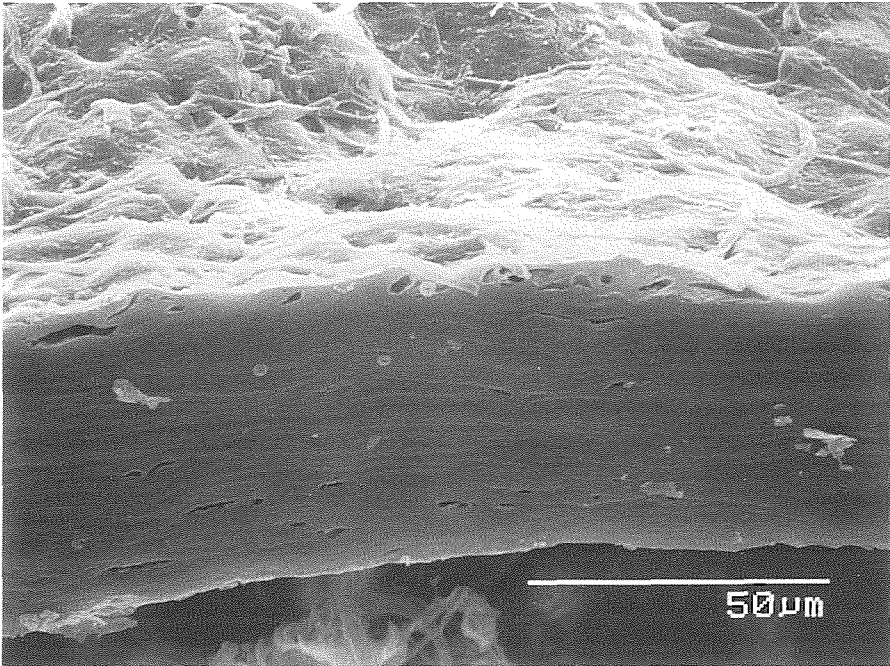


Fig. 56. *C. angraeci*, female test ; a cross section.

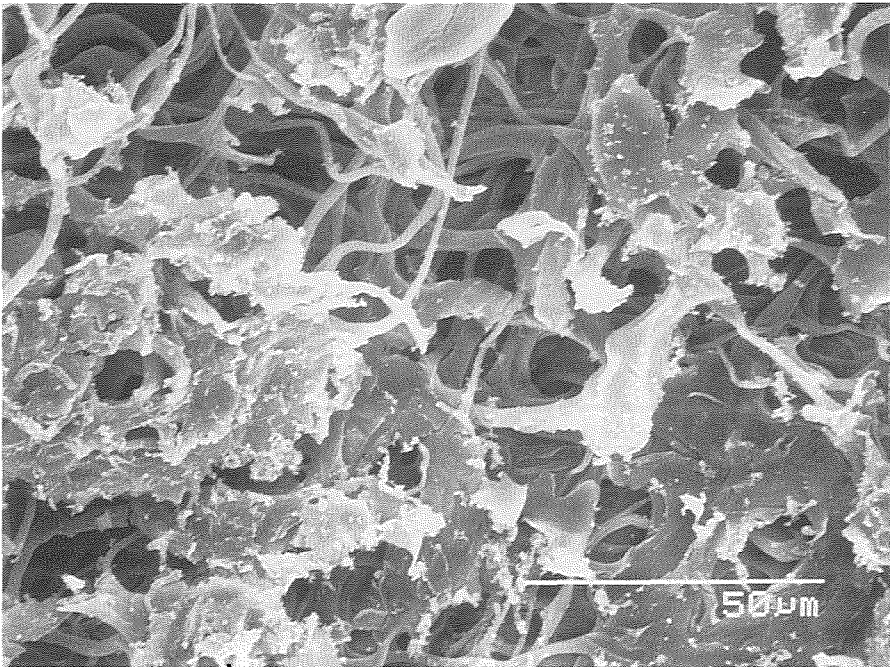


Fig. 57. *C. angraeci*, female test : outer surface of ventral portion.

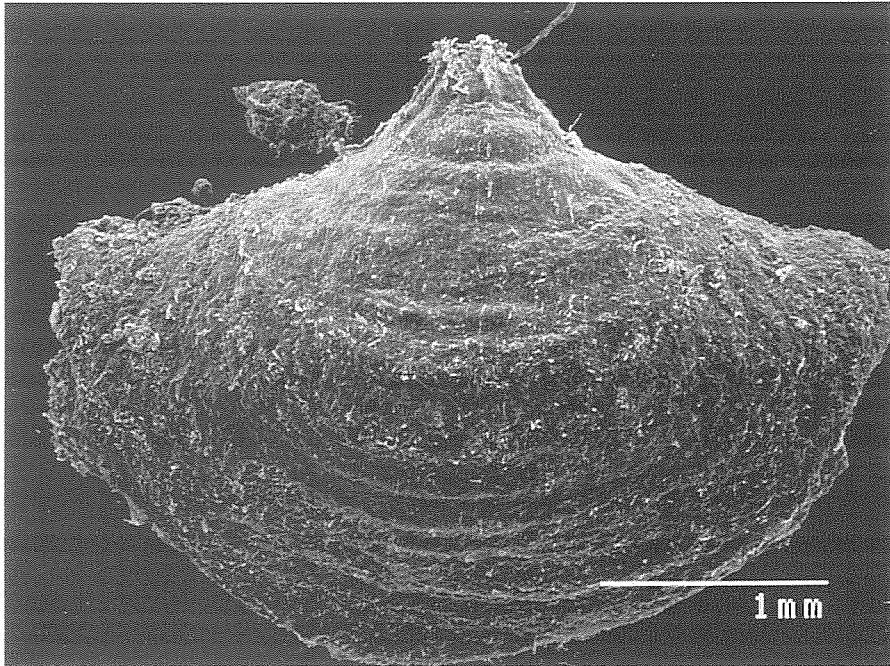


Fig. 58. *C. garciniae*, female test (cypraeiform): lateral view [90ML-186].

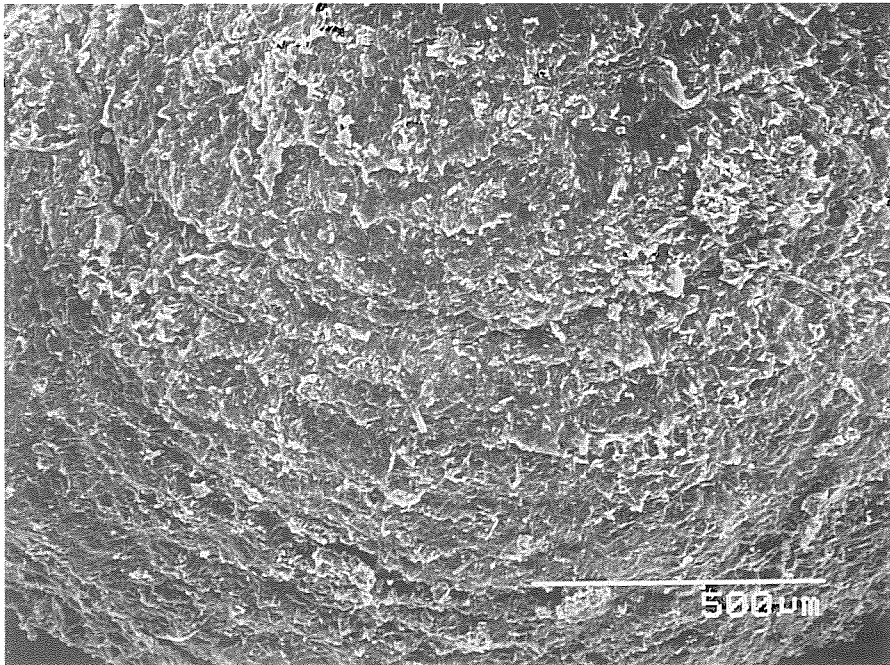


Fig. 59. *C. garciniae*, female test: part of Fig. 58, showing the dorsal surface.

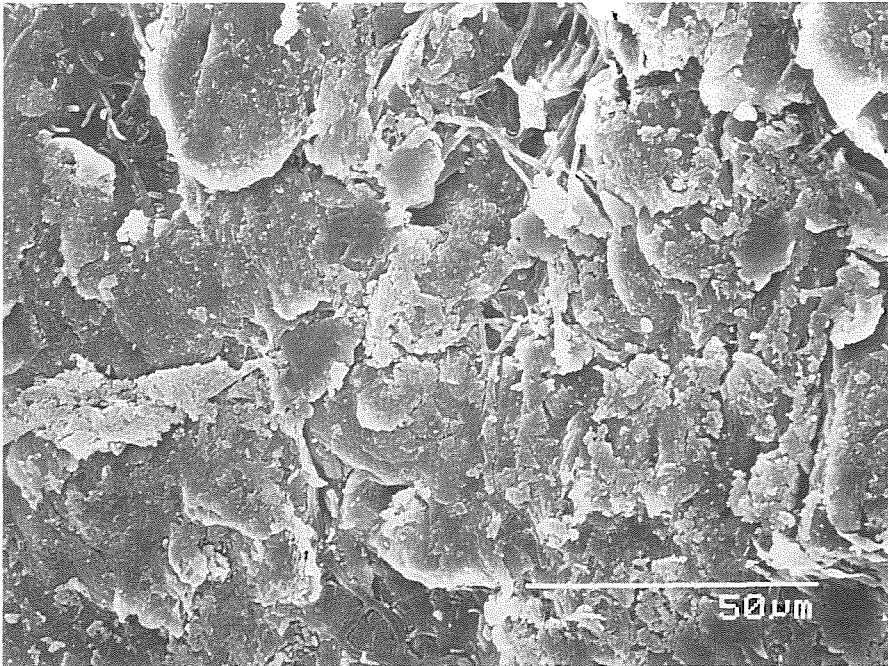


Fig. 60. *C. garciniae*, female test : part of Figs. 58 and 59, further magnified.

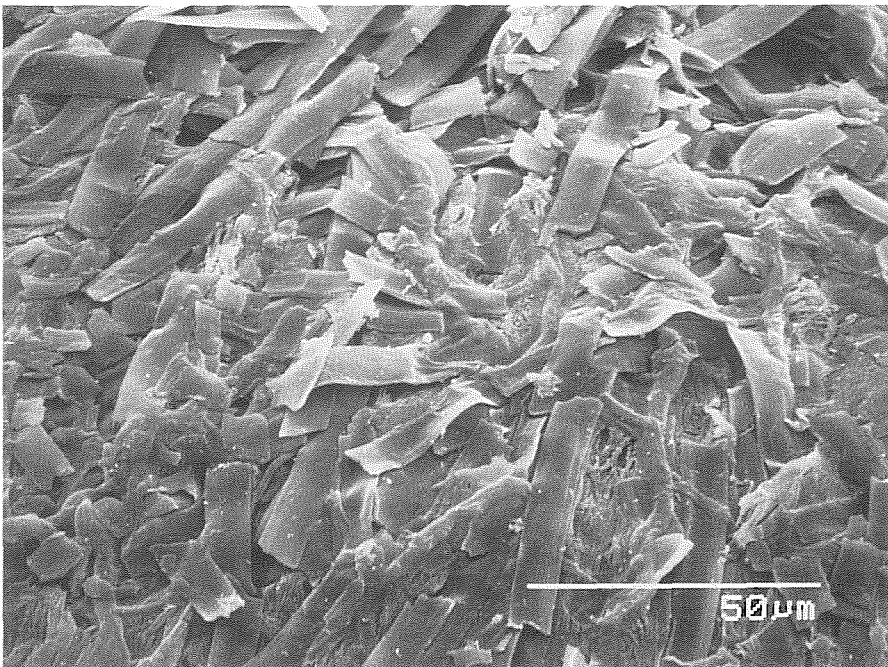


Fig. 61. *C. garciniae*, female test : part of Fig. 58 near the top, showing wax filaments exposed.

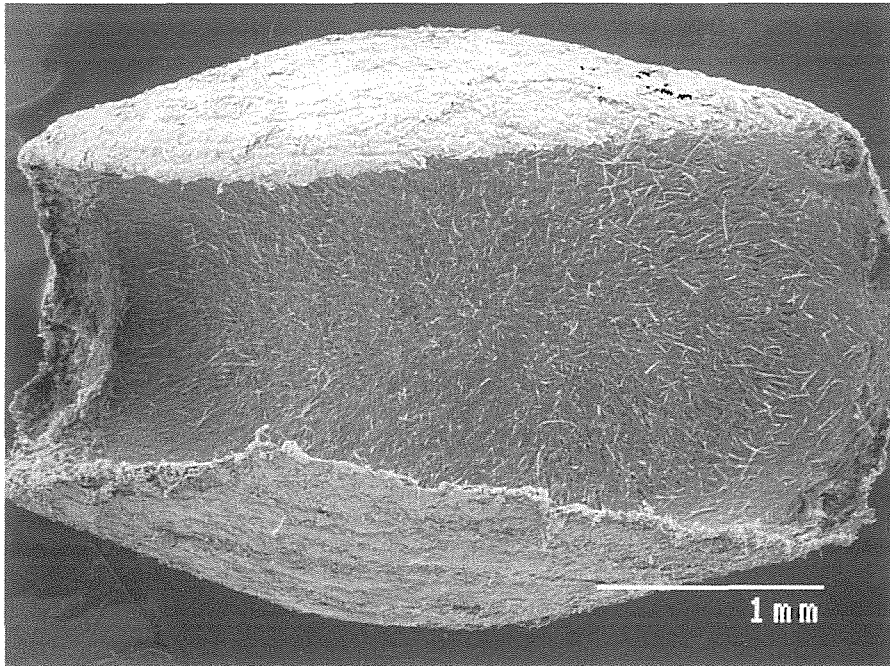


Fig. 62. *C. garciniae*, female test (cypraeiform) : ventral view [90ML-186].

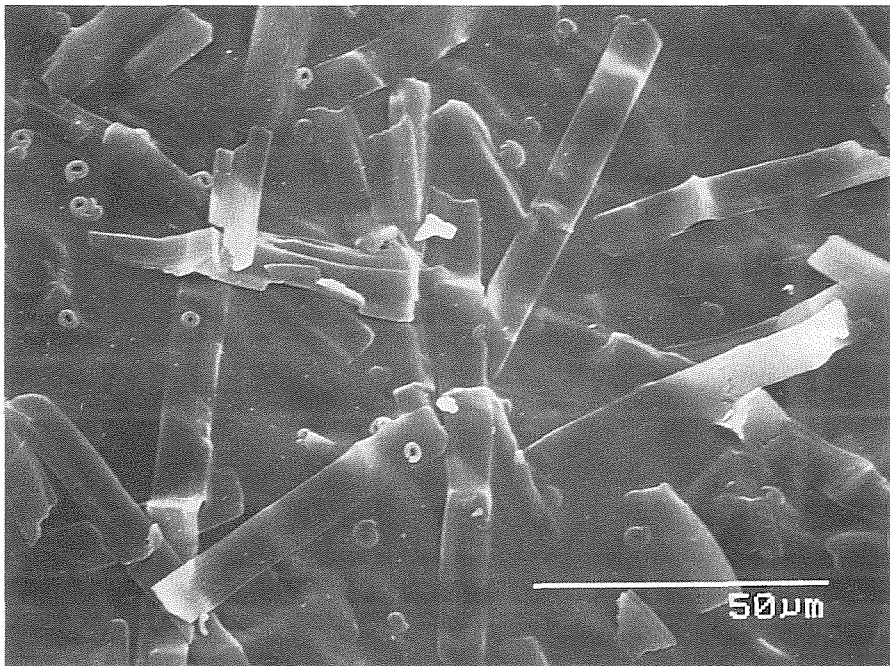


Fig. 63. *C. garciniae*, female test : inner surface about middle of Fig. 62.

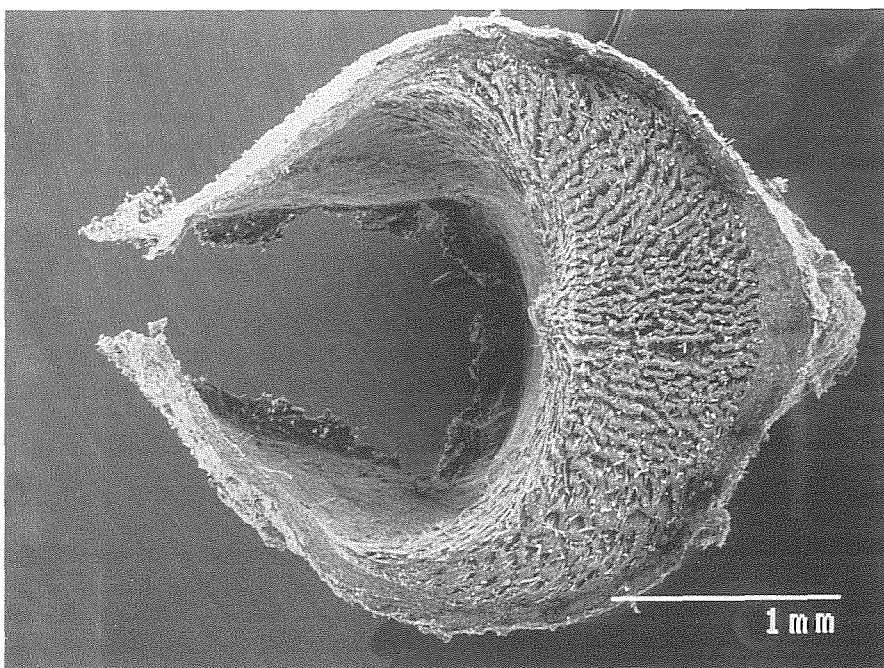


Fig. 64. *C. garciniae*, female test (cypraeiform): a cross section [90ML-186].

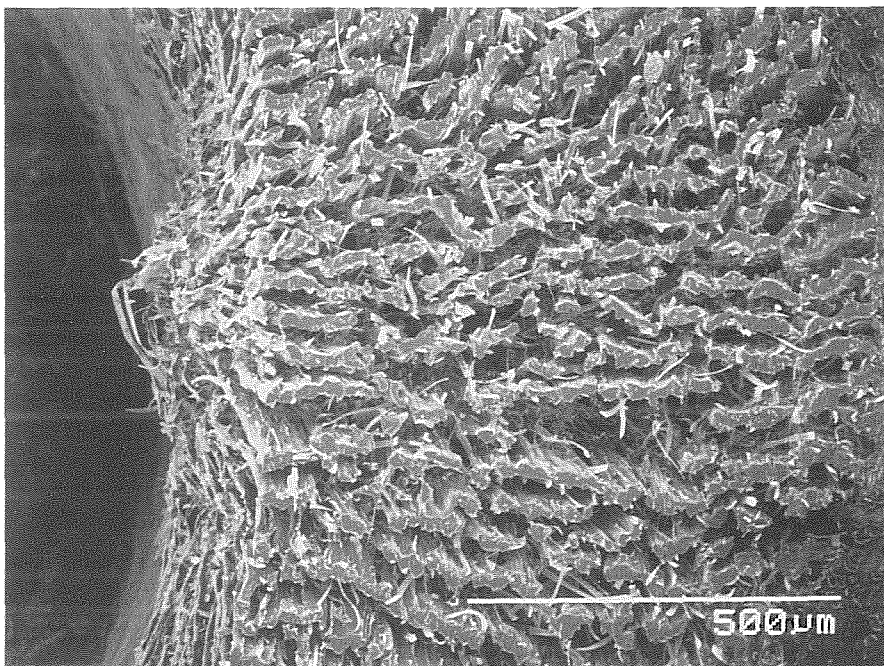


Fig. 65. *C. garciniae*, female test : part of Fig. 64.

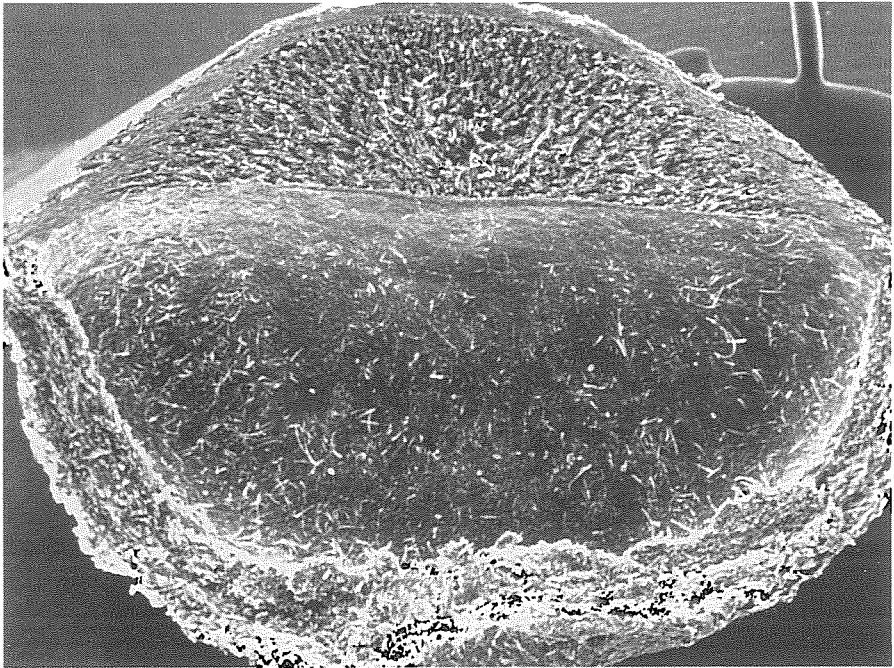


Fig.66. *C. garciniae*, female test (cypraeiform): a longitudinal section [90ML-186].
×30.

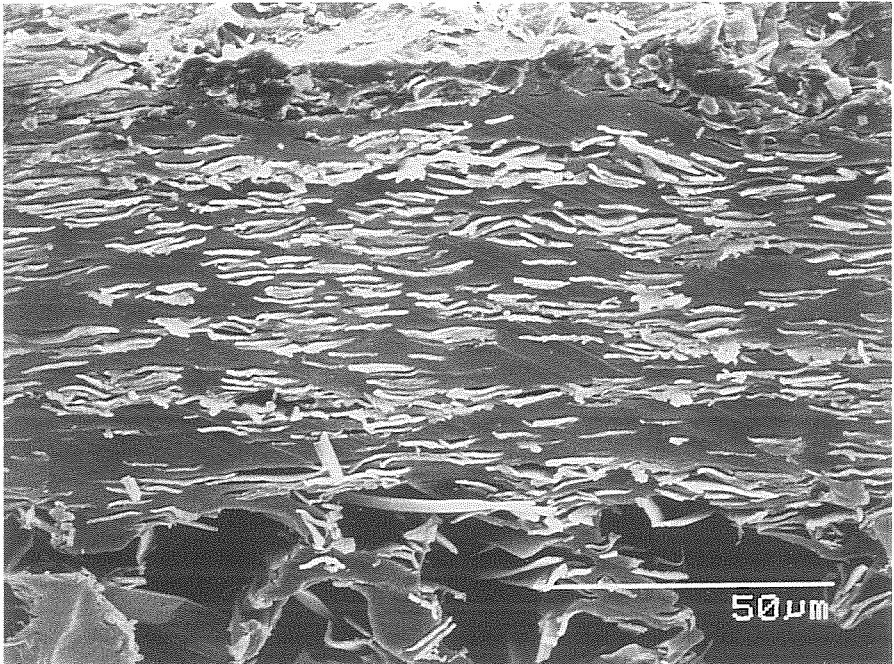


Fig.67. *C. garciniae*, female test: part of Fig.66, showing the outermost zone of the dorsal portion.

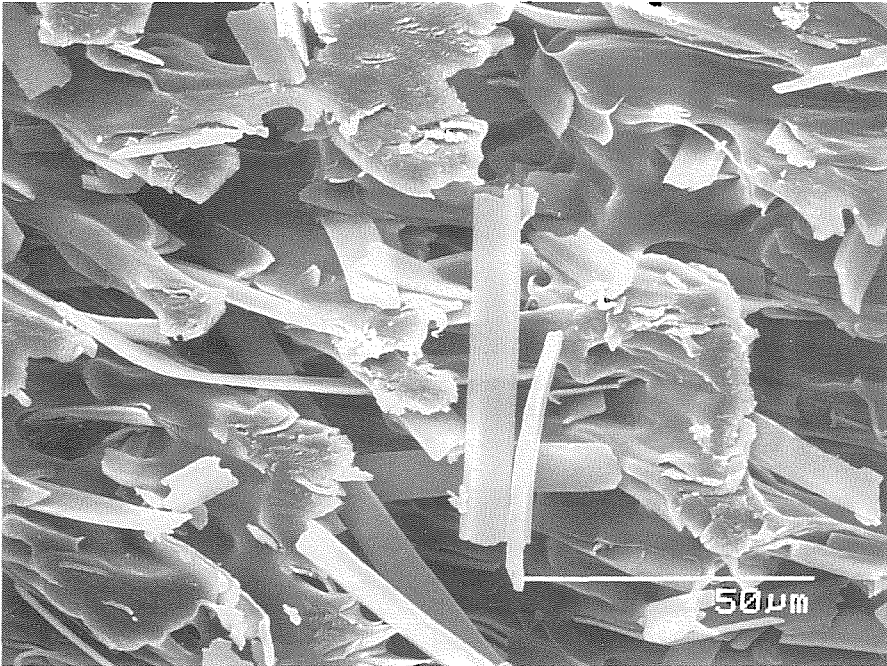


Fig. 68. *C. garciniae*, female test : part of Fig. 66, showing the intermediate zone of the dorsal portion.

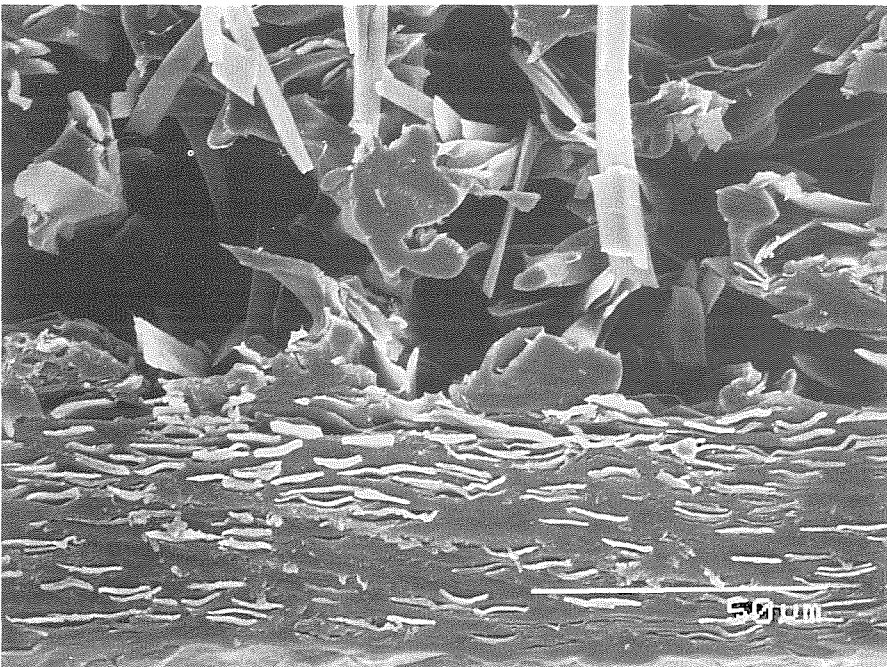


Fig. 69. *C. garciniae*, female test : part of Fig. 66, showing the intermediate zone (upper half) and the innermost zone of the dorsal portion.

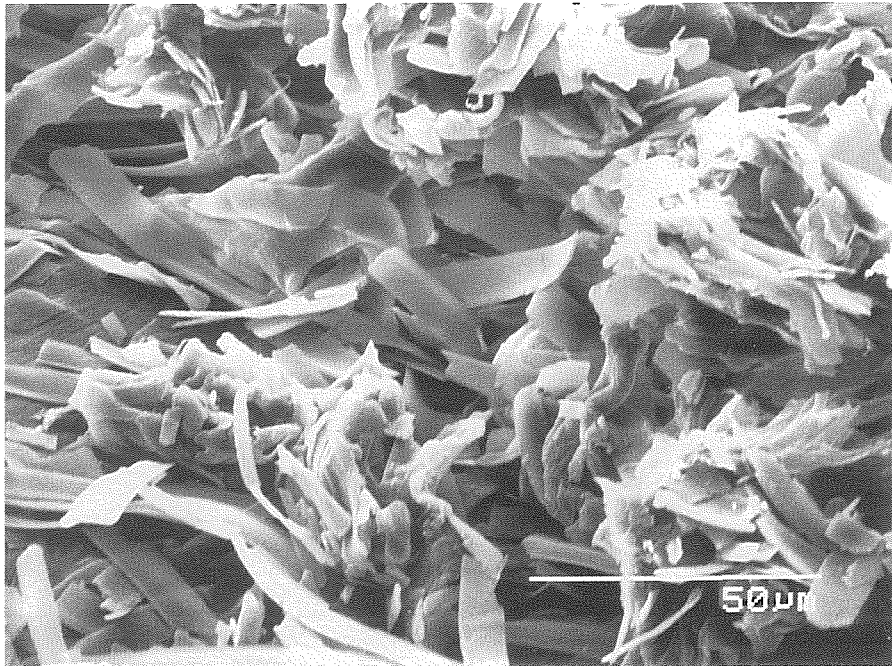


Fig. 70. *C. garciniae*, female test : part of Fig. 66, showing part of the surface in contact with the host plant.

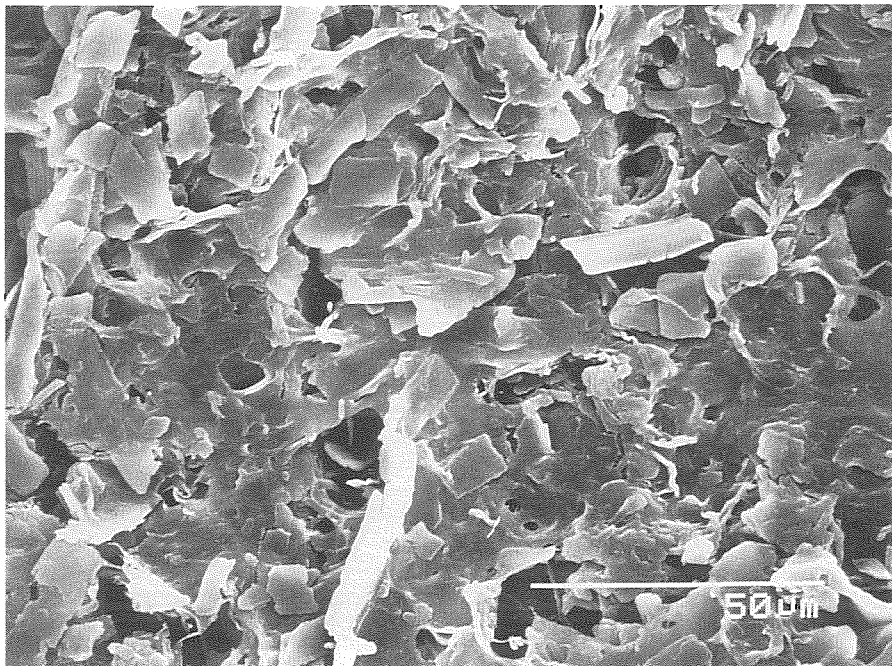


Fig. 71. Anal substance and wax filaments on the host plant : remains of a *C. garciniae* female test removed [90ML-186].

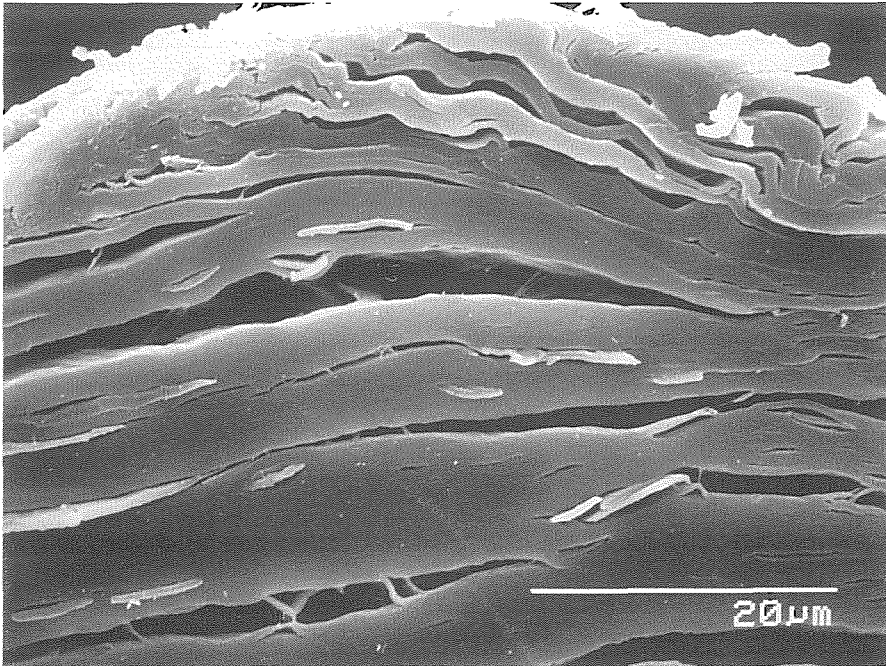


Fig. 72. *C. garciniae*, larval test : a cross section, showing the internal structure just below the top [90ML-187].

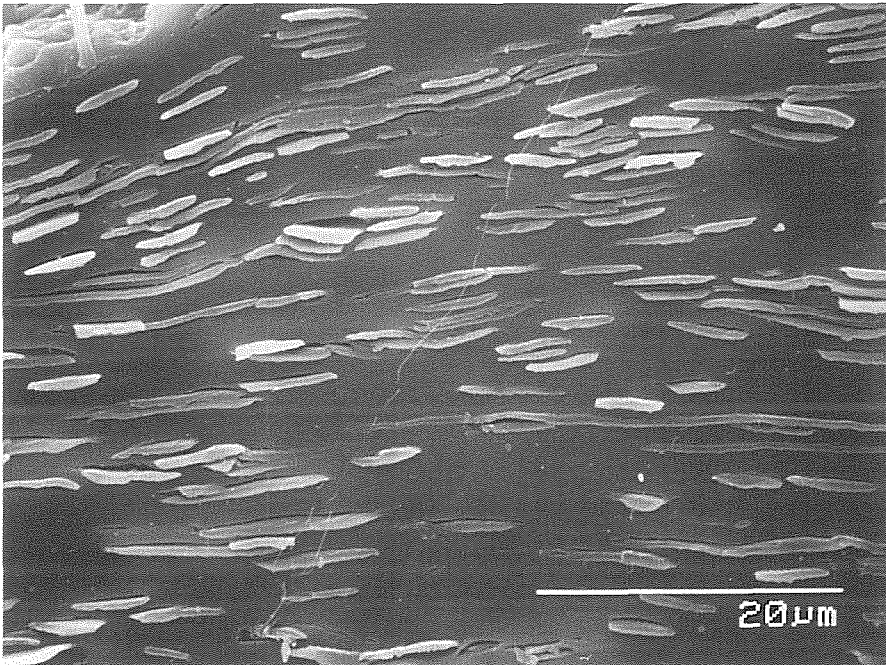


Fig. 73. *C. garciniae*, larval test, same as Fig. 72 : part lateral to the top.

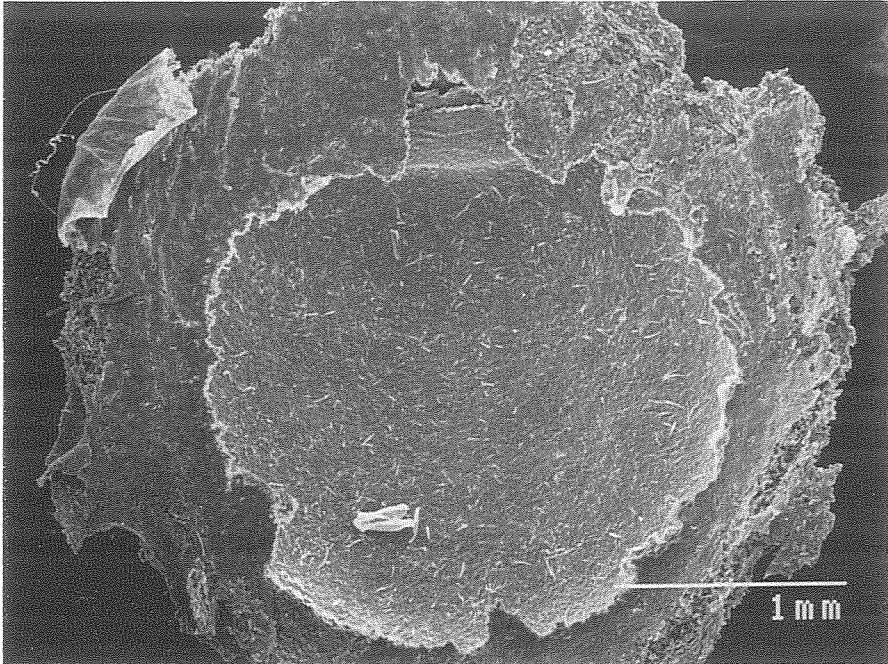


Fig. 74. *C. garciniae*, female test (patelliform): ventral view [90ML-187]. (Note the presence, on the upper side, of a tunnel for copulation and the escape of crawlers.)

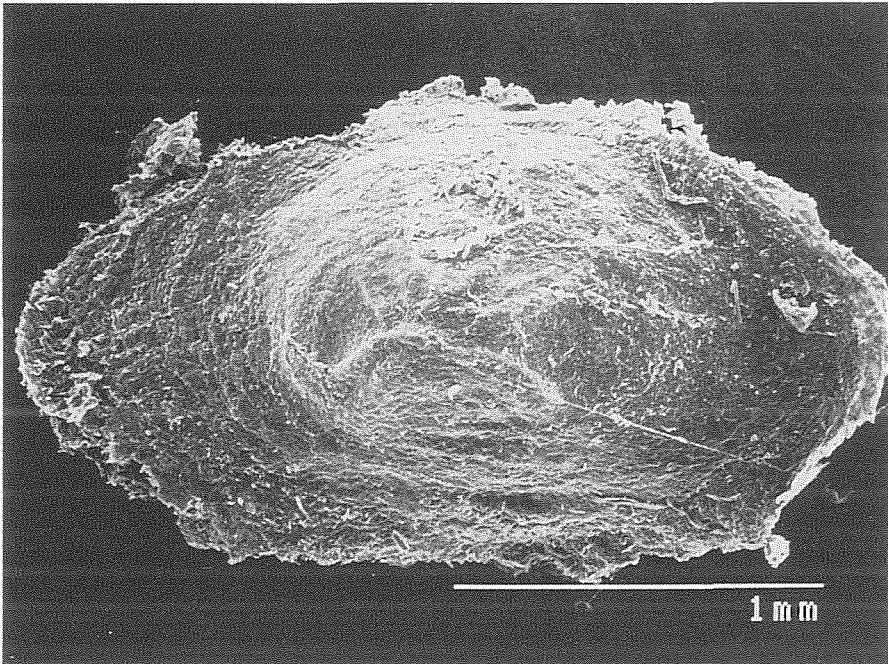


Fig. 75. *C. garciniae*, male test: dorsal view [90ML-186].

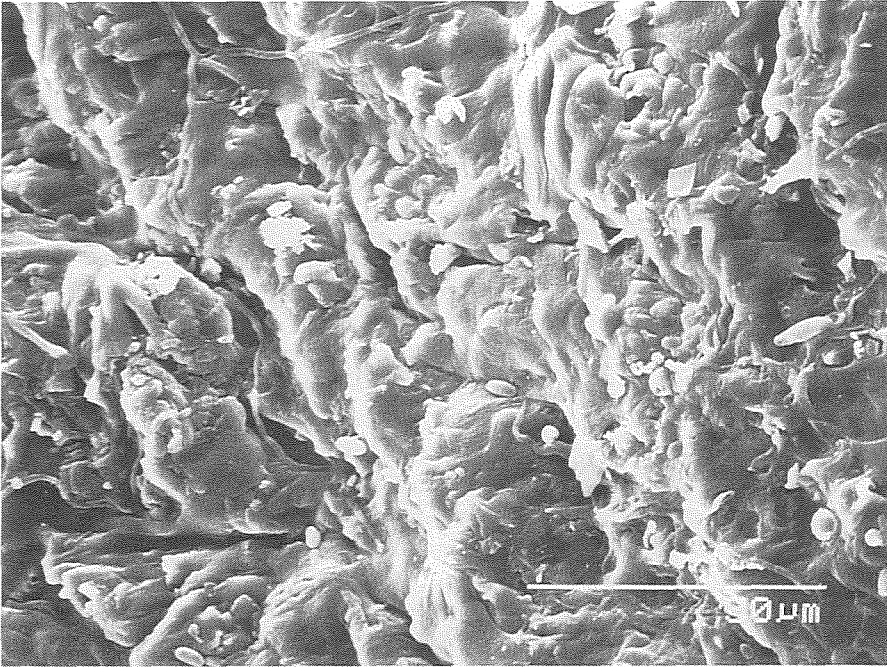


Fig. 76. *C. garciniae*, male test : part of Fig. 75.

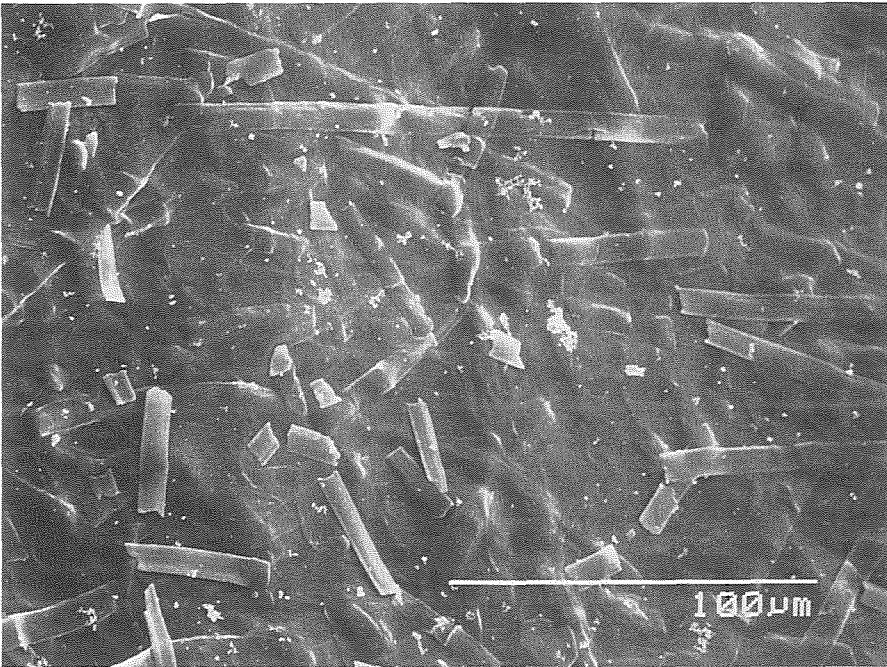


Fig. 77. *C. garciniae*, male test : inner surface of dorsal portion [90ML-186].

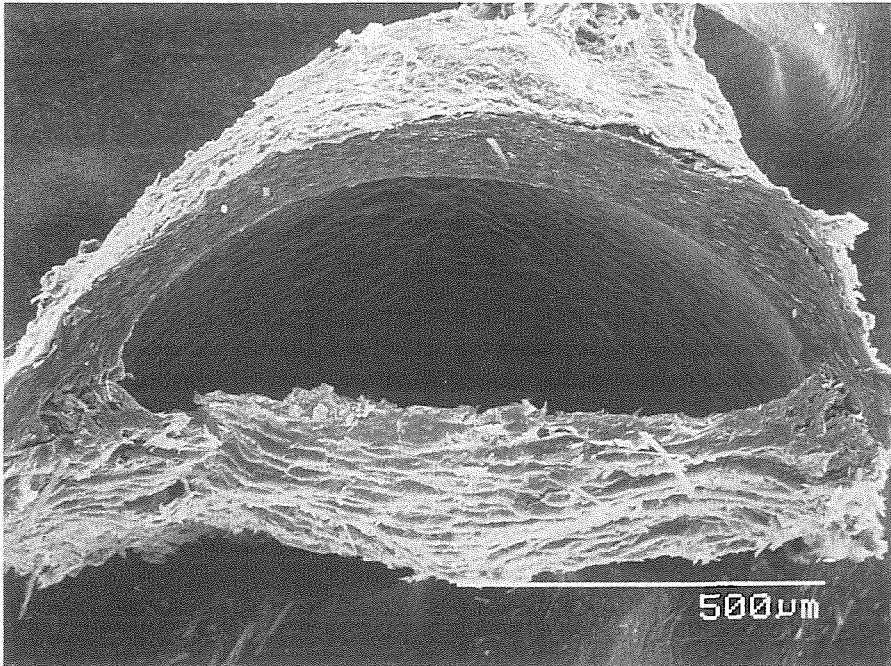


Fig. 78. *C. garciniae*, male test : a cross section [90ML-186].

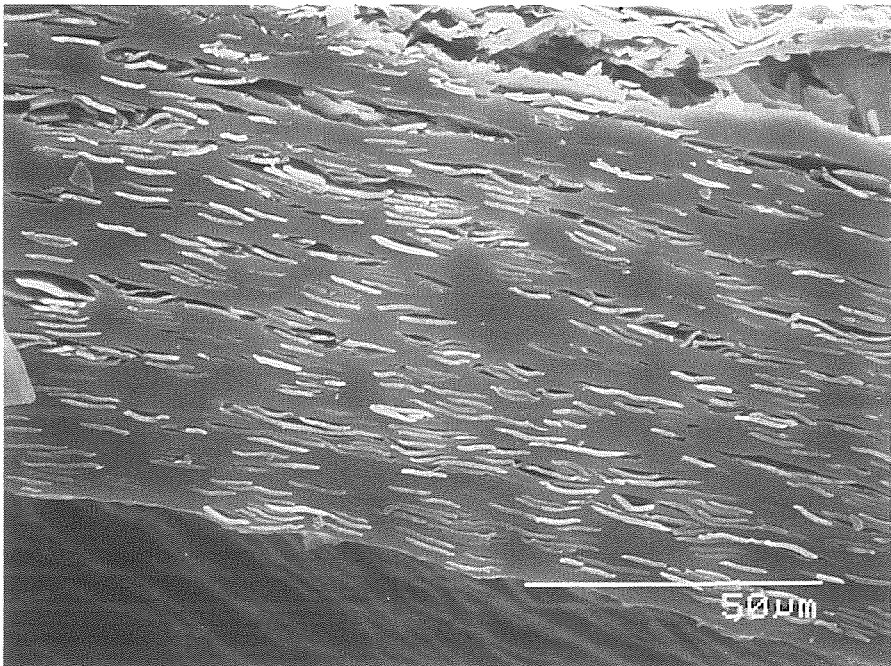


Fig. 79. *C. garciniae*, male test, same as Fig. 78 : internal structure of the dorsal portion.

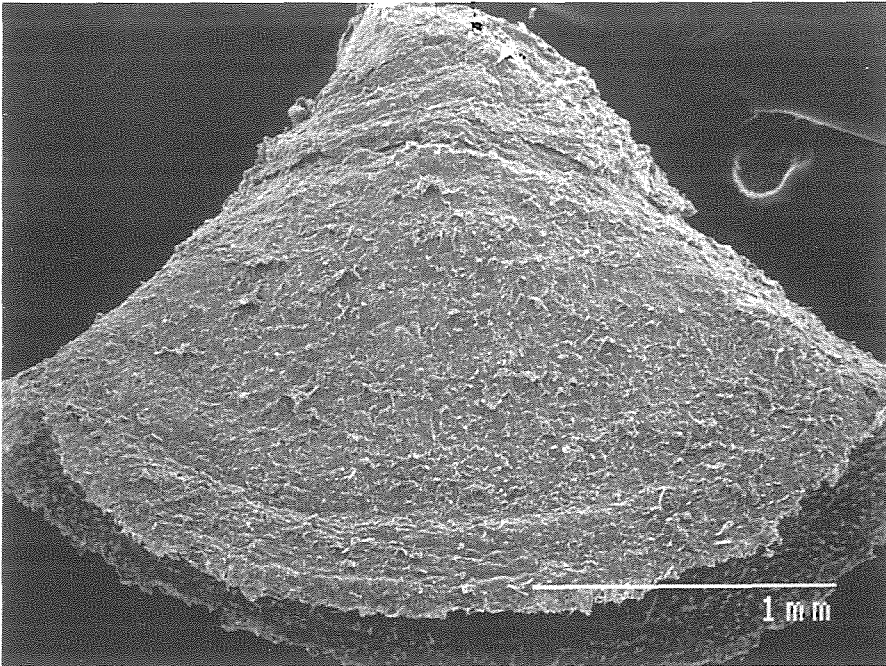


Fig. 80. *C. vaccinii*, female test : lateral view [90ML-545].

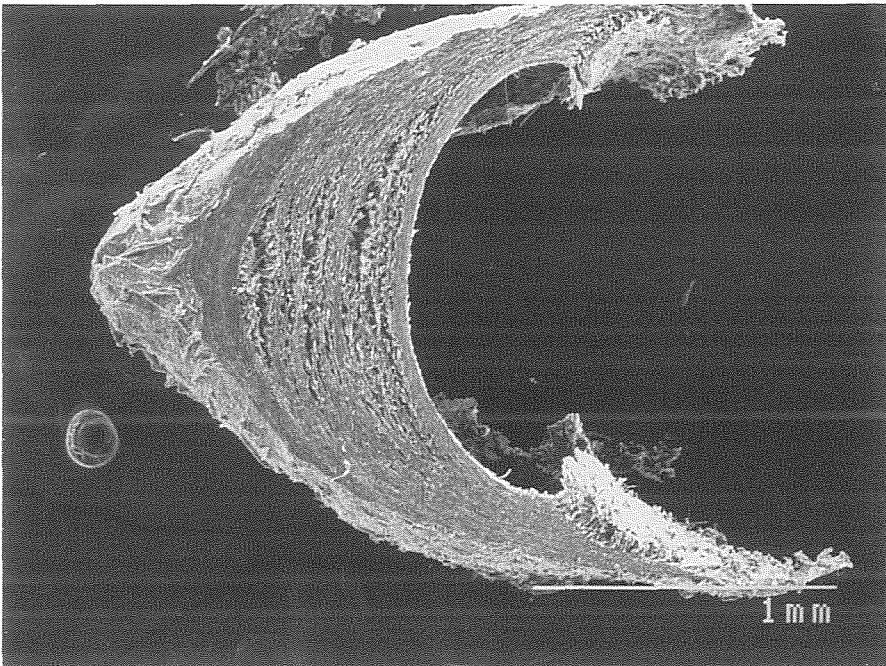


Fig. 81. *C. vaccinii*, female test : a cross section [90ML-545].

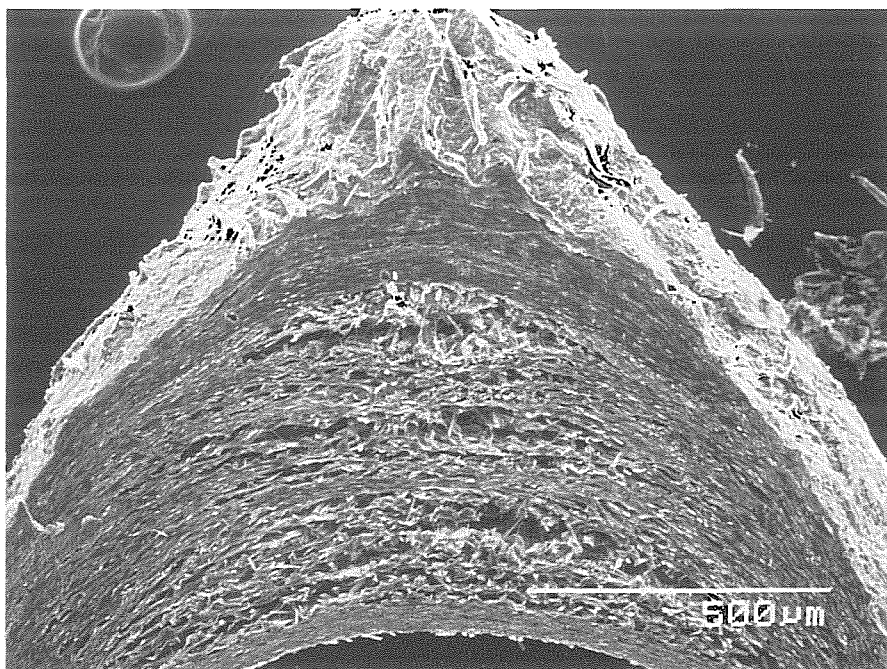


Fig. 82. *C. vaccinii*, female test : part of Fig. 81, showing the 3 internal zones.

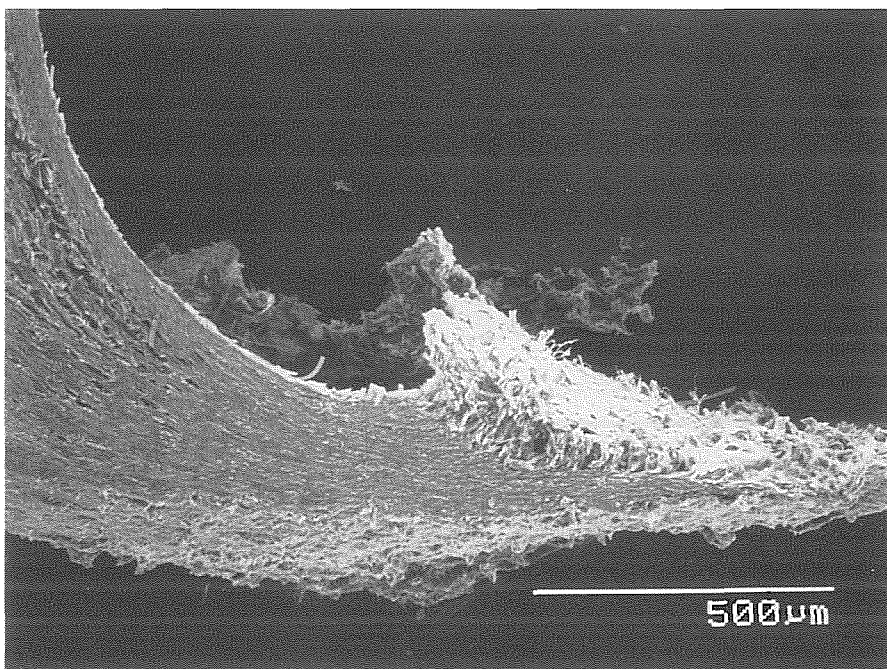


Fig. 83. *C. vaccinii*, female test : part of Fig. 81, showing a lower extension.

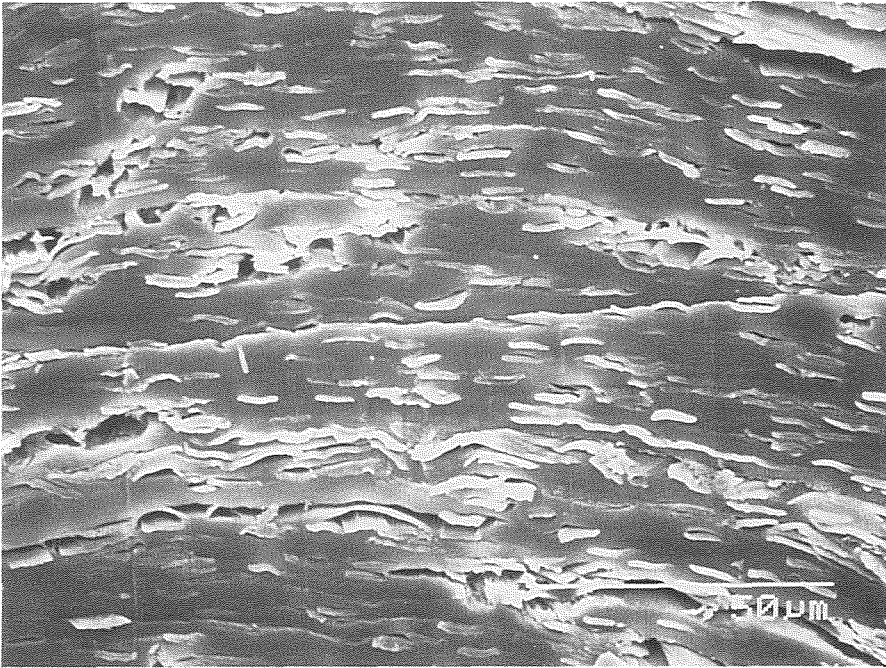


Fig. 84. *C. vaccinii*, female test : part of Fig. 81, showing the outermost zone.

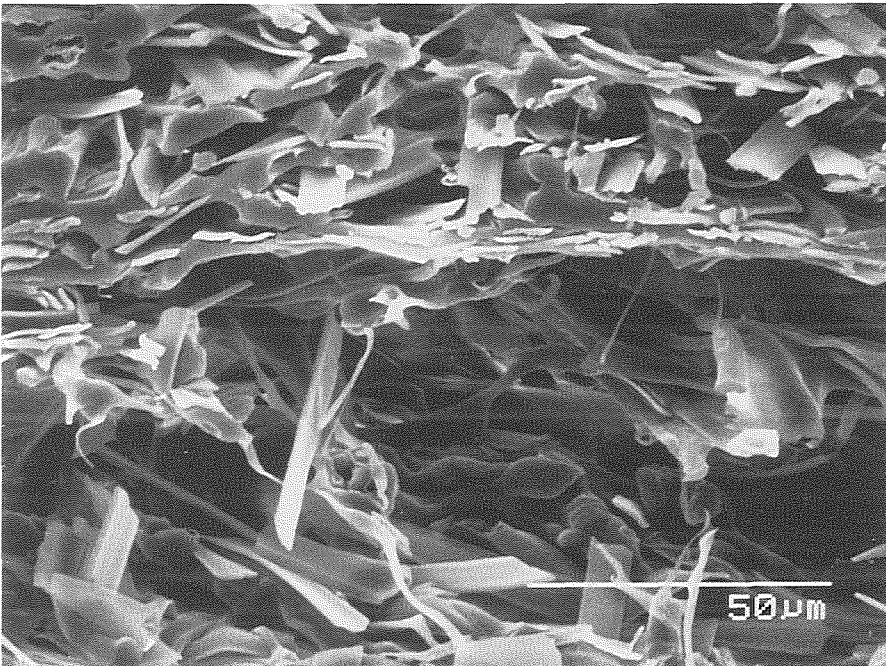


Fig. 85. *C. vaccinii*, female test : part of Fig. 81, showing the intermediate zone.

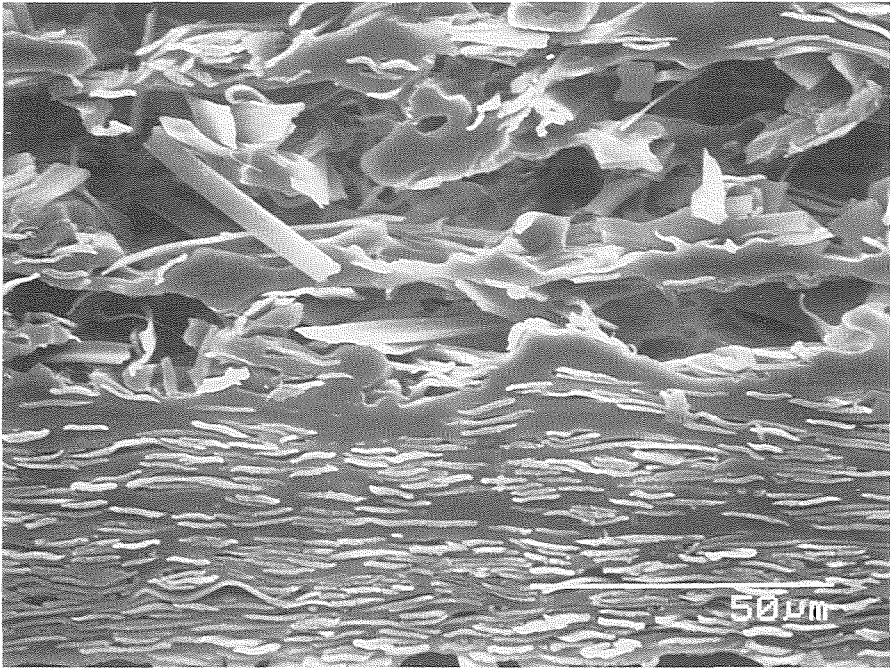


Fig. 86. *C. vaccinii*, female test : part of Fig. 81, showing the intermediate zone (upper half) and the innermost zone.

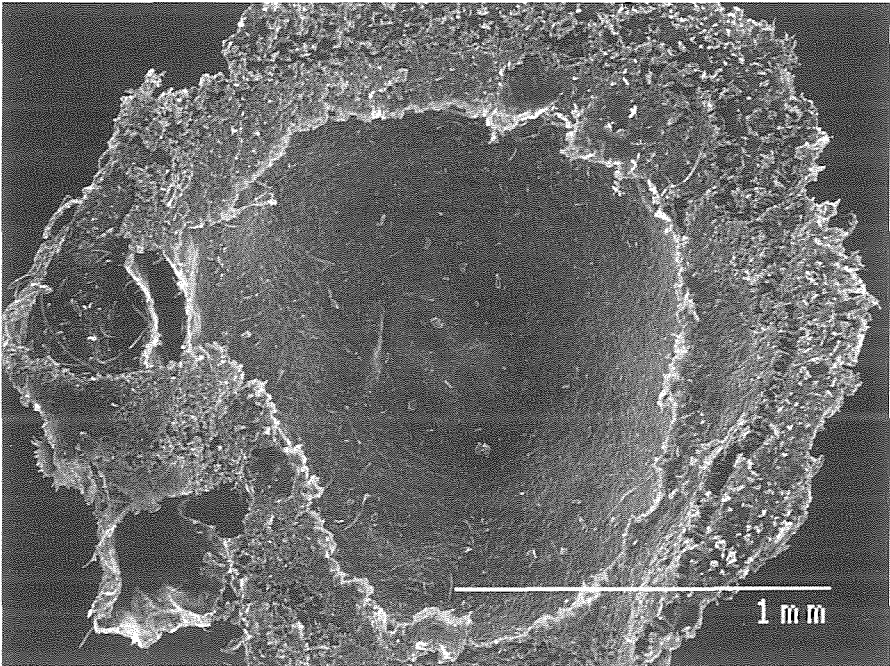


Fig. 87. *C. buchanae*, female test : ventral view. (Note the presence, on the left side, of a tunnel for copulation and the escape of crawlers.)

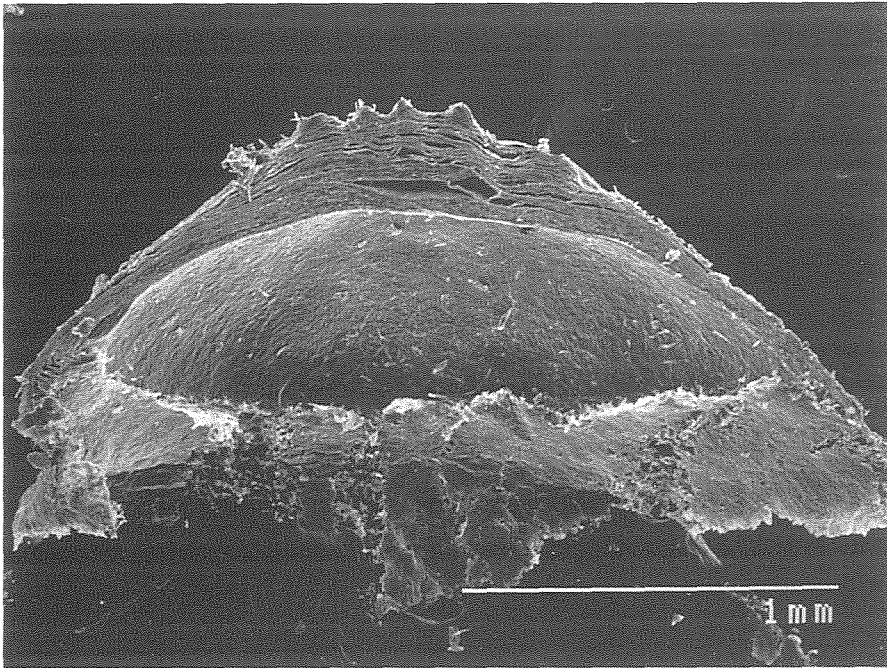


Fig. 88. *C. buchananiae*, female test : a cross section.

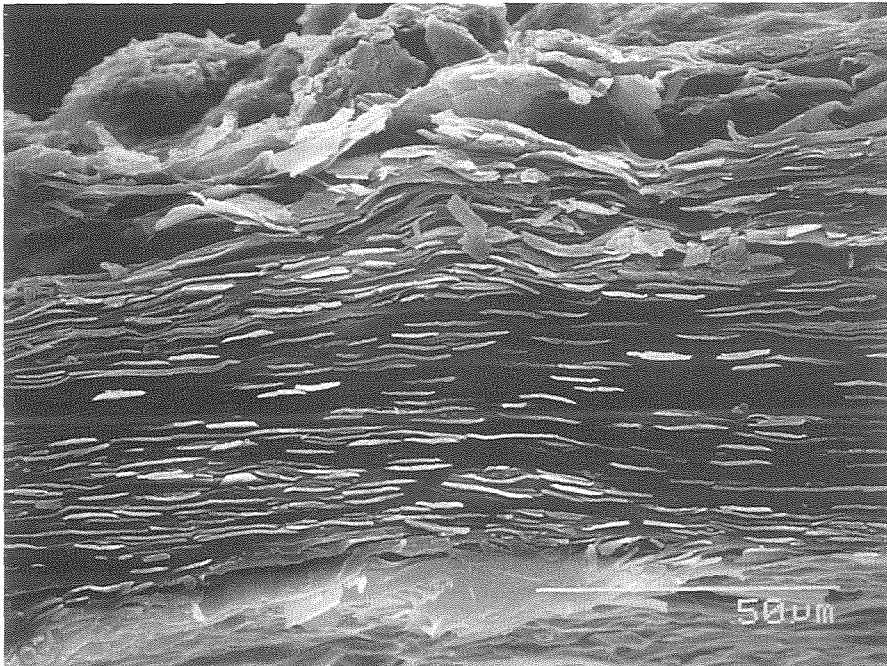


Fig. 89. *C. buchananiae*, female test : part of Fig. 88, showing the internal structure of the dorsal portion.