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**SEM OBSERVATIONS ON THE TESTS OF SOME DIASPIDIDAE  
(HOMOPTERA : COCCOIDEA)**

By SADAO TAKAGI

*Abstract*

TAKAGI, S. 1990. SEM observations on the tests of some Diaspididae. *Ins. matsum. n. s. 44* : 17-80, 117 figs. (in 48 plates).

The tests of 10 species of the family Diaspididae were observed in a scanning electron microscope, and photomicrographs are presented for them. Highly magnified tests are mainly composed of wax filaments, but not uniform in structure among the species observed. An evolutionary trend of the test from a loose mass of filaments to a thin, tight and broad covering is recognized, and in parallel in different groups of the family. Advanced types of tests are made by oscillatory or nearly rotatory movements of the insects, but in the Diaspidini the male test shows no trace of such movements. Attempts to connect structures of the test with external characters of the insect body have not wholly been successful, but still support the view that the external characters have largely evolved in association with test formation.

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*Contents.* Introduction—Material and methods—Observations [*Ulucoccus gombakensis*, *Megacanthaspis langtangana*, *Nikkoaspis shiranensis*, *Chionaspis alnus*, *Pseudaulacaspis prunicola*, *Thysanaspis perkinsi*, *Lopholeucaspis japonica*, *Parlatoria abieticola*, *Microparlatoria itabicola* and *Pseudaonidia paeoniae*]—Discussions—References—Plates.

## INTRODUCTION

Diaspididae or armoured scale insects are uniquely characterized by their protecting coverings called tests, scales, etc., which are composed partly of larval skins and partly of secretory material. The tests are variable in shape and colour, and characteristic of taxonomic groups to some degree. Published observations on the test are abundant, but scanning electron microscopy has been limited to several species. In a recent work on a diaspidine species (Takagi, 1989) it has been shown that in a SEM the test is rather complicated in structure. Comparative studies of tests based on SEM observations may, therefore, be promising.

It is the main purpose of the present work to approach the evolutionary development of diaspidid tests on the basis of SEM observations. Species were selected to represent some evolutionary stages from the viewpoint of body characters, but the forms available are still very insufficient for the purpose. I restrict this paper to 10 species, of which five are referable or related to the tribe Diaspidini, the subfamily Diaspidinae, and the other five to the subfamily Aspidiotinae. Another purpose of this paper is to present SEM photomicrographs of the tests, because our knowledge is very meagre as to the highly magnified structure of diaspidid tests. For this purpose a complete series of photomicrographs for every test observed may be the best means to convey information, but it needs too many pages. In this paper, therefore, photomicrographs are limited to some representative parts of the tests.

## MATERIAL AND METHODS

Growing or completed tests were observed. Material was prepared with the purpose of making observations on both the test and the insect body within it. Alcohol-preserved or dried material was used. Dried material was kept in humid atmosphere (with creosote in a vial) for some days; after the insect bodies within the tests absorbed enough moisture to become plump, the material was dehydrated in alcohol. Dehydrated material, originally alcohol-preserved or dried, was critical point dried and coated with gold. Observations were made in a Hitachi S-2100A scanning electron microscope.

Treatment of tests with alcohol may allow some substance to melt away, but extract in alcohol if any may be negligible so far as the visual structure of the test is concerned.

The following 10 species of armoured scale insects are dealt with in this paper.

*Uluococcus gombakensis*\*. Malaysia (Selangor), on *Gigantochloa scortechinii*. Figs. 1-3.

*Megacanthaspis langtangana*. Nepal (Langtang Valley), on *Persea duthiei*. Figs. 4-12.

*Nikkoaspis shivanensis*. Japan (Kyōto-hu), on *Sasa* sp. Figs. 13-23.

*Chionaspis alnus*. Japan (Sapporo), on *Alnus japonica*. Figs. 24-44.

*Pseudaulacaspis prunicola*. Japan (Sapporo), on *Prunus lannesiana* (partly on *Prunus mume*).

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\* Systematic and Ecological Surveys on Some Plant-parasitic Microarthropods in Southeast Asia, Scientific Report No. 10B.

Figs. 45-72.

*Thysanaspis perkinsi*. Taiwan (Kuan-tzu-ling), on *Litsea akoensis*. Figs. 73-77.

*Lopholeucaspis japonica*. Japan (Sapporo), on *Betula platyphylla*. Figs. 78-87.

*Parlatoria abieticola*. Nepal (Langtang Valley), on *Abies spectabilis*. Figs. 88-96.

*Microparlatoria itabicola*. Japan (Okinawa), on *Ficus pumila*. Figs. 97-111.

*Pseudaonidia paeoniae*. Japan (Osaka), on *Camellia sasanqua*. Figs. 112-117.

## OBSERVATIONS

Highly magnified tests usually show a mass of filaments, which may be called wax filaments. These are variable in breadth, and broader filaments may be called wax ribbons when necessary. ('Filaments' may, therefore, mean only fine filaments or both fine filaments and ribbons.) Wax ribbons, flat stripes in shape, are apparently produced by macroducts. It may not be easy, however, to distinguish fine filaments according to their supposed secretory organs (small macroducts, microducts and gland spines or plates).

Sometimes there are on the test irregular lumps of a substance which looks like wax once melted. They were removed by treating with chloroform for one night or one day, and may be called wax lumps. However, filaments remained unaffected by the treatment. According to Foldi (1983), the secretion of ducts contains a glyco-proteinaceous substance in addition to the waxy component. Further, it has been stated that wax filaments are coated by or embedded in a substance discharged by the anus, and the substance was called "glutinous liquid" (Baranyovits, 1953), "hardening non-waxy component" (Ebstein and Gerson, 1971) or "substance agglomérante" (Foldi, 1982). In fact, wax filaments often appear to be agglutinated together by an amorphous substance. Sometimes filaments themselves appear to be fused together. Material forming wax lumps may primarily be secreted as filaments (so far as secreted by ducts), but no trace of fused filaments has been observed in them.

### *Ulucoccus gombakensis*

Five of the species dealt with have gland spines and are referable or related to the tribe Diaspidini. Among them *Ulucoccus gombakensis* is the most primitive in some features. The adult female is simple in external structure, with ducts all geminate at the inner end; it has no marginal appendages on the pygidium except for small gland spines and, in *U. danumensis*, rudimentary irregular processes. The 2nd instar male and female are similar to the adult female.

The male and female of *U. gombakensis* secrete white and fluffy wax. When magnified, the growing adult female is covered by a loose mass of filaments, with the 1st instar exuvial cast on the anterior end (Fig. 1). (The 2nd instar exuvial cast is broken into 2 pieces, only the anterior piece being kept under the 1st exuvial cast.) Very fine filaments are mingled among much thicker ones (Fig. 2); these must be discharged by the macroducts, which are rather abundant dorsally, while the fine filaments may originate from microducts. At full growth the filaments are denser but the mass is still fluffy. The growing male is also covered with filaments, which, however, form a rather compact mass, with the 1st exuvial cast on the anterior end (Fig. 3).

*Megacanthaspis langtangana*

In this species and the succeeding three the ducts are 2-barred at the inner end and the pygidium is provided with well-developed marginal appendages. This species has plate-like marginal appendages around the pygidial margin in the adult female and the 2nd instar male and female, but lacks sclerotized lobes. The female test is elongate, narrow, highly convex dorsally, fluffy and dark brown, with the 1st and 2nd exuvial casts at the anterior end. The male test appears quite different, being depressed dorsally, and white and smooth except medially, where it is fluffy and dark brown. It is provided with the 1st instar exuvial cast at the anterior end.

In a low-magnified SEM observation the tests still appear fluffy (Fig. 4). At a higher magnification the whole dorsal surface of the female test is ragged with wax ribbons which project up and then bend down more or less abruptly (Figs. 5 and 6). The male test is similarly ragged medially, but laterally much less (Fig. 9). When growing, the female test shows on the inner surface a lot of running and bending ribbons (Fig. 8); later these ribbons are agglutinated together (Fig. 7). The ventral portion of the female test is limited to lateral sides in accordance with the ventral macroducts which occur only on the lateral sides of the adult female. On the other hand, the male test is complete, with a well-formed ventral portion in accordance with the occurrence of macroducts over the venter of the 2nd instar, thus enclosing the male insect, for which it becomes a cocoon (Fig. 10). The inner surface of the male test is lined with entangled filaments.

In the adult female the marginal gland spines are all enlarged, each having 2-7 microducts. However, it seems that they take a small part if any in the formation of the test, which appears to be composed at least largely of ribbons secreted by macroducts. When the test is removed, it leaves on the host leaf a white patch, which is formed by entangled wax filaments (Fig. 11). These filaments are various in breadth (Fig. 12), but much narrower than the ribbons composing the test; it is possible, though not certain, that each of these filaments are discharged from 2 or more microducts running through a gland spine. Filaments originated from ducts must also be mingled there, because some small ducts are present on the ventral surface of the pygidium.

*Nikkoaspis shiranensis*

This species has sclerotized lobes in addition to plate-like marginal appendages in the adult and 2nd instar females. The female test is thick in accordance with the fact that abundant macroducts occur dorsally in the adult female; it is elongate, expanding posteriorly, convex dorsally and white, with some remarkable growing ridges running across, and with the exuvial casts at the anterior end. The 2nd instar male is much different from the female, and especially characterized in having a set of communal ducts marginally on each side of the supposed 7th abdominal segment. The male test is elongate and depressed, with a median carina dorsally throughout, and with the 1st exuvial cast at the anterior end (Fig. 21).

Fused or agglutinated filaments run longitudinally, obliquely or rather irregularly on the dorsal surface of the female test (Figs. 14-16). The growing female discharges filaments around the body (Fig. 18); at the posterior end of the body the filaments are directed backward (Figs. 19 and 20) and even projected outside (Figs. 13 and 17). Filaments discharged from the macroducts and marginal gland spines

are mingled together (Figs. 19 and 20). The ventral portion of the test covers the cephalothorax and the base of the abdomen (Fig. 18); it must be formed by the ventral macroducts, which occur on the metathorax and the base of the abdomen. The completed test is lined by entangled filaments on the inner surface except about the posterior end.

The median carina of the male test is formed by projecting filaments; laterally to the carina the surface of the test is rather smooth and obscurely imbricated (Figs. 21 and 22). The inner surface of the test is, however, covered with entangled filaments and irregular patches of the glutinous substance (Fig. 23). The ventral portion is formed for the whole length of the test and similar to the dorsal portion in structure, but with no carina and with filaments appearing here and there on the outer surface. The filaments forming the median carina may be produced by the communal ducts, which are, however, located on the supposed 7th abdominal segment, thus laterally to the median line of the body.

#### *Chionaspis alnus*

The adult female is fusiform or elongate pyriform, with many ducts, which are variable in size, on the dorsal surface in addition to marginal macroducts on the pygidium and lateral macroducts on prepygidial segments. The pygidium is provided with lobes and gland spines, but with no plate-like appendages. The 2nd instar male is much different in external features and is, in comparison with the female, peculiar in having cup-like ducts on the 2nd to 4th abdominal segments and also on the 7th. The female test is elongate pyriform, moderately convex dorsally and white, with the exuvial casts at the anterior end; the male test is elongate, depressed, longitudinally tricarinate dorsally and white, with the 1st exuvial cast at the anterior end.

When magnified, the female test is speckled on the dorsal surface with fragments of the uppermost layer of the bark; beneath them ribbons and fine filaments run across the test, forming curved lines (Figs. 24-27). On the inner surface the test is lined by irregularly entangled filaments (Figs. 28 and 29) except about the posterior end, where ribbons are exposed (Fig. 30); at the posterior end filaments are embedded in a thin layer of the glutinous substance (Fig. 31). The ventral portion of the test is well developed; on the outer surface it is formed by filaments which are more or less agglutinated together but still show some transverse tendency in running (Figs. 32 and 33).

The male test is covered dorsally by irregular lumps of wax, which are coarser on the median and lateral carinae (Figs. 34-37). It seems that the median carina corresponds to the cup-like ducts of the 7th abdominal segment and the lateral carinae to those of the 2nd to 4th. In cross section these lumps are superimposed on a layer of filaments and show no internal structure. When treated with chloroform for one day, all the lumps disappear and filaments below them are exposed (Figs. 38-40). The inner surface is lined by entangled filaments (Figs. 41 and 42). The ventral portion of the test is also formed by irregularly entangled filaments (Figs. 43 and 44).

#### *Pseudaulacaspis prunicola*

This species differs from all the preceding species in the broadly obovoid body of the adult female; this stage has many submedian and submarginal dorsal

macroducts, which are as large as the marginal macroducts, and many lateral macroducts, and is provided with well-developed lobes and gland spines. The female test is rounded, white, with the exuvial casts subcentral to submarginal; no ventral portion is formed. The 2nd instar male is elongate ovoid, much different from the adult female in the ducts and marginal appendages, and characterized by having a set of communal ducts and surrounding cluster ducts on the margin of the 6th and 7th abdominal segments on each side of the body; the male test is elongate, with a well-developed ventral portion.

The female test shows a concentric growing pattern (Fig. 45). This pattern is formed by ribbons (Fig. 48), which are, however, not clearly detected at a higher magnification owing to their agglutination (Figs. 46-48). Fine filaments are running along the margin; it seems that they are secreted along the margin of a growing test and then agglutinated within the already constructed part of the test (Figs. 46-48). There are no organs other than the marginal gland spines of the pygidium to secrete these filaments. Free filaments are also seen around the margin of the 2nd instar exuvial cast (Fig. 49). They may be remains of filaments secreted by the full-grown 2nd instar, because the 2nd instar female seems to form her test in much the same way (Figs. 54-56).

The female in forming her test scrapes the bark to pick up or remove the uppermost layer. When the test and the insect body are removed, there remains on the bark a well-bounded trace with a concentric pattern within (Fig. 50). This pattern is formed by filaments (Figs. 52 and 53), which are, however, irregular in running around the point where the rostral loop is inserted (Fig. 51). These filaments may be secreted by lateral macroducts or prepygidial gland spines or, more probably, by both; microducts are also present on the ventral surface, but they are too few to produce the main part of the filaments.

The female test is apparently formed by nearly rotatory or wide and compound oscillatory movements of the insect. It is also apparent that even the 1st instar female is not immobile (Figs. 57-60).

On the other hand, the male test is elongate, with the 1st exuvial cast at the anterior end, and appears to extend only posteriorly as the insect grows; the ventral portion is well developed, thus the test completely encloses the insect (Figs. 61 and 64). It is formed by irregularly entangled ribbons which are agglutinated together (Figs. 63 and 67), and also by filaments on the lateral sides (Figs. 62 and 66). On the dorsal surface ribbons tend to project along the lateral margins, forming, however, no obvious carinae (Figs. 61 and 62). The inner surfaces of the dorsal and ventral portions are lined by filaments, but rather sparsely (Figs. 68-72) except below the 1st exuvial cast (Fig. 65).

#### *Thysanaspis perkinsi*

The remaining 5 species have plates instead of gland spines on the pygidial margin. Usually the plate is glandulous like the gland spine, but in *Thysanaspis perkinsi* and *Lopholeucaspis japonica*, which represent primitive forms among the species, the plates are nonglandulous. Further, *T. perkinsi* is provided with no sclerotized lobes on the pygidium, thus comparable to *Megacanthaspis langtangana* in the preceding group so far as the pygidial fringe is concerned (the latter is provided with plate-like appendages and gland spines). In the 5 species the ducts are 2-barred

at the inner end except the enlarged marginal ducts of *Thysanaspis perkinsi*.

*Thysanaspis perkinsi* is, however, pupillarial, the adult female being enclosed within the 2nd instar exuvial cast, which is plump and heavily sclerotized, and being simplified in external structure. The 2nd instar female has remarkable plates and 3 enlarged marginal ducts, which are geminate at the inner end, on the pygidium and small gland tubercles and scattered ducts on the ventral side; the exuvial cast is almost naked, lying on a small amount of wax.

The 2nd instar male is similar to the 2nd instar female in the pygidial margin and is provided with segmental series of macroducts on both dorsal and ventral surfaces in addition to the enlarged marginal ducts. It forms a complete test, which is elongate, with the 1st exuvial cast at the anterior end (Fig. 73). The outer surfaces of the dorsal and ventral portions are covered by curved filaments (Figs. 74 and 75), while the inner surfaces are lined by irregularly entangled filaments (Figs. 76 and 77). It seems that both the outer and the inner filaments are secreted by the dorsal and ventral macroducts, because these macroducts are the only secretory organs responsible for abundant filaments. (The 2nd instar female is almost devoid of dorsal ducts, and the exuvial cast is nearly naked dorsally.) Gland tubercles are present on the thoracic ventrum, but they are small and too few. Then the question may be raised what role the enlarged marginal ducts have in test formation. They are only 3 in all, but remarkable in size. (They are well developed in the 2nd instar female, too.) They probably have some role, which, however, has not been found out in the present study.

#### *Lopholeucaspis japonica*

This species also has nonglandulous plates on the pygidium, but is provided with sclerotized pygidial lobes; in this character it is more advanced than the preceding species. It is pupillarial, but the adult female is not enclosed within the 2nd instar exuvial cast but entirely covered by the latter. The 2nd instar female forms a good test, which is elongate, with the 1st exuvial cast at the anterior end (Fig. 78). The dorsal surface of the test appears somewhat disorderly owing to agglutinated ribbons mixed with minute flakes originated from the uppermost layer of the bark (Figs. 81 and 82). In the ventral view, ribbons obviously run across the test (Fig. 84) and the test under construction is much bigger than the body of the 2nd instar female (Fig. 83); this indicates that the 2nd instar female makes oscillatory movements in forming the test. The inner surface is largely lined by entangled filaments except about the posterior end (Fig. 85). These filaments may be secreted by small ducts scattered in the prepygidial abdomen, while the ribbons by the macroducts which are mostly located on the pygidium. The ventral portion of the test is formed only anterolaterally (Fig. 83) and corresponds in position to the gland tubercles and small ducts which occur on the ventrum along the margin.

The 1st instar exuvial cast is covered by a mat of filaments; these run longitudinally in the anterior third of the mat, then suddenly change the direction to run transversely (Figs. 78-80). The 1st instar larva is provided with a series of marginal macroducts on the abdomen and with smaller ducts, also along the margin, on the head and thorax. It may be supposed that the insect projects filaments anteriorly from the ducts of the head, but it can be hardly imagined how it secretes filaments across the body without any movement.

No obvious difference has been found in the structure of the male test (Figs. 86 and 87).

#### *Parlatoria abieticola*

The female test is more or less rounded and moderately convex dorsally, with exuvial casts located marginally. At a low magnification the dorsal surface shows curved growing lines, but, when more magnified, the growing pattern is very obscure owing to agglutinated ribbons (Fig. 88). In a growing test free ribbons may be found somewhere on the inner surface, but they are to be agglutinated together to form a smooth surface (Figs. 89 and 90). The ventral portion of the test is formed narrowly along the anterior to lateral margin. It shows no structure except for filaments appearing under the 2nd exuvial cast (Fig. 91) and at some other parts (Fig. 92).

The male test is different from the female one, being much smaller and elongate, with the 1st exuvial cast at the anterior end. But in magnified structure it is much the same as the latter. It differs from the female test by having abundant filaments lining the inner surface (Figs. 93-95). Abundant filaments also remain on the host leaf when the test is removed (Fig. 96).

The female test is no doubt formed by the secretion of the macroducts which are numerous on the dorsal surface of the adult female; the ventral portion may be formed by the gland tubercles and small macroducts which occur submarginally on the ventrum of the thorax and the base of abdomen. However, the secretion of the plates, which are rather well represented on the pygidial margin, could not be identified.

The 2nd instar male has not been examined, but it must be very similar to the known 2nd instar male of *P. tsugicola*, a closely related species. It must, then, be similar to the adult female, differing mainly in having much fewer ducts and gland tubercles. As stated above the male test is lined by abundant filaments, which may be secreted from the gland tubercles, microducts, or plates, or from all of them.

#### *Microparlatoria itabicola*

In the adult female the plates are well developed and glandulous, the marginal macroducts are comparatively very large, occurring in 4 pairs and with the orifice set longitudinal, and the other dorsal ducts are all microducts and scattered along the body margin mainly on the abdomen. The 2nd instar male is similar to the female, differing mainly in the marginal macroducts occurring in 3 pairs, in having much fewer microducts, and in having some macroducts marginally on the thorax.

The female test is elongate obovoid, with the exuvial casts at the anterior end. The dorsal surface of the secreted part is crossed by many curved lines (Figs. 97 and 98). When highly magnified, the surface is covered across by overlapping board-like structures; each of these appears to be composed of tightly agglutinated ribbons, and bears many spots or interrupted lines running in parallel with it (Figs. 99 and 100; the spots and lines come out white in the photomicrographs). These spots and lines disappeared after a treatment with chloroform for one night, leaving pits and grooves (Figs. 101 and 102). Irregular lumps of wax are deposited between the 1st and 2nd exuvial casts (Figs. 103 and 104); they also disappeared by the treatment. The inner surface of the test is covered by rather irregularly entangled ribbons and, further, lined by filaments except about the posterior end (Figs. 105-107).

The ribbons cannot be secreted by any organs other than the marginal macroducts, and the spots and lines on the agglutinated ribbons may originate from the plates. Then the filaments lining the inner surface must be produced at least mainly by the dorsal microducts. The ventral portion of the test is formed only along the anterior to lateral margin, corresponding to gland tubercles and microducts which occur on the ventrum along the margin.

The male test is elongate and a little smaller than the female test. In magnified structure, however, it is very similar to the latter (Figs. 108-111).

#### *Pseudaonidia paeoniae*

In this species the plates are much reduced, the ducts are all small, and there are no gland tubercles on the thoracic ventrum and no differentiated marginal ducts on the pygidium.

The female test is circular, but the expected concentric pattern of growth is rather obscure owing to the agglutination of filaments (Fig. 112). The inner surface appears more irregular as to the running direction of filaments (which are secreted for lining) (Fig. 113), but some filaments may be seen running along the margin (Fig. 114). The central area is further lined by fine filaments (Fig. 115), which may be produced by microducts occurring submedially and submarginally in the prepygidial region. The male test is smaller and elongate (Fig. 116), but, when magnified, much the same as the female test in both the dorsal (Fig. 116) and ventral (Fig. 117) views.

### DISCUSSIONS

It is known that diaspidids make some movement in forming their tests (Matsuda, 1927 and 1929; Dickson, 1951; Baranyovits, 1953). However, not all diaspidids move.

The 5 species with gland spines are referable or related to the tribe Diaspidini, the subfamily Diaspidinae. They are remarkably different in the female test. The test of *Uluccoccus gombakensis* is merely a loose mass of filaments. The test of *Megacanthaspis langtangana* is a more compact mass; however, when highly magnified, it is still a rough assemblage of filaments. In *Nikkoaspis shiranensis* the composing filaments are agglutinated together to form a tight covering, which, however, fits the body of the insect and shows no trace of the movement of the insect. In all these species the female test is formed as the stationary insect grows.

The elongate pyriform female test of *Chionaspis alnus* represents a usual type in the Diaspidini. It is as narrow as the test of *Nikkoaspis shiranensis*. Nevertheless, the running of filaments shows that the outer layer of the test is formed by oscillatory movements of the female. The layer thus formed is thin and tight. The inner surface is lined by filaments, which are apparently deposited after the formation of the outer layer and show no trace of oscillatory movements.

The female of *Pseudaulacaspis prunicola* forms a circular test, for which rotatory or compound oscillatory movements of the insect are expected. The magnified structure supports this expectation. Disorderly entangled ribbons are occasionally seen on the inner surface; otherwise, there is on the test no trace of stationary secretion.

Thus a graded series is formed from a loose mass of filaments to a thin, tight and

broad covering. It must show an evolutionary trend of the female test, because the species correspondingly represent evolutionary stages in the characters of the adult female. It is not difficult to explain the adaptive significance of this evolutionary trend, which, therefore, may be expected also for other groups of the Diaspididae.

The remaining 5 species form another group and are referable or related to the subfamily Aspidiotinae. No form comparable to *Uluococcus gombakensis* is available in this group. *Thysanaspis perkinsi* is the most primitive among the species, but the female is pupillarial and does not form a covering. In the structure of its male test it nearly corresponds to *Megacanthaspis langtangana*. The 2nd instar male of *T. perkinsi* seems to be stationary, projecting filaments to form a rather loose mass. In the other species the females apparently move when forming their tests, and there may be recognized, though not so obviously as in the preceding group, a trend toward a tight and broad test. In fact, circular tests are prevailing in the Aspidiotini, an advanced taxon in the subfamily.

There is a noteworthy difference between the 2 groups. In all the species of the 1st group the 2nd instar males do not move when forming their tests, which are cocoon-like and more or less different from the female tests in appearance and structure. On the other hand, in the species of the 2nd group except *Thysanaspis perkinsi* the 2nd instar males apparently move, and the male tests are little different from the female ones in magnified structure. In fact, the 2nd instar males of the Diaspidini are usually much different from the females in the external structure of the body, and are supposed to approach some ancestral form (or forms) (Takagi et al., 1989). On the other hand, the 2nd instar males of the Aspidiotinae are generally similar to the females.

It is well known that female diaspidids retain both the 1st and 2nd instar exuvial casts on the test. But in *Uluococcus gombakensis* the 2nd exuvial cast is broken into 2 pieces, and only the anterior piece is kept under the 1st. This may be no more than a character specific to *U. gombakensis*, for in the other known species of the genus, *U. danumensis*, the adult female retains the entire 2nd exuvial cast and the 1st. It is possible, however, that *U. gombakensis* represents a transitional stage toward the retention of both the exuvial casts.

The Odonaspidini are a peculiar group. They are primarily cryptic, occurring beneath the leaf-sheath of the host, and are much modified in accordance with this mode of life. A species of *Odonaspis* has been observed (and some difference has been found between the male and female tests in highly magnified structure), but it is not treated here.

The Lepidosaphedini, the subfamily Diaspidinae, are characterized by having gland spines in common with the Diaspidini. In this tribe the 2nd instar male is, so far as known, similar to the adult and 2nd instar females (especially in the pygidial margin). Several species of *Lepidosaphes* have been observed. They show an obvious trace of oscillatory movements of the insect body in the male and female tests, which are little different in highly magnified structure. No other forms of the tribe, however, have been observed for comparison.

The present work shows that the tests of the species examined are variable in highly magnified structure in accordance with the diversity in the external charac-

ters of the insects. However, it has still been uncertain how external organs and their characters are concerned with test formation. Undoubtedly ducts are the main source of the test material, but even their role may not be fixed throughout the family. For example, in *Microparlatoria itabicola* the dorsal ducts are differentiated into 2 distinct groups: the marginal macroducts are enlarged, with the orifice set longitudinal like the "mégapores" of the Lepidosaphedina, and apparently play a major role in test formation (in fact, the male and female tests are similar to those of *Lepidosaphes* in magnified structure); the other dorsal ducts, all reduced in size, seem to have changed their role to the lining of the test.

In *Pseudaulacaspis prunicola* abundant filaments are discharged from the pygidial gland spines on the margin of a growing female test, and may play some role in test formation. Fine filaments are also observed running together with ribbons in *Chionaspis alnus*. In *Ulucooccus gombakensis*, *Megacanthaspis langtangana* and *Nikkoaspis shiranensis* no abundant fine filaments were observed in the female test. However, the fact that gland spines are present even in *U. gombakensis*, a very primitive form, and well developed in many advanced Diaspidinae suggests a significant role of the gland spine.

Gland spines are absent in the Aspidiotinae, and glandulous plates in this subfamily may be comparable in their role to gland spines in the Diaspidinae. In fact, in *Microparlatoria itabicola*, which has remarkably developed plates, the supposed secretion of the plates is found on the board-like structures formed by agglutinated ribbons. However, in the female test of *Parlatoria abieticola* no secretion from the plates was identified. In *Pseudaonidia paeoniae* the plates are reduced in number and size. In the Aspidiotini many species have well-developed plates, but others are provided with a few much reduced ones or none and thus may be derivative. The female Odonaspidini usually have no plates. Apparently, in various forms, the plates tend to be reduced.

What is, then, the role of nonglandulous membranous appendages such as the plates of *Thysanaspis perkinsi* and *Lopholeucaspis japonica* and the plate-like processes of *Megacanthaspis langtangana* and *Nikkoaspis shiranensis* in the formation of the test? These processes are well developed in the species mentioned, which, except *L. japonica*, are stationary in forming the test. It may be imagined that they are used to help wax ribbons under secretion to extend in the right direction (see Figs. 18 and 19). Whatever role they have, these appendages may be of no use for species which oscillate or rotate in forming their tests, because in those species they are replaced by glandulous plates (in the Aspidiotinae) or lost (in the Diaspidini). The Leucaspidini as represented by *Lopholeucaspis japonica* make oscillatory movements in the 2nd instar, which still retain well-developed nonglandulous plates. They are a primitive group of the Aspidiotinae, which has survived probably owing to their pupillarial mode of life.

It has generally been assumed that the lobes, sclerotized appendages on the pygidial margin, are used like a trowel in test formation. On the other hand, female tests are often constructed partly or entirely under a thin (or sometimes thick) layer of the host plant epidermis, and the lobes are probably used like a knife or saw in burrowing into the plant epidermis. In any case, the lobes may be useful only when the insect moves. However, *Nikkoaspis shiranensis* is provided with lobes in spite of the fact that it does not move. Did the lobes first appear with another function?

In approaching the formation of the test the nature of the wax secreted is also essential, but it is conspicuously lacking in our knowledge. The chemical composition of wax may differ according to species or groups. Further, it has been known that the composition differs between the sexes in *Pseudaulacaspis pentagona* (Sugiyama and Kuwana, 1967; Hashimoto et al., 1971; Hashimoto and Kitaoka, 1971); indeed, the 2nd instar male of this species remarkably differs from the female in having communal ducts and cluster ducts. Cup-like ducts and other unusual ducts are found in other male Diaspididae. The male test of *Chionaspis alnus* is composed of wax lumps superimposed on a layer of wax filaments; it is possible that the wax lumps are produced by the cup-like ducts and different from the filaments in chemical composition. We need also to know about other components of the test. The agglutinating substance observed on various parts of tests is supposed to be excreted by the anal opening. Then the question may arise how it gets even to the ventral portion of the test (does it simply overflow?).

Lastly, the mechanism of movement in test formation has not been taken into consideration owing to our ignorance on it. The body shape has some concern with it (Takagi and Tippins, 1972). Such external structures as crenulae and spurs may be useful in the movement, but their presence is not universal in the family.

In conclusion, the present work supports the view that in the armoured scale insects characters must have evolved largely in association with test formation. To understand this association may, therefore, be essential for advancing the systematics of this insect group. The present work, however, has approached only a few aspects of the association and raised many questions instead.

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## EXPLANATION OF PLATES

*Ulucoccus gombakensis*. Fig. 1, growing female covered by a mass of filaments ( $\times 150$ ). Fig. 2, wax filaments of female ( $\times 800$ ). Fig. 3, male enclosed by filaments ( $\times 150$ ).

*Megacanthaspis langtangana*. Fig. 4, male and female tests ( $\times 60$ ). Fig. 5, female test, wax filaments on dorsal surface ( $\times 800$ ). Fig. 6, female test, wax filaments on dorsal surface at posterior end of test ( $\times 800$ ).

*Megacanthaspis langtangana*. Fig. 7, female test, inner surface of dorsal portion, posterior end ( $\times 800$ ). Fig. 8, growing female test, inner surface of dorsal portion, posterior end ( $\times 800$ ). Fig. 9, male test, wax filaments on dorsal surface ( $\times 800$ ).

*Megacanthaspis langtangana*. Fig. 10, male test, ventral surface ( $\times 800$ ). Fig. 11, trace of female test on host plant, posterior end ( $\times 800$ ). Fig. 12, filaments in the trace ( $\times 4$  k).

*Nikkoaspis shiranensis*, growing female test. Fig. 13, dorsal view ( $\times 60$ ). Fig. 14, dorsal surface behind 1st exuvial cast, wax secreted by 2nd instar female ( $\times 800$ ). Fig. 15, dorsal surface (posterior to the part in Fig. 14), wax secreted by 2nd instar female ( $\times 800$ ).

*Nikkoaspis shiranensis*, growing female test. Fig. 16, dorsal surface, wax secreted by adult female ( $\times 800$ ). Fig. 17, wax filaments projected posteriorly outside ( $\times 800$ ). Fig. 18, ventral view ( $\times 60$ ).

*Nikkoaspis shiranensis*, growing female test. Fig. 19, ventral view, posterior end ( $\times 800$ ). Fig. 20, ventral view, posterior end (the insect body is a little pulled anteriorly, showing that newly secreted filaments are attached to the test by their posterior ends) ( $\times 800$ ).

*Nikkoaspis shiranensis*. Fig. 21, growing male test, dorsal view ( $\times 100$ ). Fig. 22, growing male test, dorsal surface (median carina at top) ( $\times 800$ ). Fig. 23, male test, inner surface of dorsal portion ( $\times 800$ ).

*Chionaspis alnus*, female test. Fig. 24, dorsal surface ( $\times 200$ ). Fig. 25, dorsal surface, posterior end ( $\times 800$ ).

*Chionaspis alnus*, female test. Fig. 26, dorsal surface ( $\times 800$ ). Fig. 27, ditto ( $\times 3$  k).

*Chionaspis alnus*, female test. Fig. 28, inner surface of dorsal portion, middle area ( $\times 800$ ). Fig. 29, ditto ( $\times 3$  k).

*Chionaspis alnus*, female test. Fig. 30, inner surface of dorsal portion, near posterior end ( $\times 800$ ). Fig. 31, inner surface of dorsal portion, posterior end ( $\times 800$ ).

*Chionaspis alnus*, female test. Fig. 32, outer surface of ventral portion, median area ( $\times 800$ ). Fig. 33, ditto ( $\times 3$  k).

*Chionaspis alnus*, male test. Fig. 34, dorsal view ( $\times 100$ ). Fig. 35, ditto (median carina above) ( $\times 800$ ).

*Chionaspis alnus*, male test. Fig. 36, dorsal view (median carina at top) ( $\times 800$ ). Fig. 37, ditto (lateral margin at bottom) ( $\times 800$ ).

*Chionaspis alnus*, male test treated with chloroform for one day. Fig. 38, dorsal surface (median carina above) ( $\times 800$ ). Fig. 39, ditto (median carina) ( $\times 3$  k). Fig. 40, ditto (part lateral to median carina) ( $\times 3$  k).

*Chionaspis alnus*, male test. Fig. 41, inner surface of dorsal portion, middle area ( $\times 800$ ). Fig. 42, ditto ( $\times 3$  k).

*Chionaspis alnus*, male test. Fig. 43, inner surface of ventral portion ( $\times 800$ ). Fig. 44,

outer surface of ventral portion ( $\times 800$ ).

*Pseudaulacaspis prunicola*, growing female test. Fig. 45, inner surface ( $\times 80$ ). Fig. 46, ditto, margin ( $\times 800$ ).

*Pseudaulacaspis prunicola*, nearly completed female test (on *Prunus mume*). Fig. 47, inner surface, margin ( $\times 800$ ). Fig. 48, ditto ( $\times 800$ ).

*Pseudaulacaspis prunicola*. Fig. 49, growing female test, inner surface (2nd exuvial cast in the lower right corner) ( $\times 800$ ). Fig. 50, site of a growing female on bark (the test and insect removed) ( $\times 80$ ).

*Pseudaulacaspis prunicola*, wax filaments on growing site (Fig. 50). Fig. 51, around insertion of rostralis ( $\times 800$ ). Fig. 52, in another area ( $\times 800$ ). Fig. 53, part more distant ( $\times 800$ ).

*Pseudaulacaspis prunicola*, test formed by 2nd instar female. Fig. 54, ventral view ( $\times 150$ ). Fig. 55, ditto, part adjoining 1st exuvial cast ( $\times 800$ ). Fig. 56, ditto, margin ( $\times 800$ ).

*Pseudaulacaspis prunicola*, growing 1st instar female. Fig. 57 and Fig. 58, showing different stages ( $\times 200$ ).

*Pseudaulacaspis prunicola*, growing 1st instar female. Fig. 59, head ( $\times 800$ ). Fig. 60, wax filaments over abdomen ( $\times 800$ ).

*Pseudaulacaspis prunicola*, male test. Fig. 61, dorsal view ( $\times 80$ ). Fig. 62, ditto, marginal area (lateral margin at top) ( $\times 800$ ). Fig. 63, ditto, mid-dorsal area ( $\times 800$ ).

*Pseudaulacaspis prunicola*, male test. Fig. 64, ventral view ( $\times 80$ ). Fig. 65, ditto, below 1st exuvial cast ( $\times 800$ ). Fig. 66, ditto, marginal area ( $\times 800$ ).

*Pseudaulacaspis prunicola*, male test. Fig. 67, ventral surface ( $\times 800$ ). Fig. 68, test opened to show inner surfaces of dorsal and ventral portions ( $\times 80$ ).

*Pseudaulacaspis prunicola*, male test. Fig. 69, inner surfaces of dorsal and ventral portions, marginal areas (dorsal portion above) ( $\times 800$ ). Fig. 70, inner surface of dorsal portion ( $\times 800$ ).

*Pseudaulacaspis prunicola*, male test. Fig. 71, inner surface of ventral portion ( $\times 800$ ). Fig. 72, ditto, near posterior end ( $\times 800$ ).

*Thysanaspis perkinsi*, male test. Fig. 73, dorsal view ( $\times 100$ ). Fig. 74, wax filaments on dorsal surface ( $\times 800$ ). Fig. 75, wax filaments on ventral surface ( $\times 800$ ).

*Thysanaspis perkinsi*, male test. Fig. 76, inner surface of dorsal portion ( $\times 800$ ). Fig. 77, ditto, near posterior end ( $\times 800$ ).

*Lopholeucaspis japonica*, female test, under construction by 2nd instar. Fig. 78, dorsal view ( $\times 80$ ). Fig. 79, wax filaments on anterior end of test ( $\times 800$ ). Fig. 80, wax filaments crossing 1st exuvial cast ( $\times 800$ ).

*Lopholeucaspis japonica*, female test, under construction by 2nd instar. Fig. 81, dorsal surface ( $\times 800$ ). Fig. 82, ditto, near posterior end ( $\times 800$ ).

*Lopholeucaspis japonica*, female test formed by 2nd instar. Fig. 83, ventral view ( $\times 80$ ). Fig. 84, inner surface of dorsal portion, near posterior end ( $\times 800$ ). Fig. 85, inner surface of dorsal portion, middle area ( $\times 800$ ).

*Lopholeucaspis japonica*, male test. Fig. 86, inner surface of dorsal portion, near posterior end ( $\times 800$ ). Fig. 87, inner surface of dorsal portion, middle area ( $\times 800$ ).

*Parlatoria abieticola*, growing female test. Fig. 88, dorsal surface (with hyphae of a fungus crossing) ( $\times 800$ ). Fig. 89, inner surface of dorsal portion ( $\times 800$ ). Fig. 90, ditto, marginal area ( $\times 800$ ).

*Parlatoria abieticola*. Fig. 91, growing female test, outer surface of ventral portion, below 2nd exuvial cast ( $\times 800$ ). Fig. 92, growing female test, outer surface of ventral portion ( $\times 800$ ). Fig. 93, male test, inner surface of dorsal portion, near posterior end ( $\times 800$ ).

*Parlatoria abieticola*, male test. Fig. 94, inner surface of dorsal portion, part somewhat anterior to Fig. 93 ( $\times 800$ ). Fig. 95, inner surface of dorsal portion, middle area ( $\times 800$ ). Fig. 96, filaments left in test site on leaf (lateral margin of the site at bottom) ( $\times 800$ ).

*Microparlatoria itabicola*, female test. Fig. 97, dorsal view (1st exuvial cast with the ventral surface turned up) ( $\times 100$ ). Fig. 98, dorsal surface ( $\times 800$ ).

*Microparlatoria itabicola*, female test. Fig. 99, dorsal surface ( $\times 3$  k). Fig. 100, ditto, posterior end ( $\times 3$  k).

*Microparlatoria itabicola*, female test treated with chloroform for one night. Fig. 101, dorsal surface ( $\times 3$  k). Fig. 102, ditto ( $\times 15$  k).

*Microparlatoria itabicola*, female test. Fig. 103, dorsal surface of 2nd exuvial cast (1st exuvial cast removed) ( $\times 300$ ). Fig. 104, ventral surface of 1st exuvial cast ( $\times 800$ ).

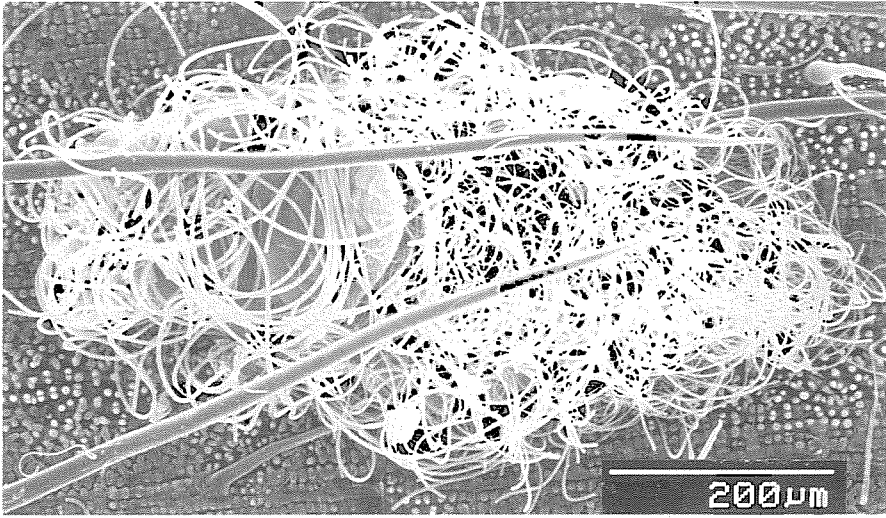
*Microparlatoria itabicola*, female test. Fig. 105, inner surface of dorsal portion, middle area ( $\times 3$  k). Fig. 106, inner surface of dorsal portion, posterior area ( $\times 3$  k). Fig. 107, inner surface of dorsal portion, near posterior end ( $\times 3$  k).

*Microparlatoria itabicola*, male test. Fig. 108, dorsal surface ( $\times 3$  k). Fig. 109, ditto, posterior end ( $\times 3$  k).

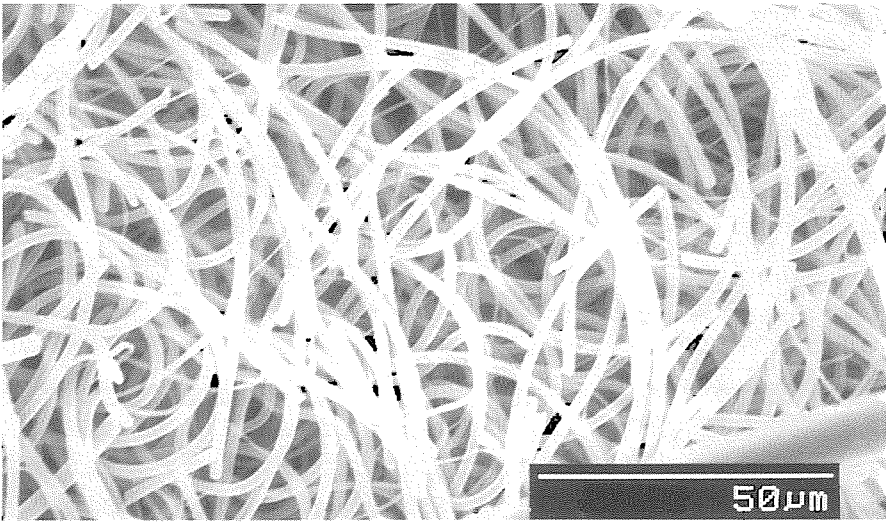
*Microparlatoria itabicola*, male test. Fig. 110, inner surface of dorsal portion, middle area ( $\times 3$  k). Fig. 111, inner surface of dorsal portion, near posterior end ( $\times 3$  k).

*Pseudaonidia paeoniae*, female test. Fig. 112, dorsal surface, marginal area ( $\times 800$ ). Fig. 113, inner surface of dorsal portion, submarginal area ( $\times 800$ ). Fig. 114, inner surface of dorsal portion, marginal area ( $\times 800$ ).

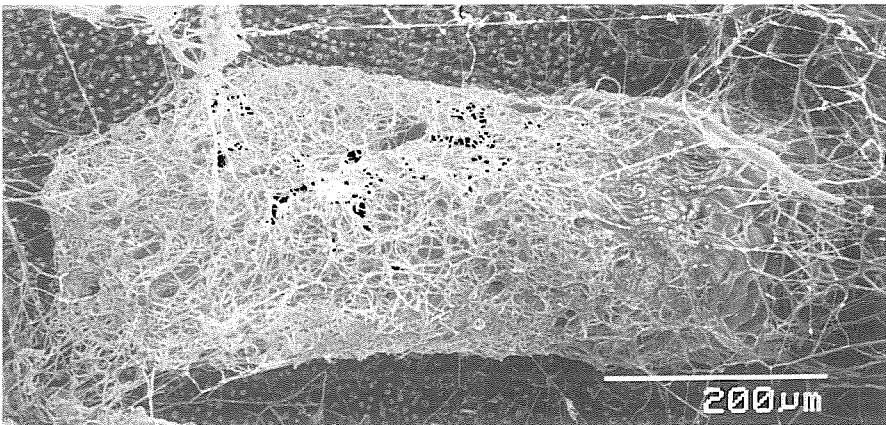
*Pseudaonidia paeoniae*. Fig. 115, female test, inner surface of dorsal portion, central area ( $\times 800$ ). Fig. 116, male test, dorsal view ( $\times 80$ ). Fig. 117, male test, inner surface of dorsal portion ( $\times 800$ ).



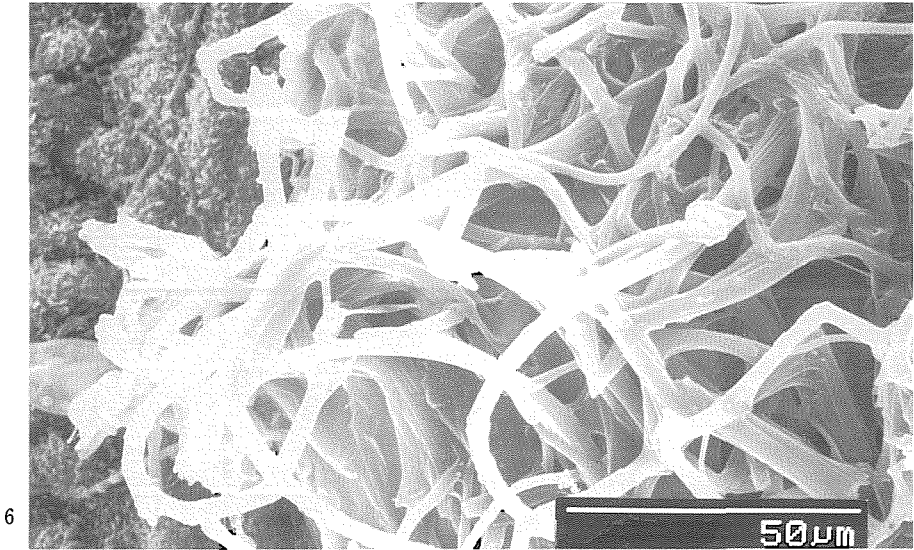
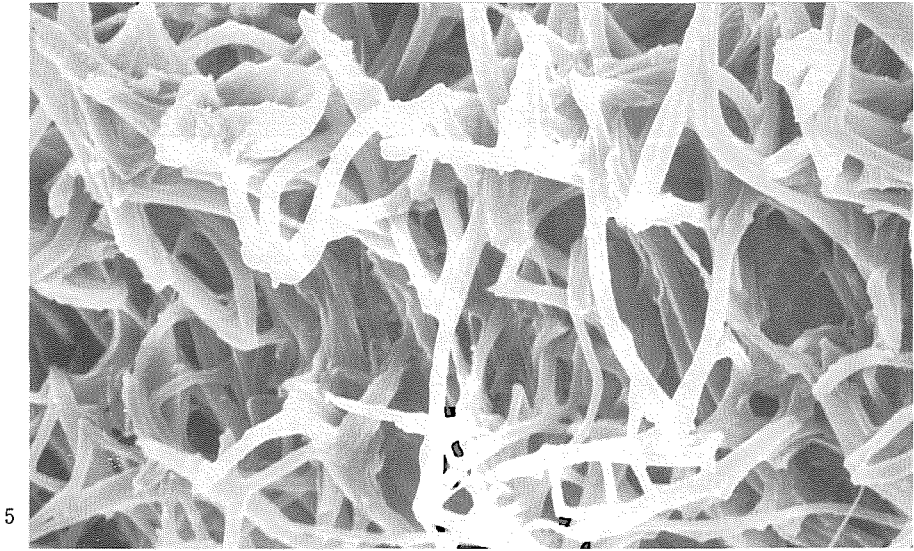
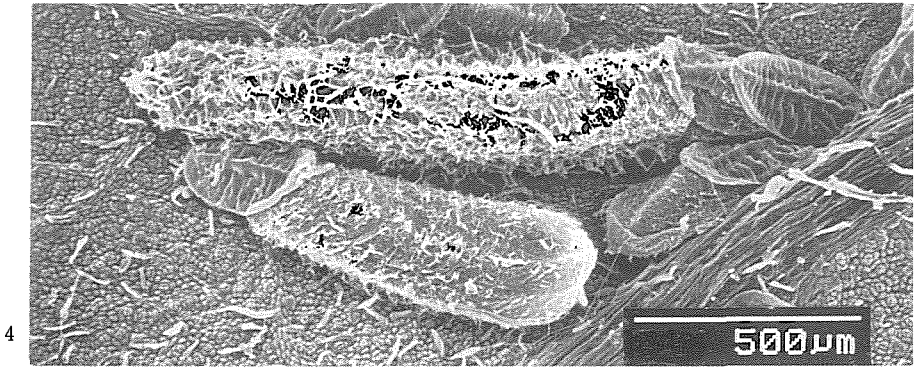
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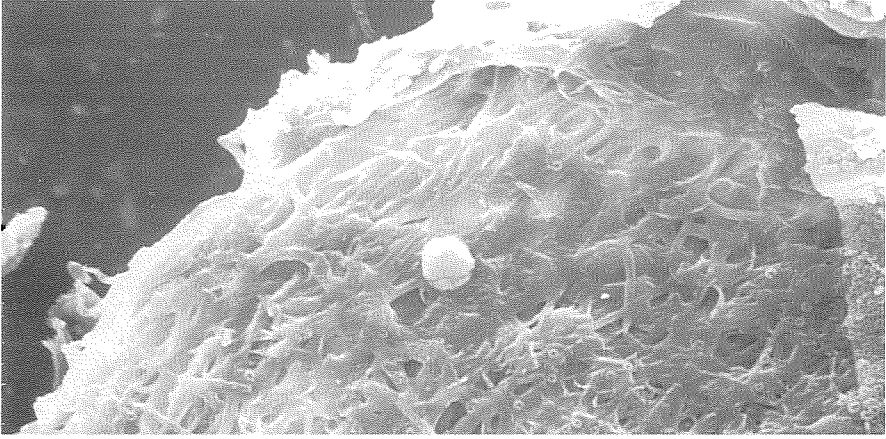


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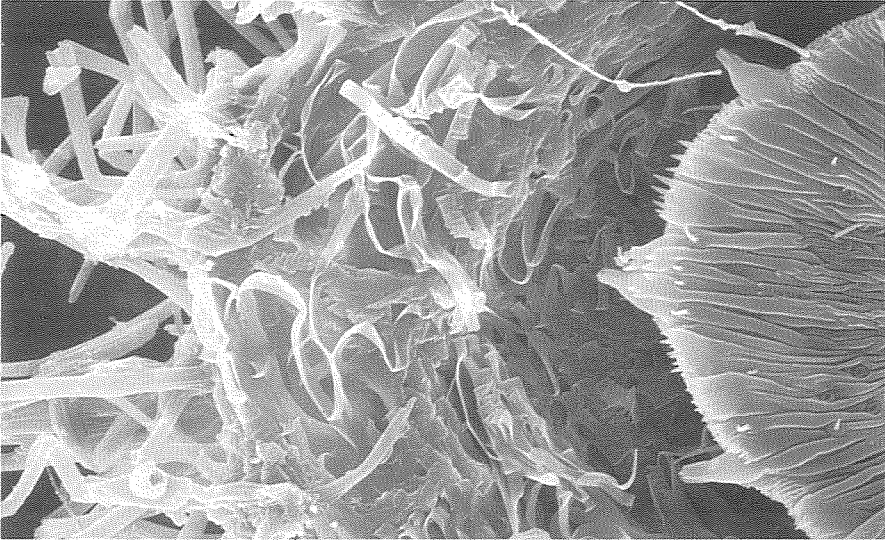


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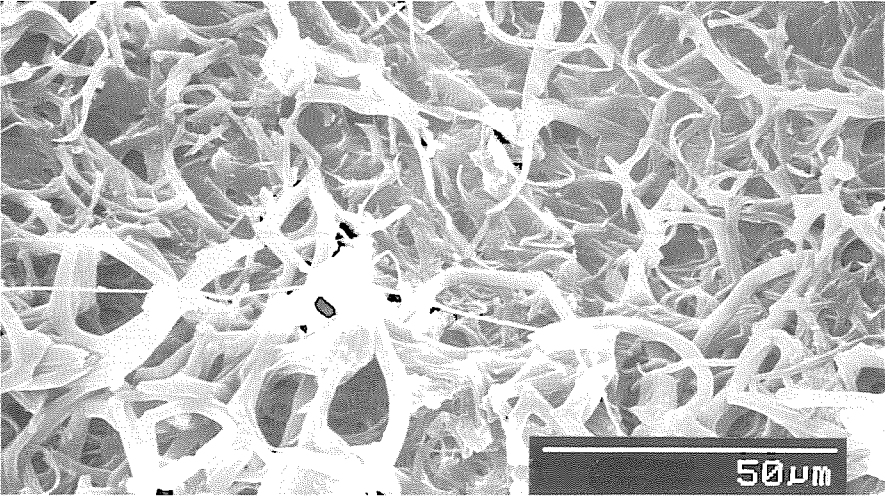




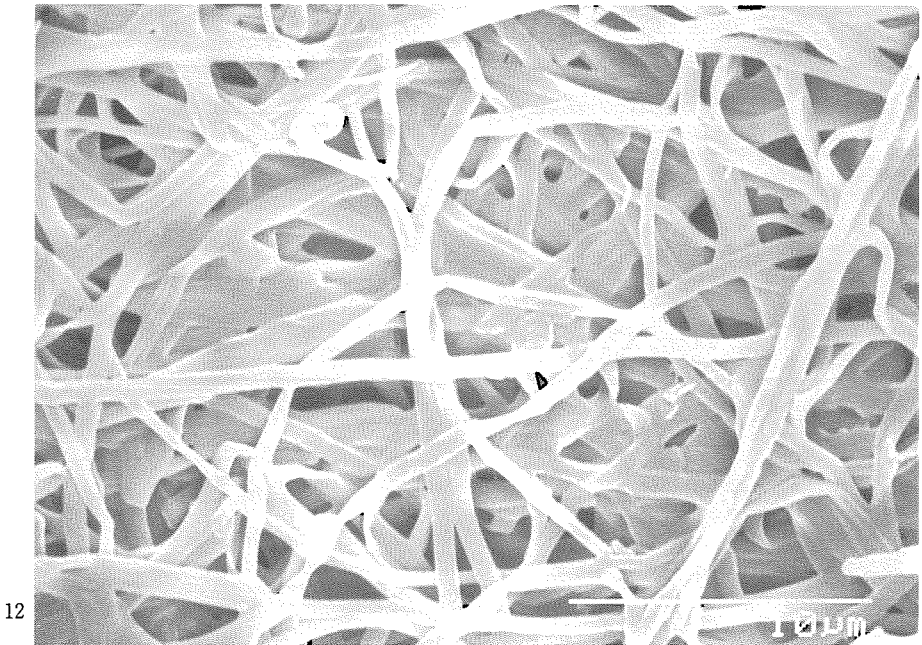
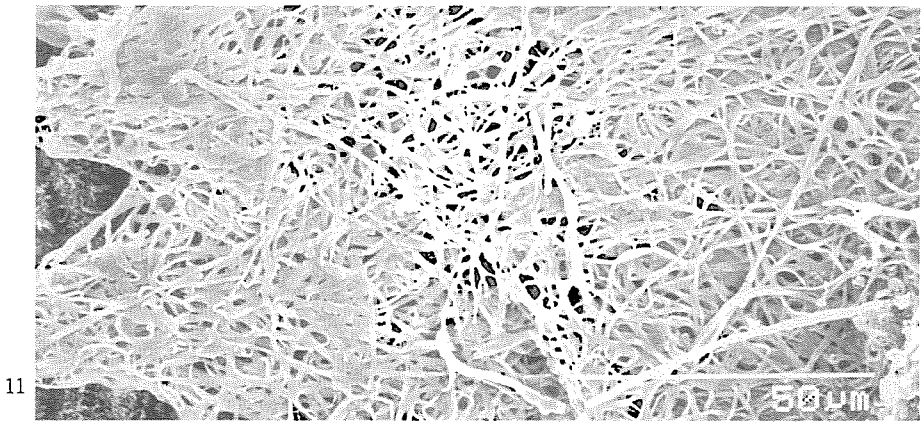
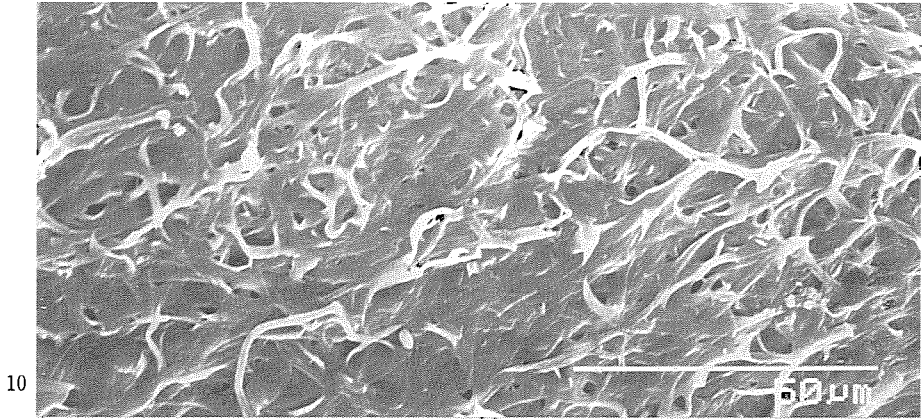
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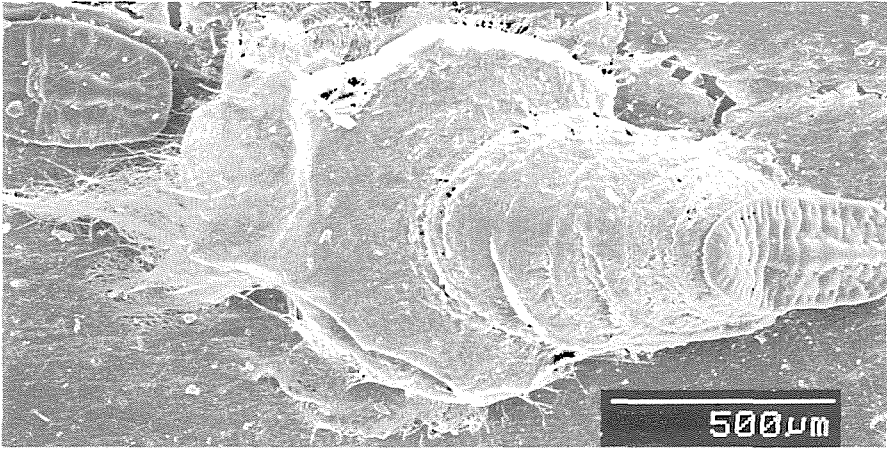


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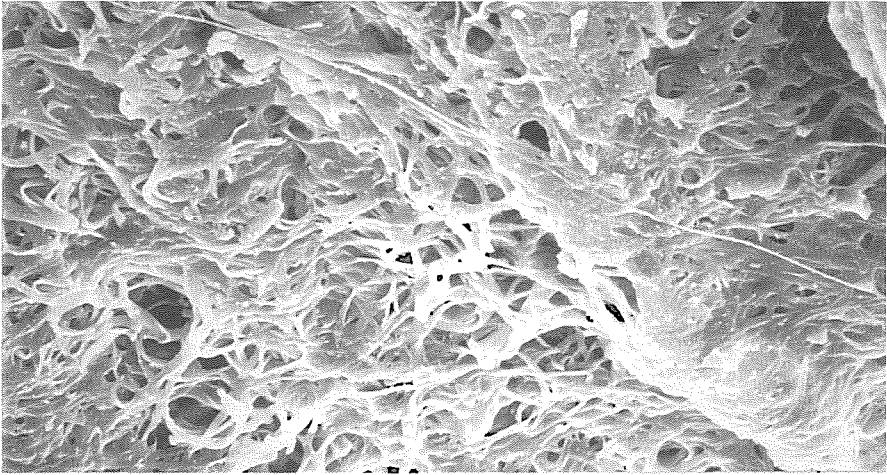


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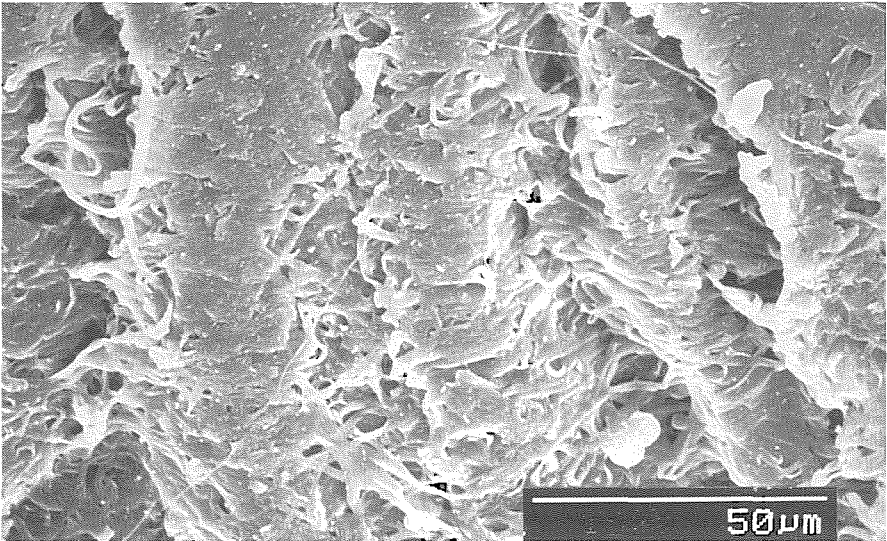




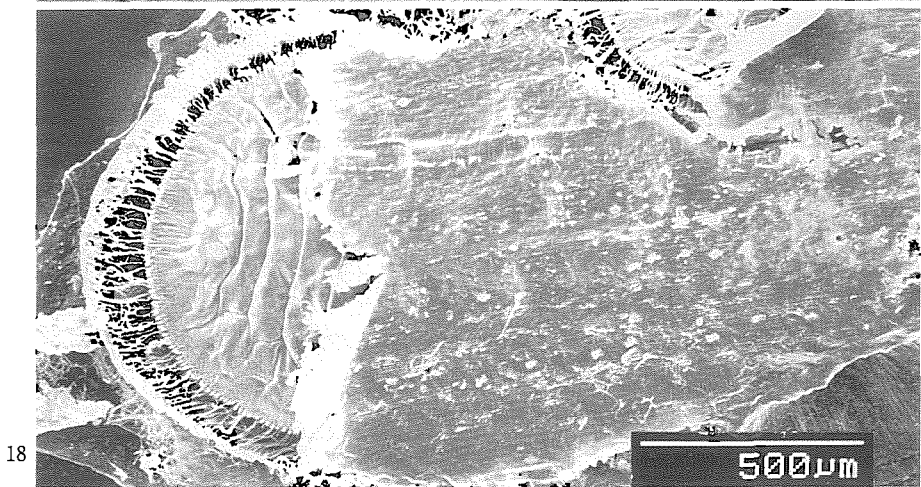
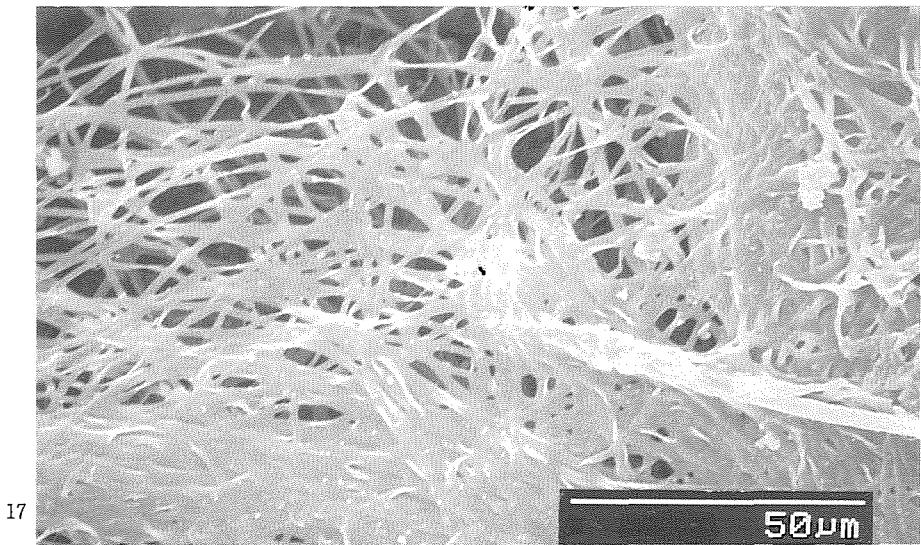
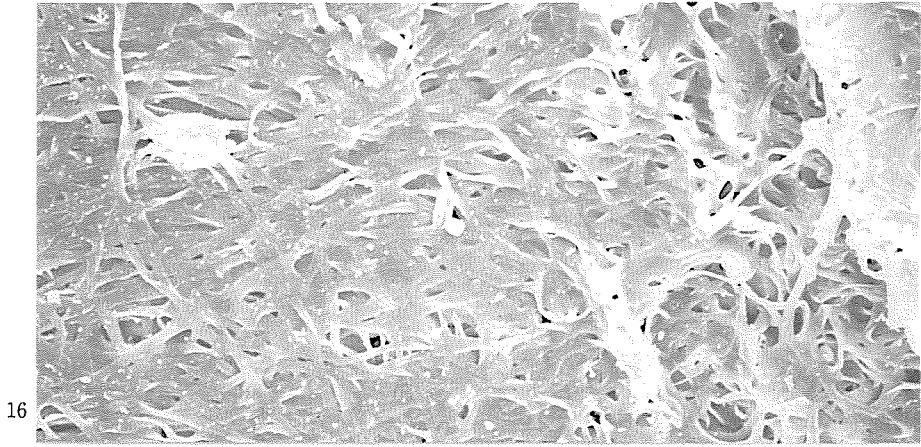
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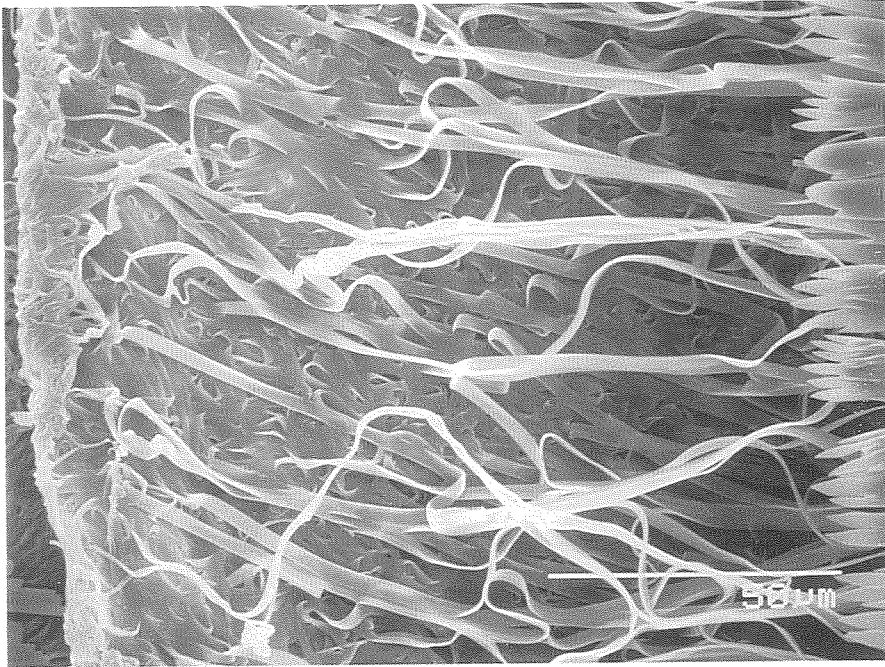


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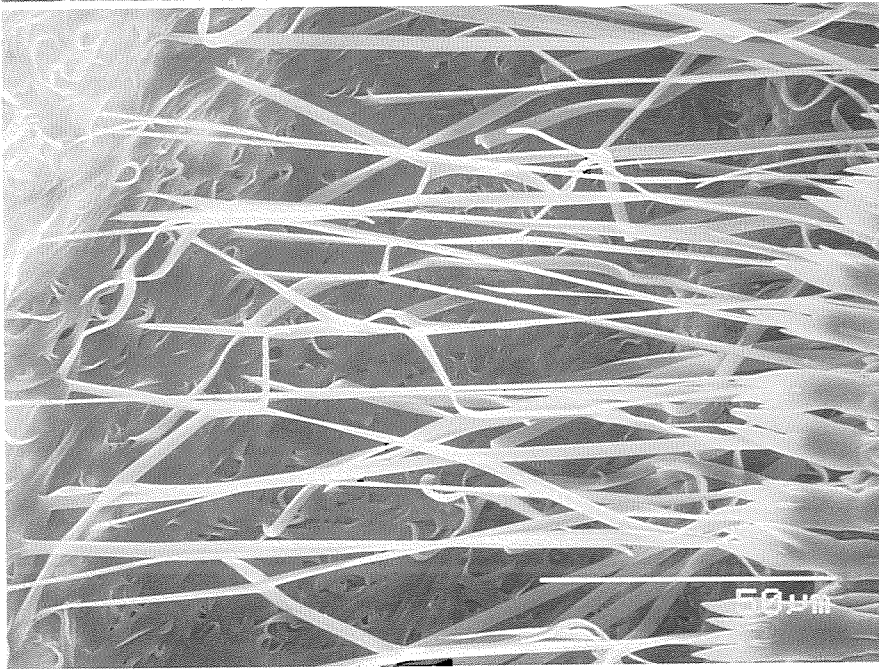


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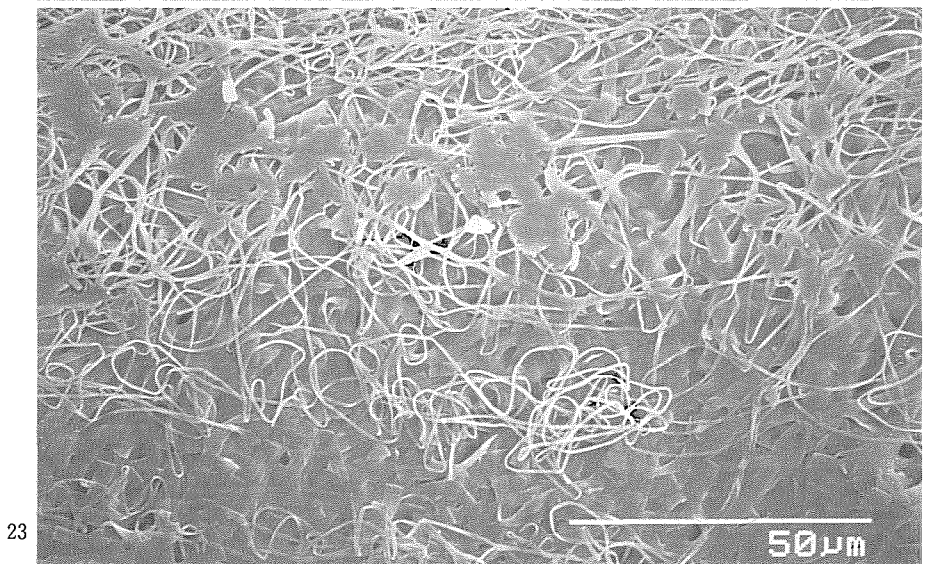
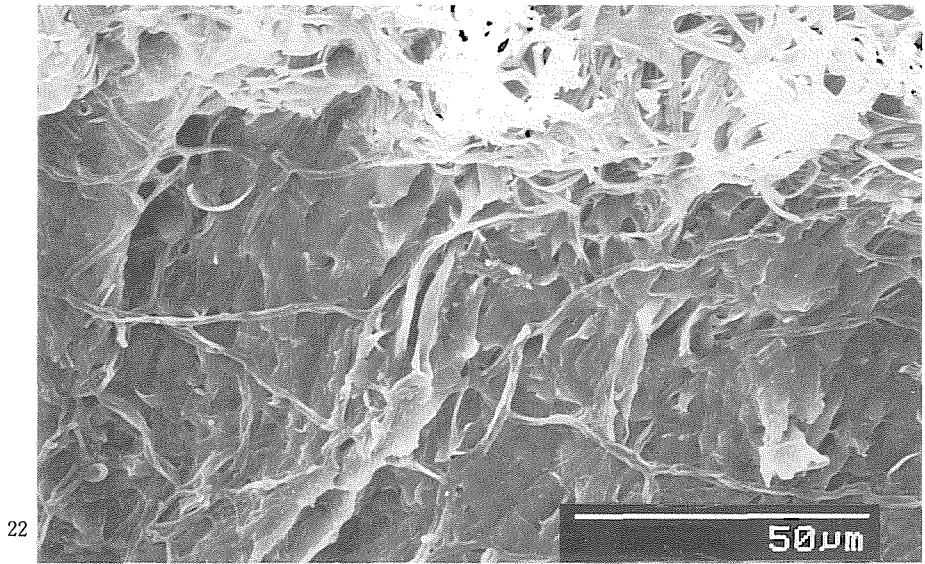
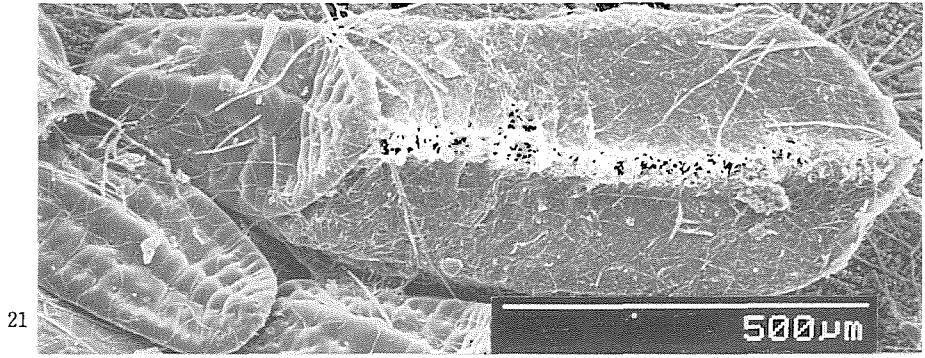


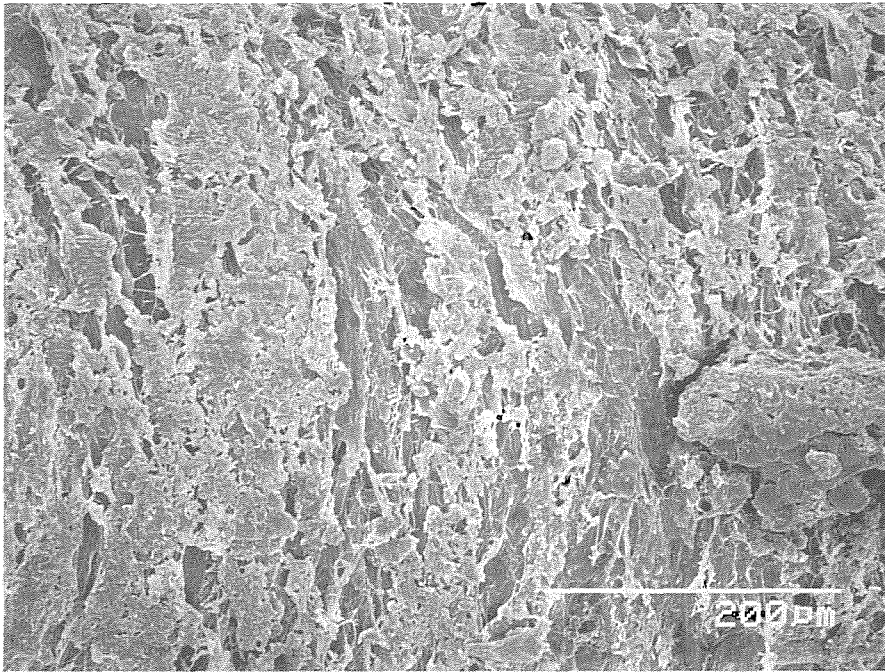


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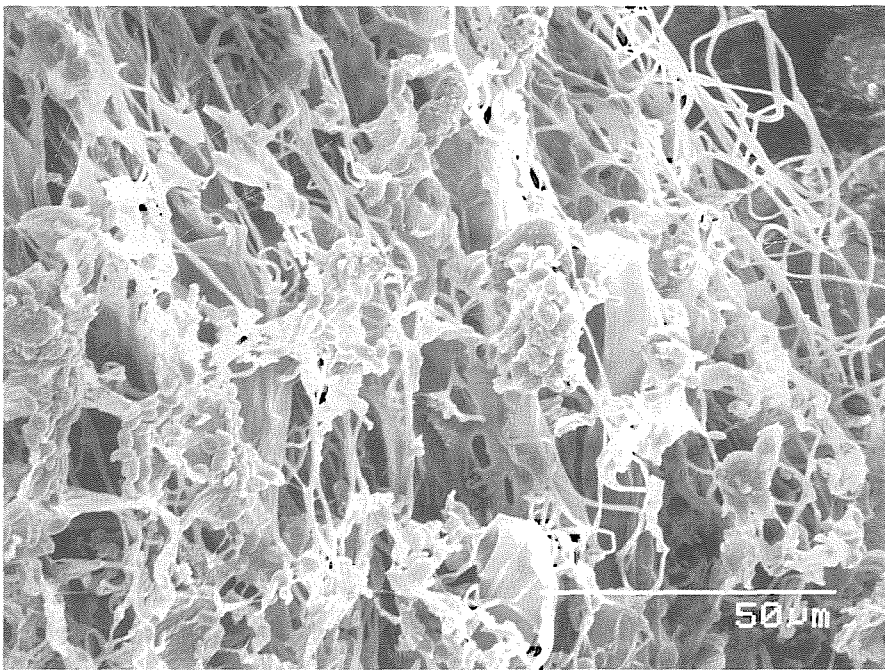


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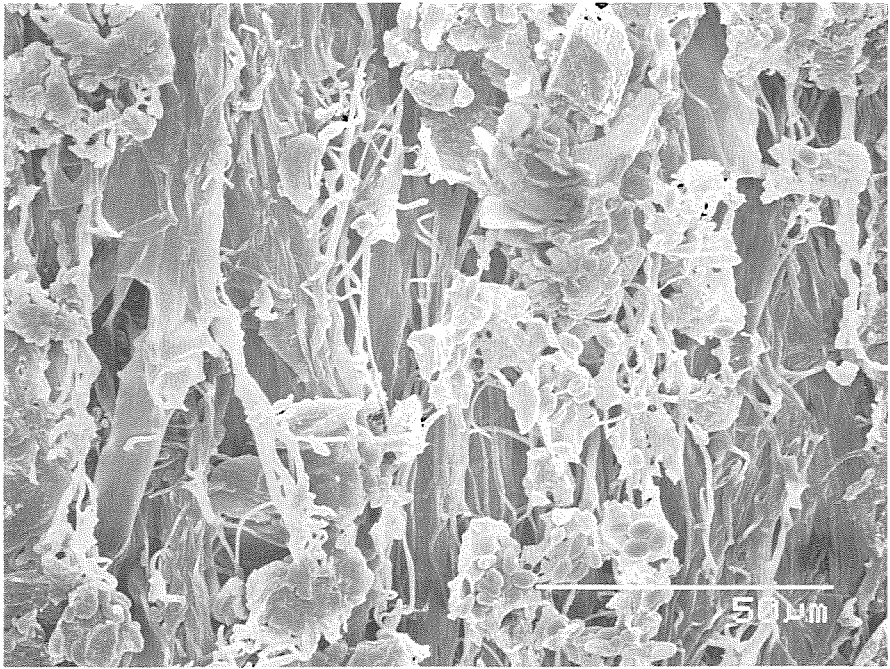


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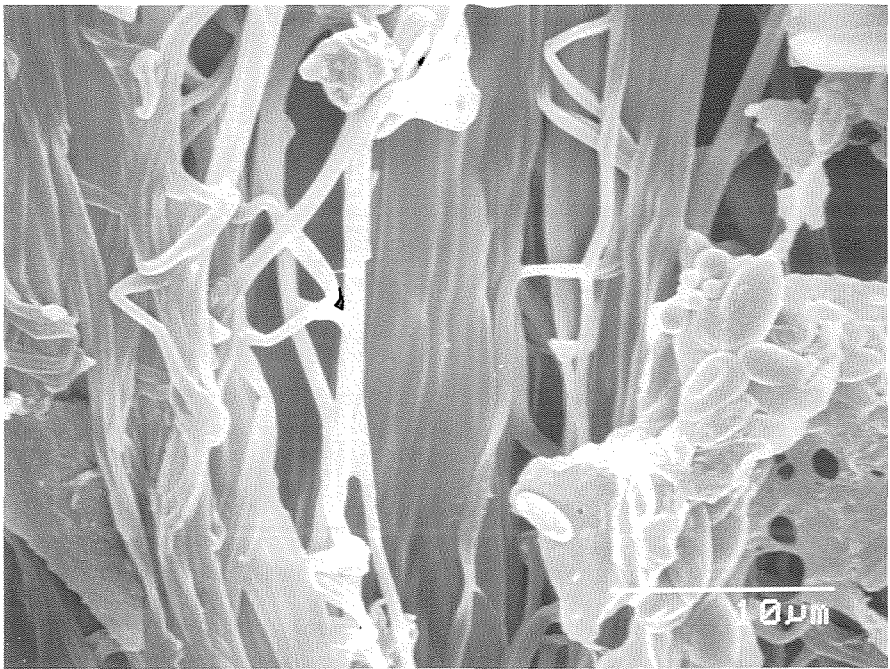


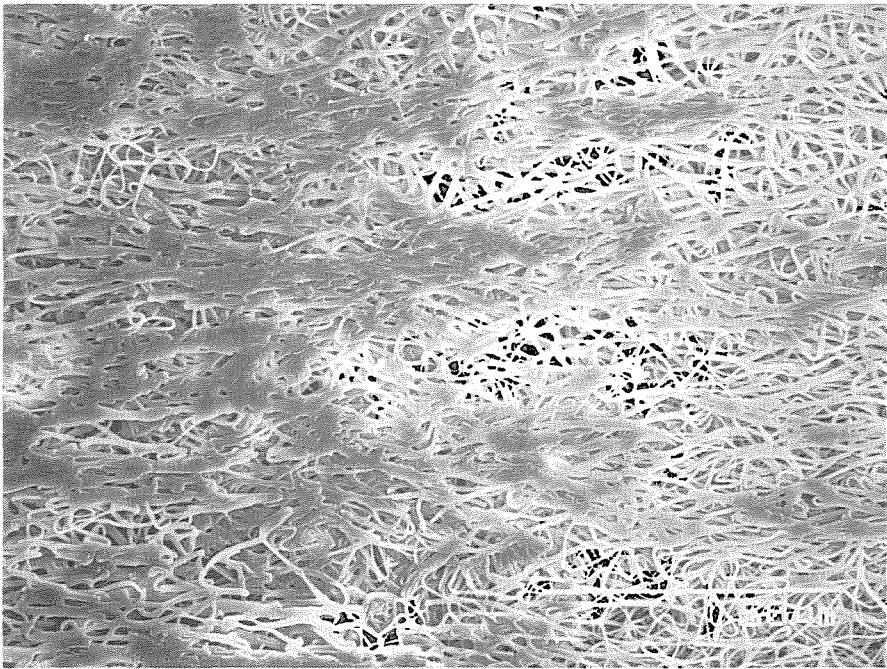
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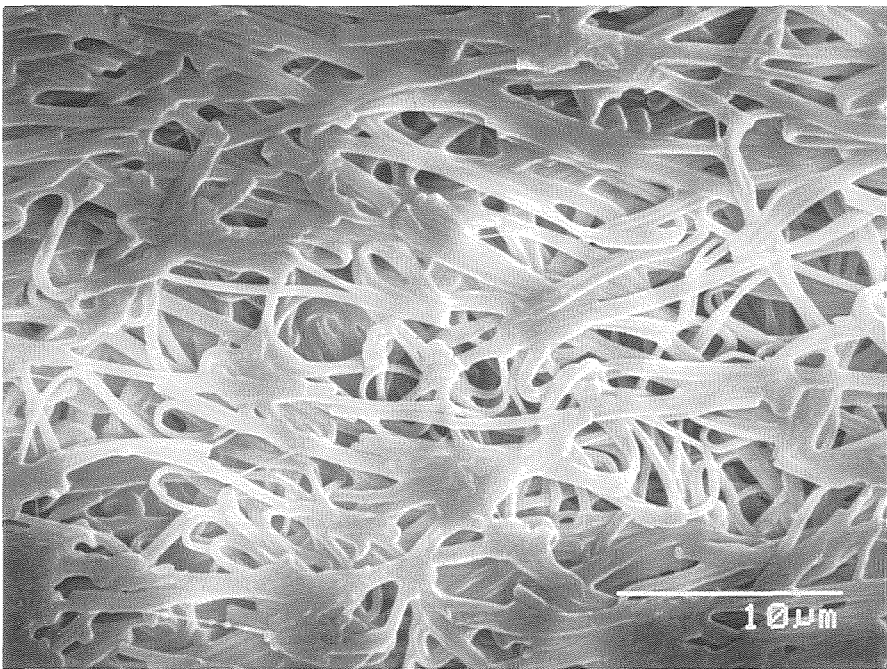


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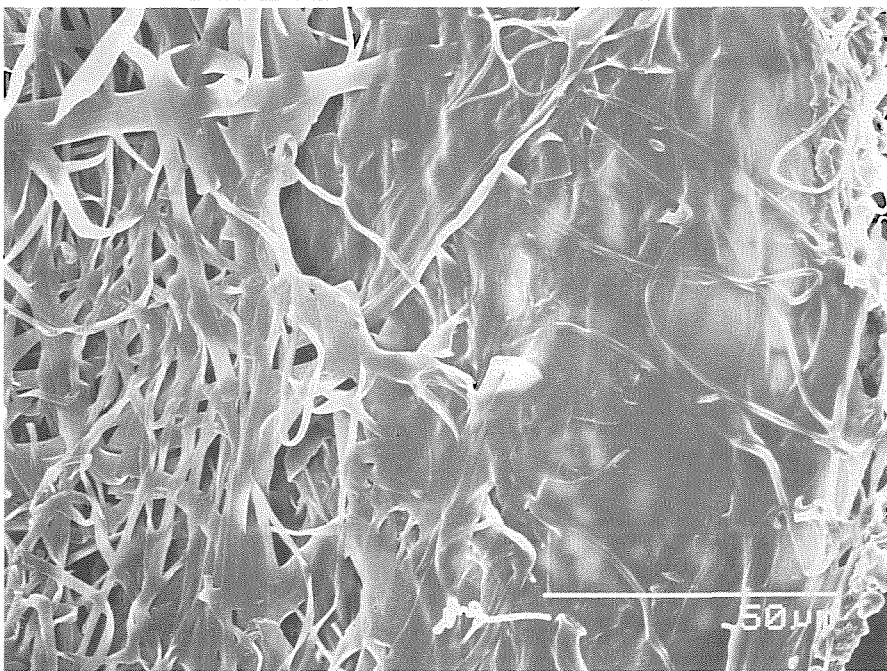
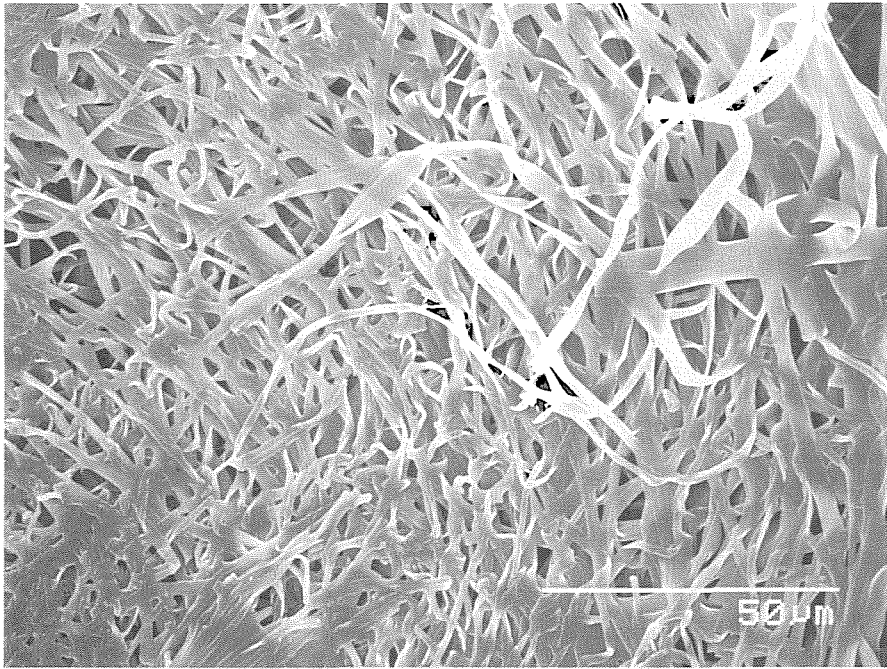


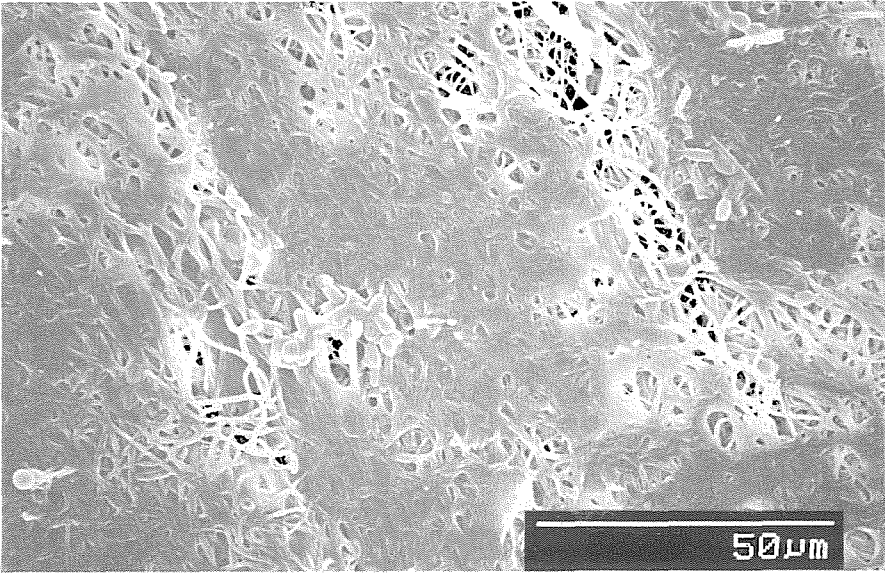


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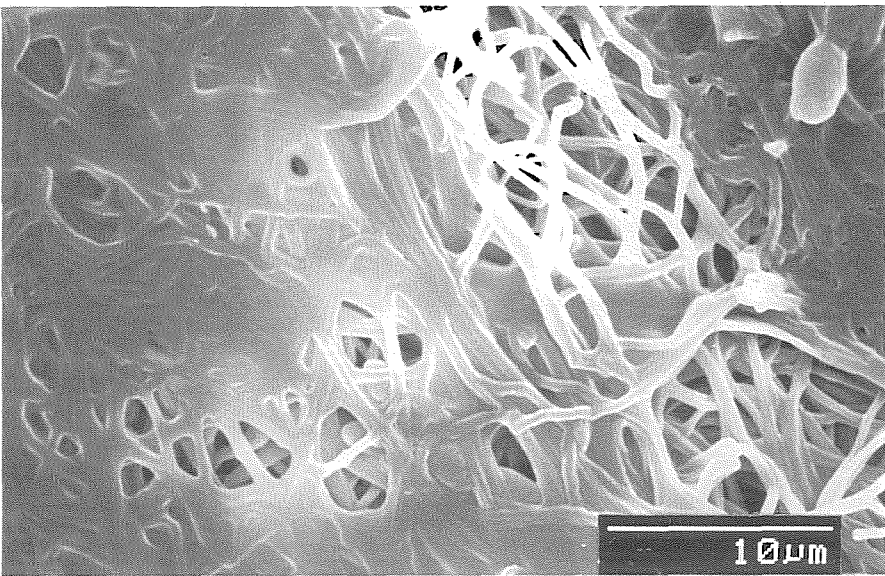


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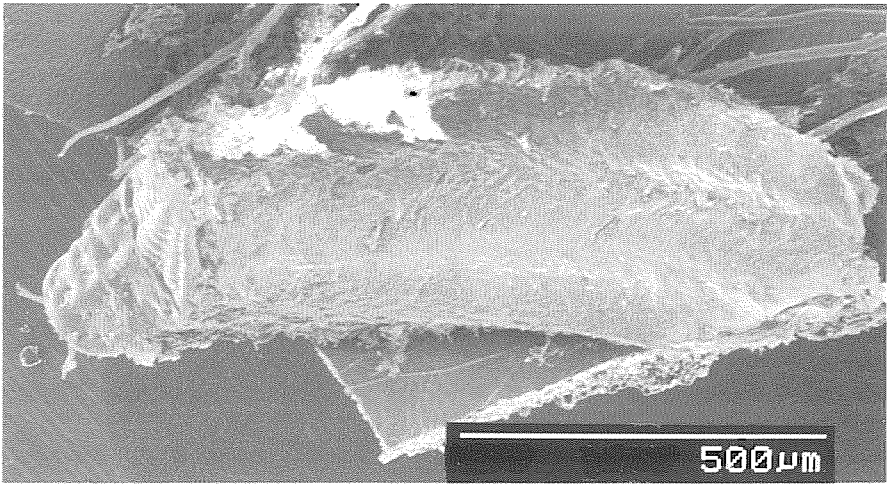




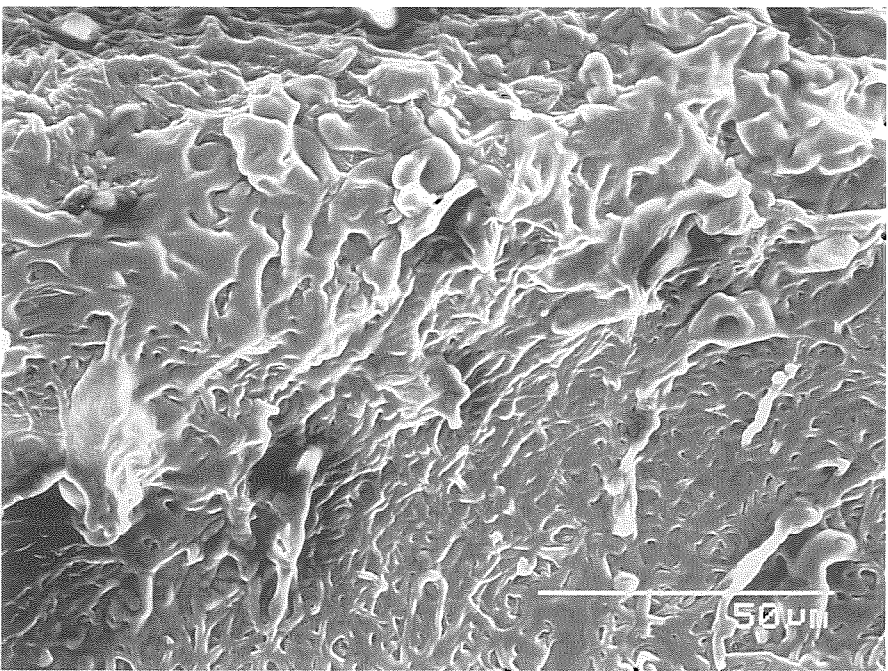
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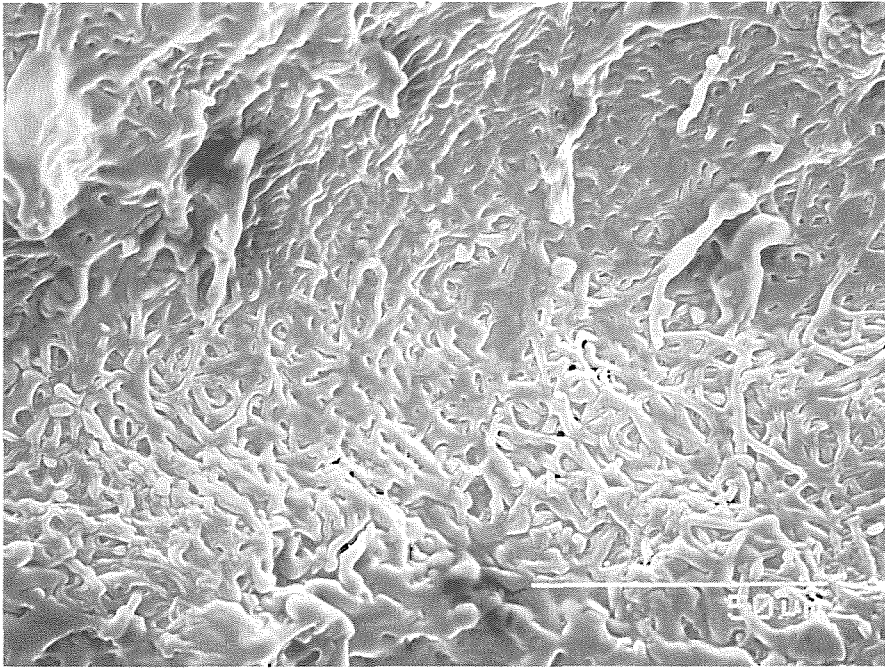
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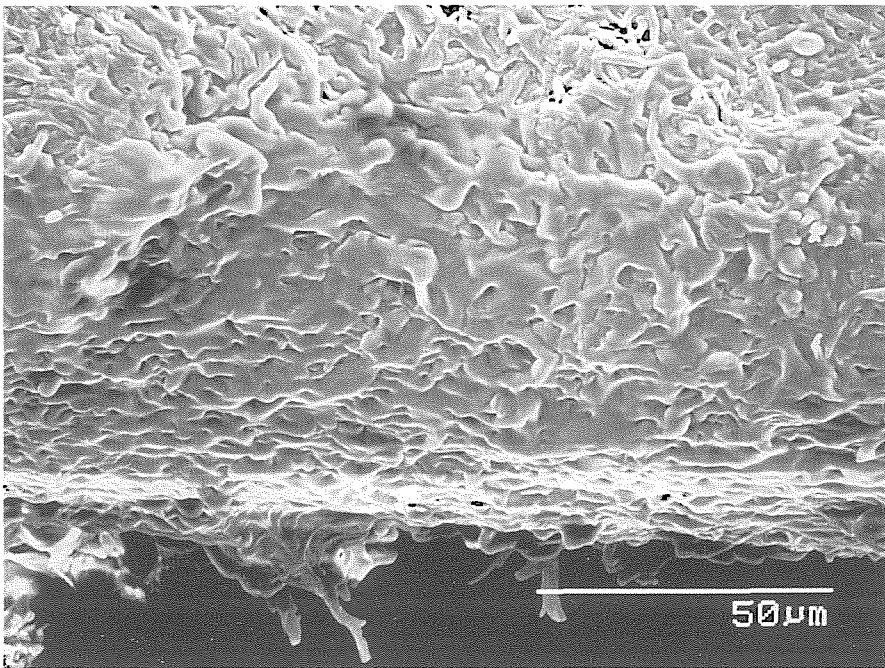
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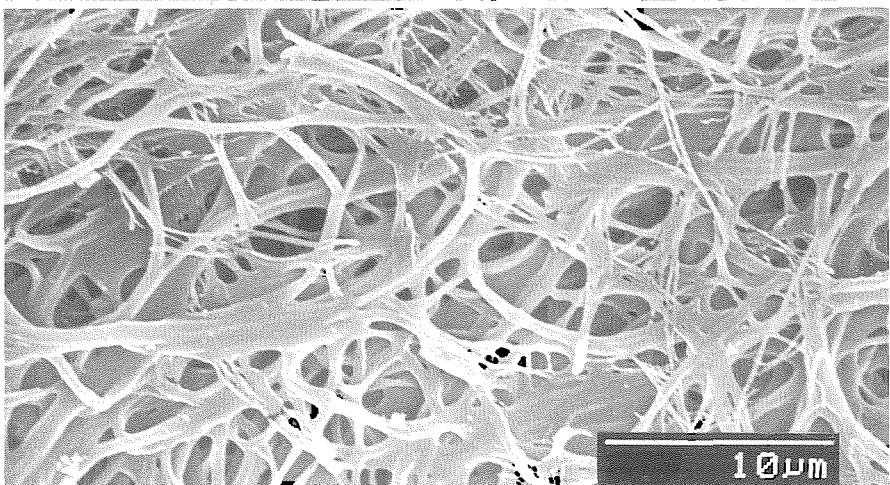
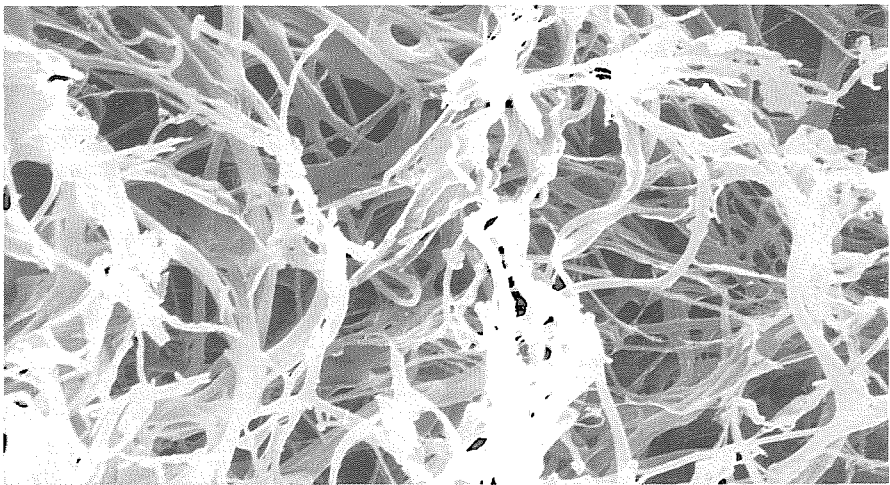
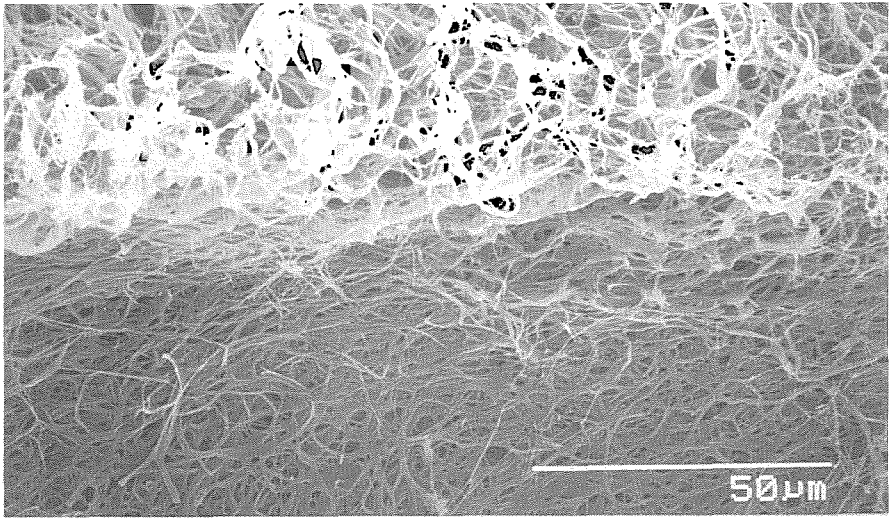
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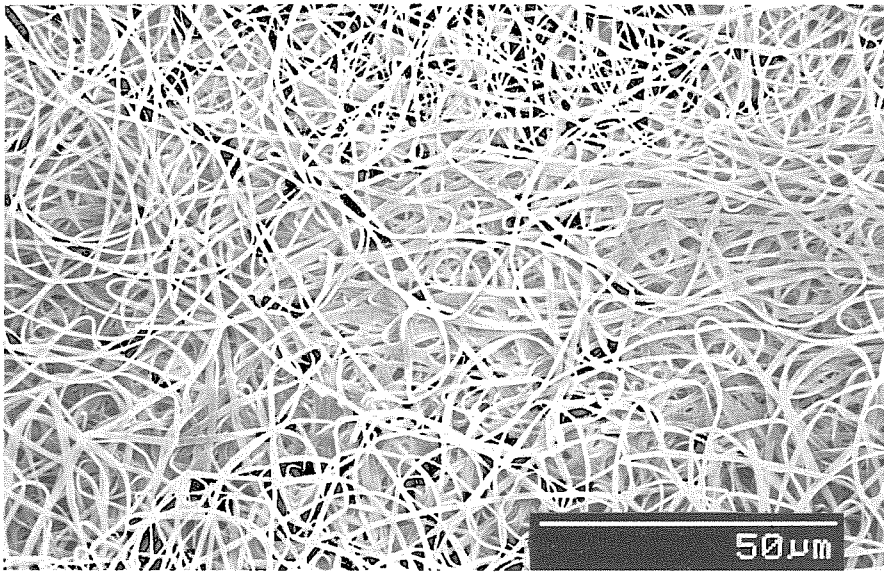


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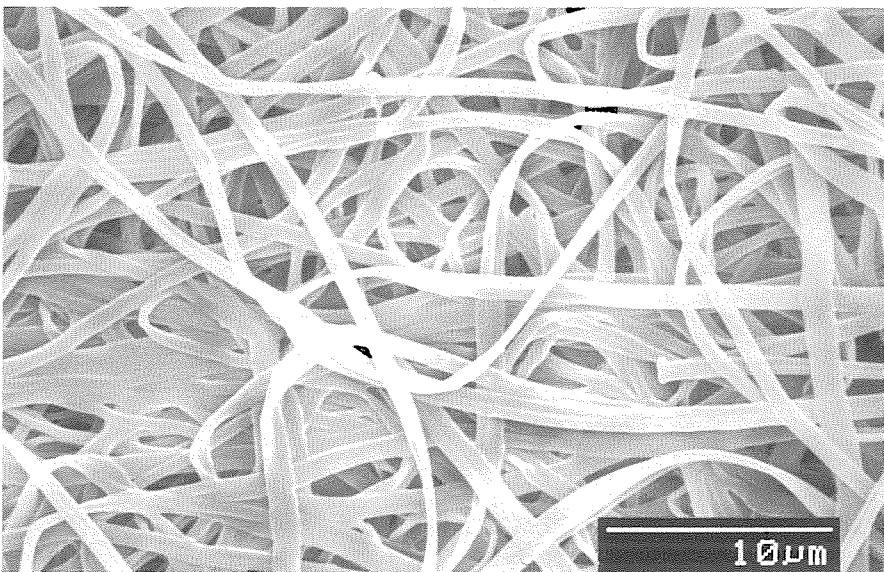


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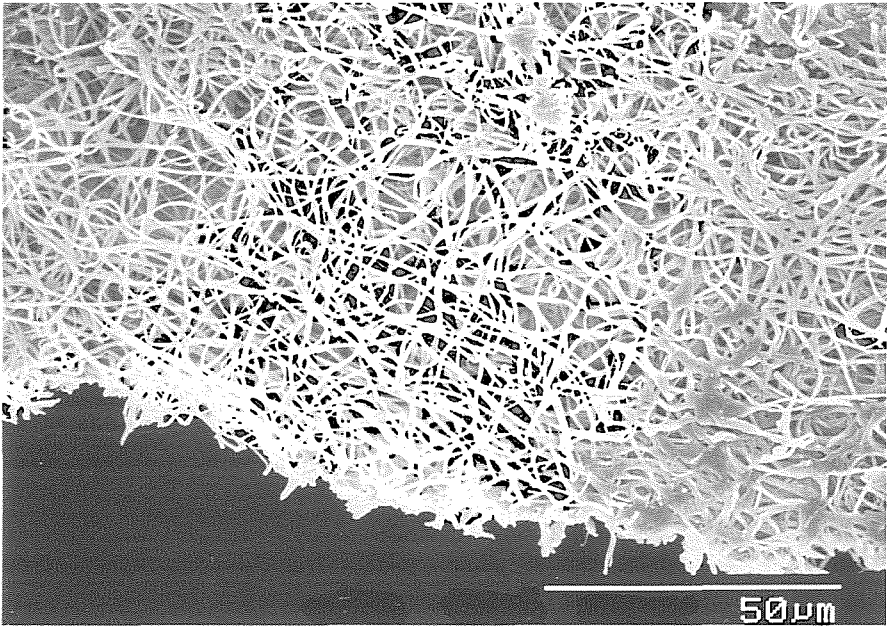




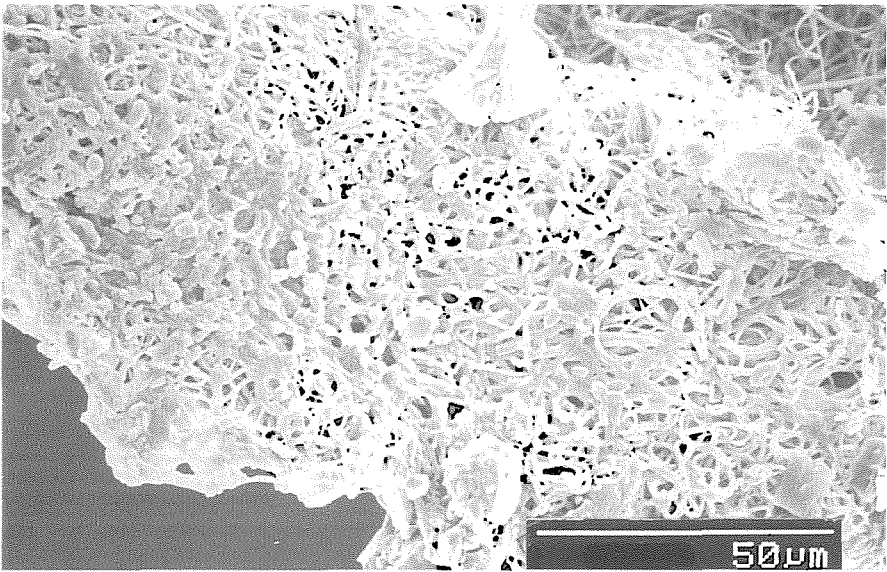
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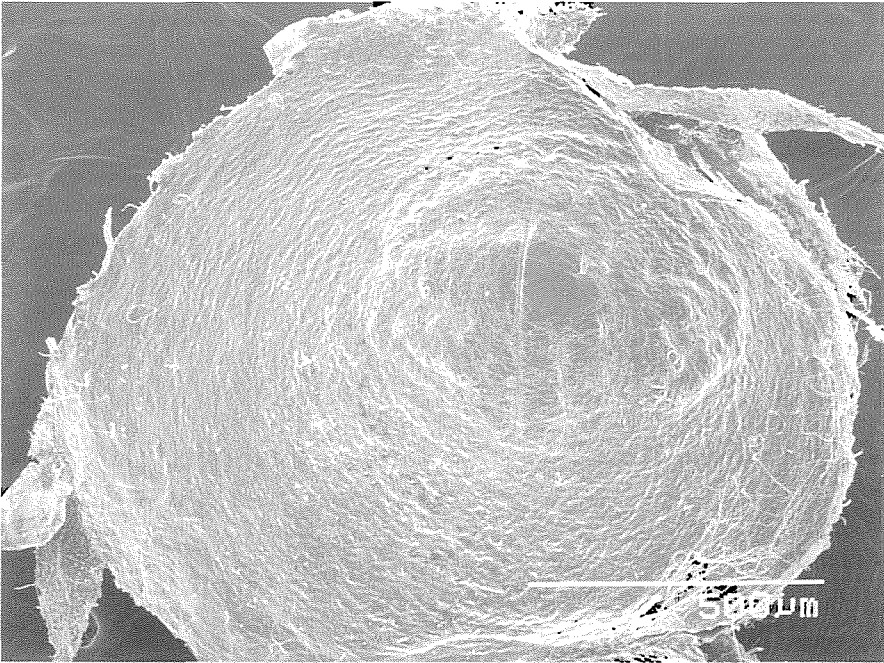
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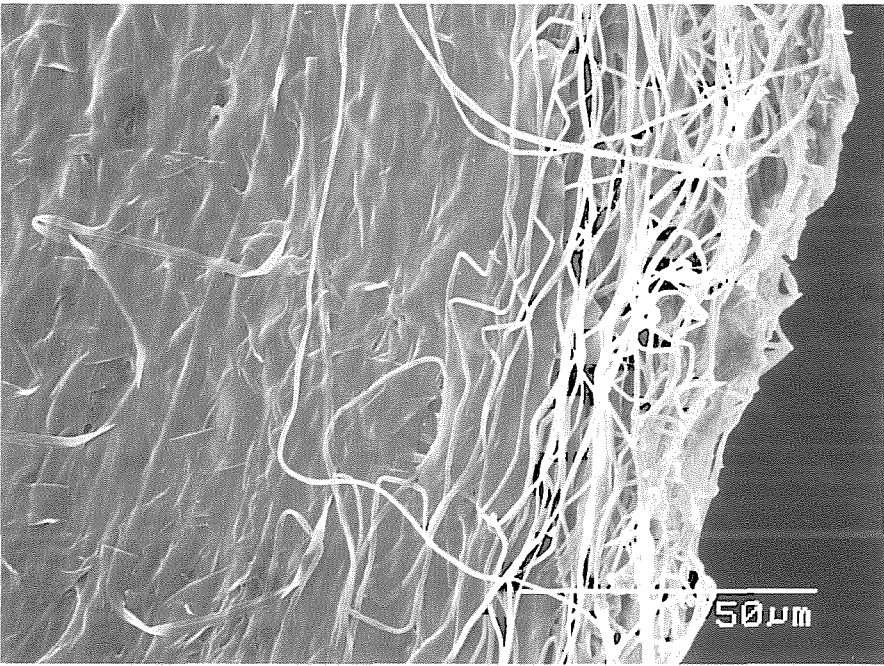
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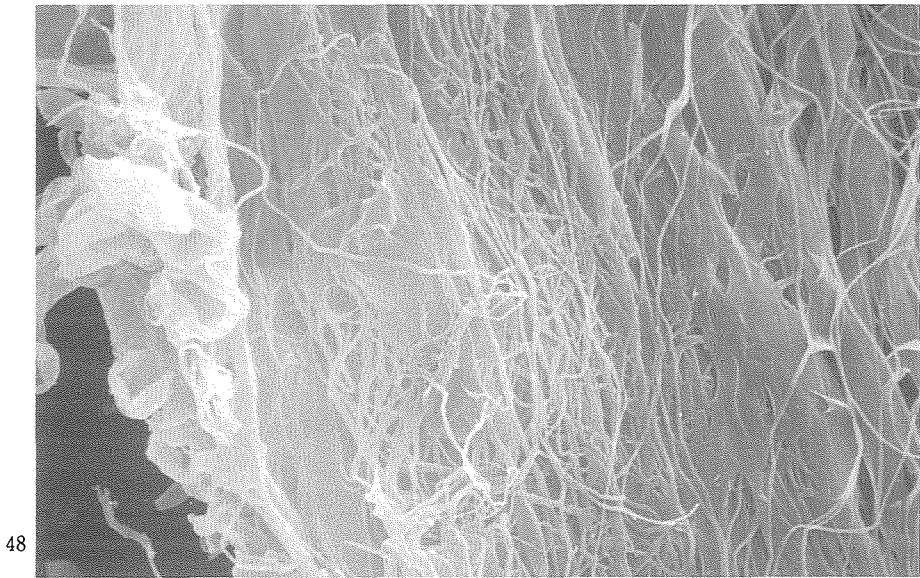
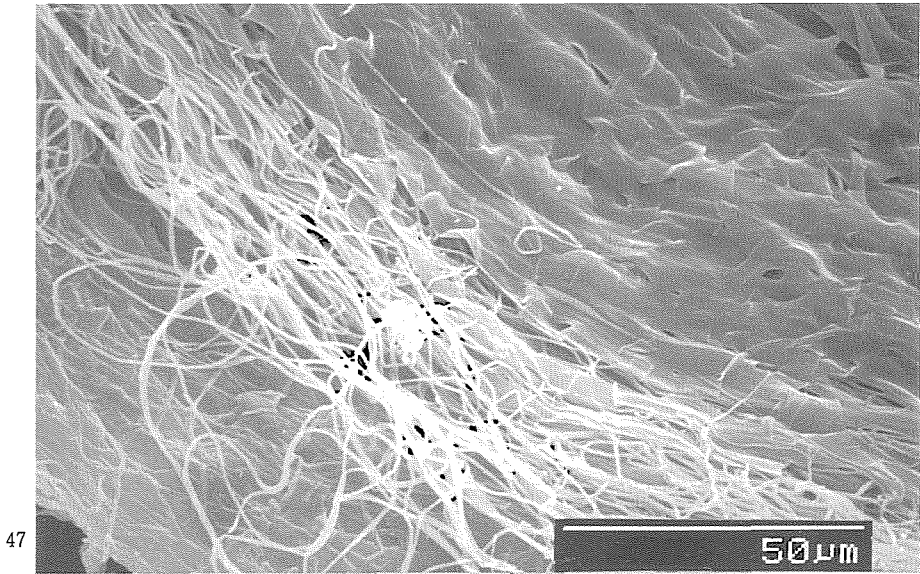
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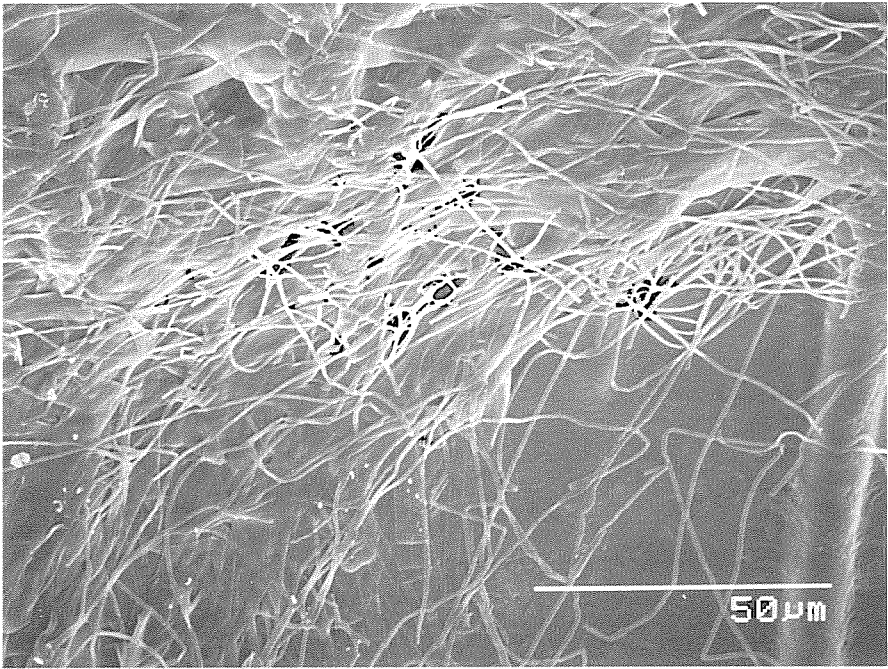


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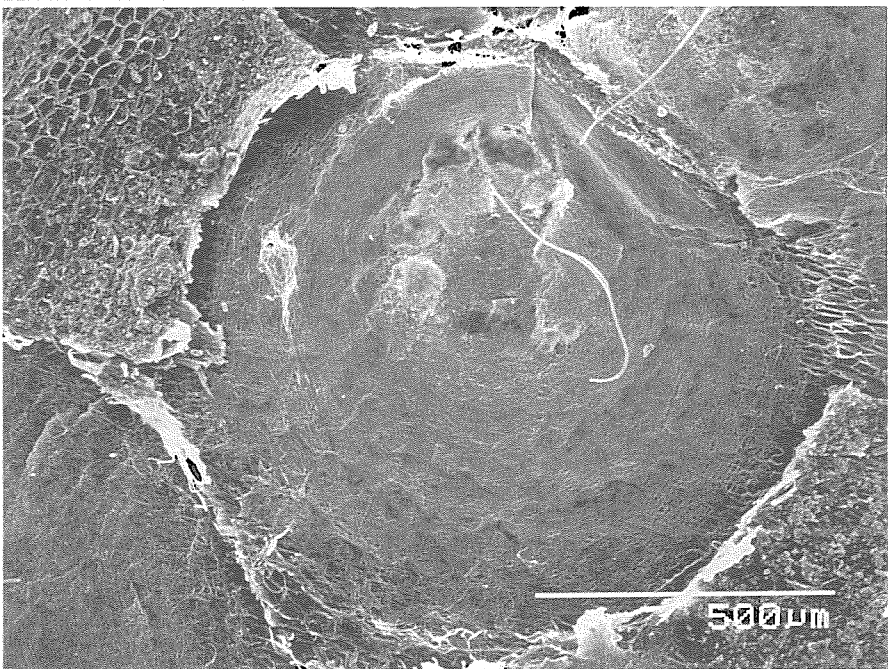


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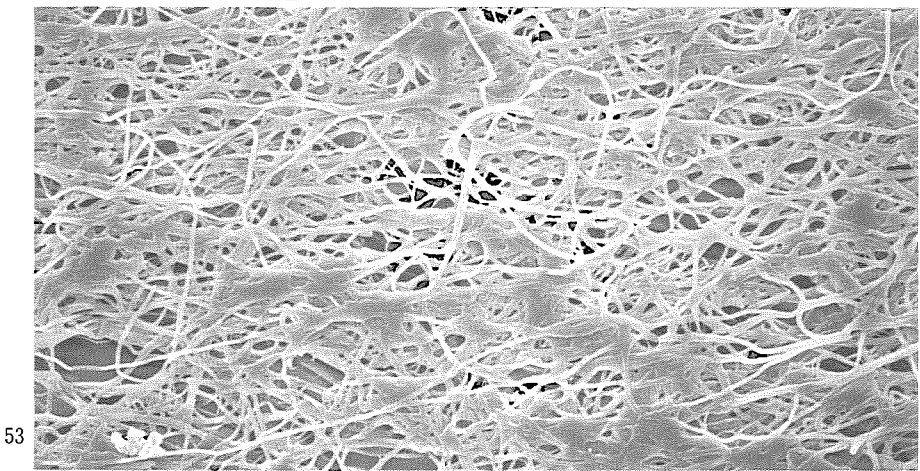
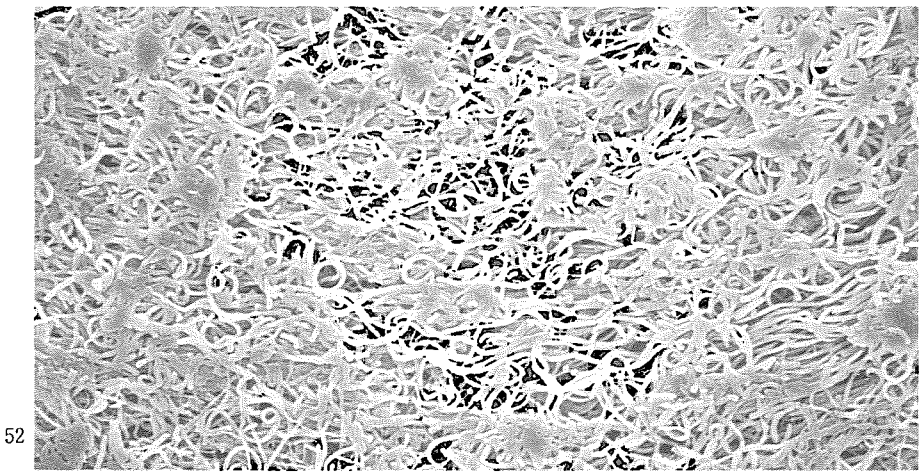
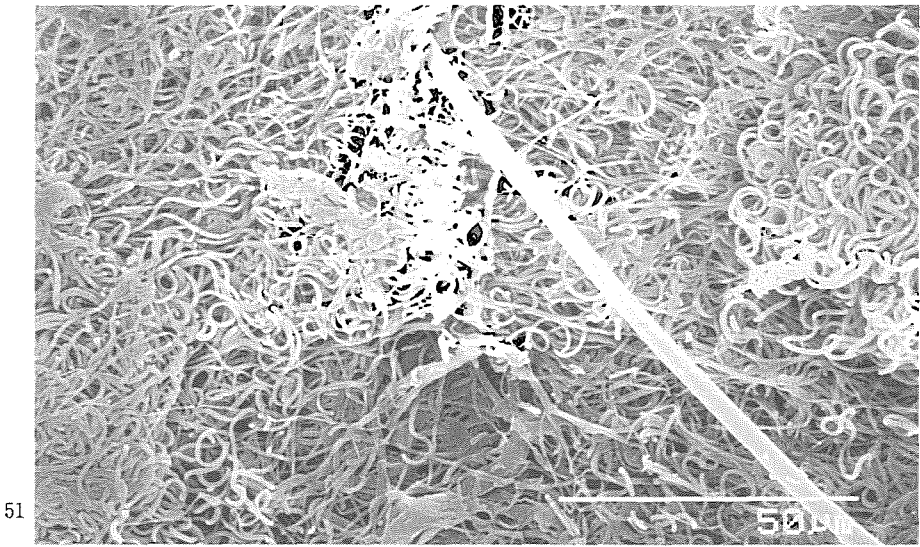


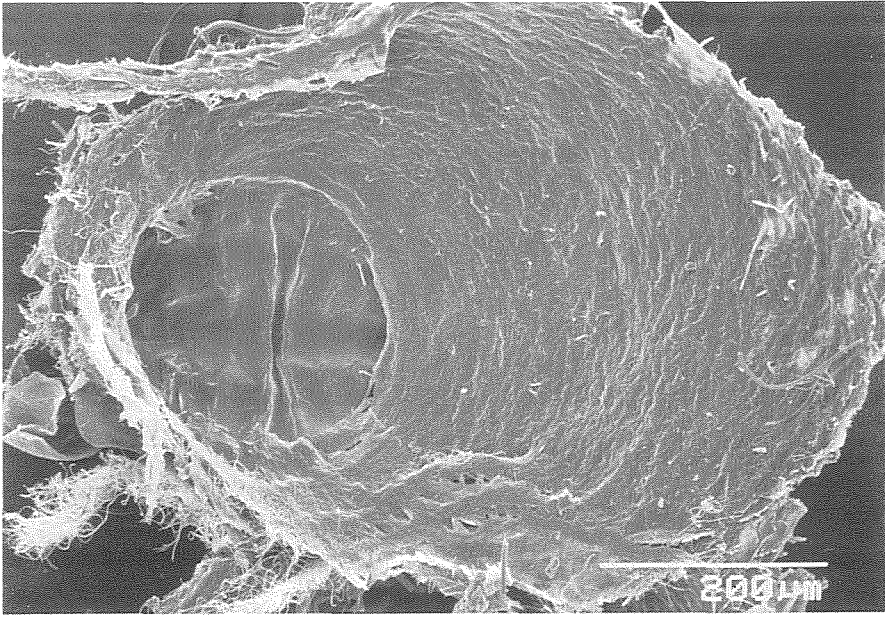


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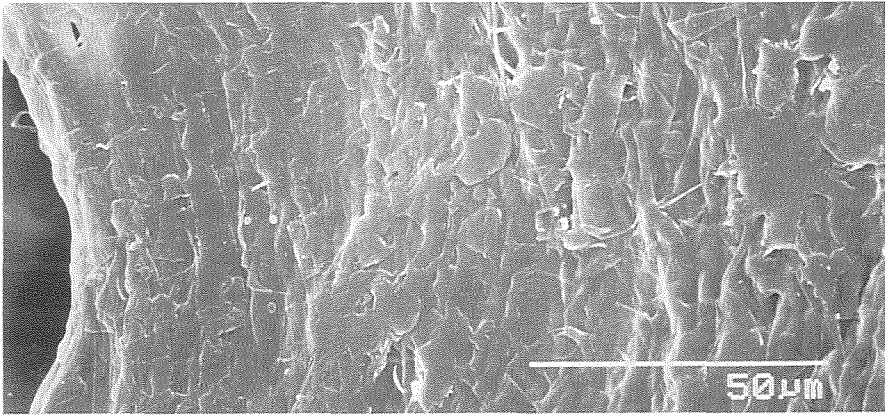


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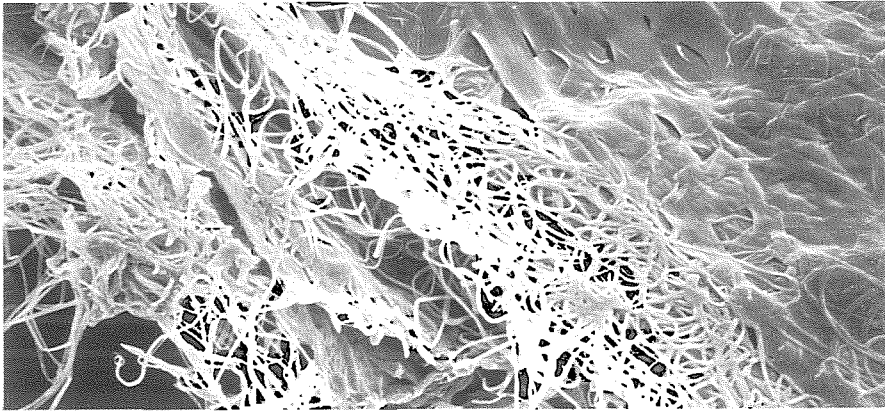




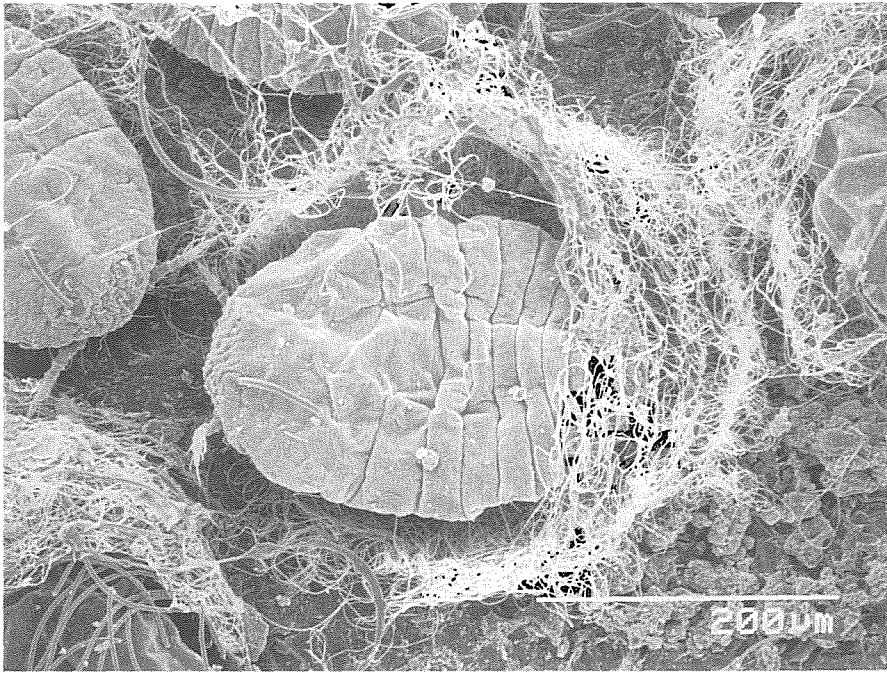
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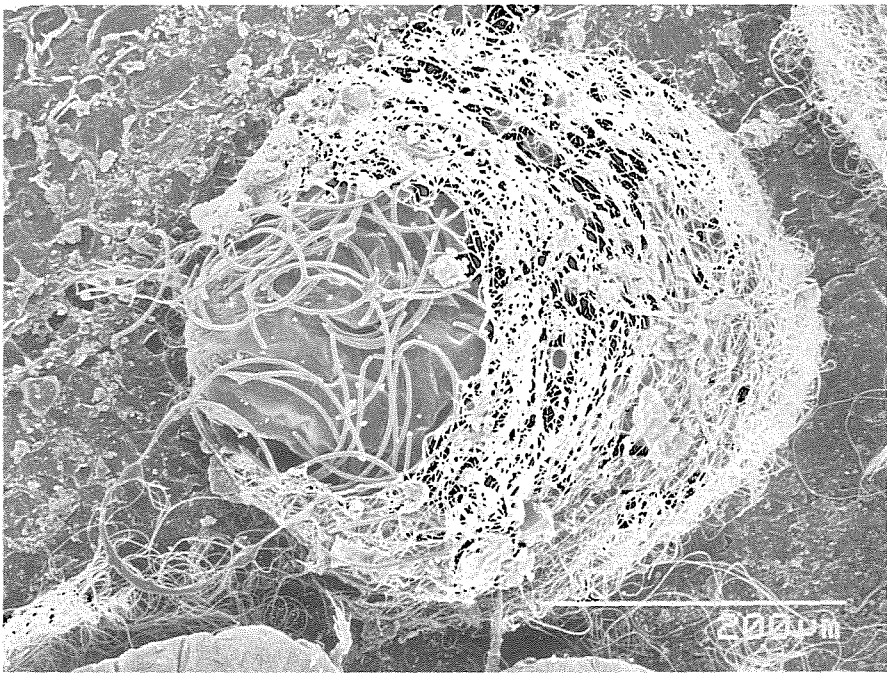
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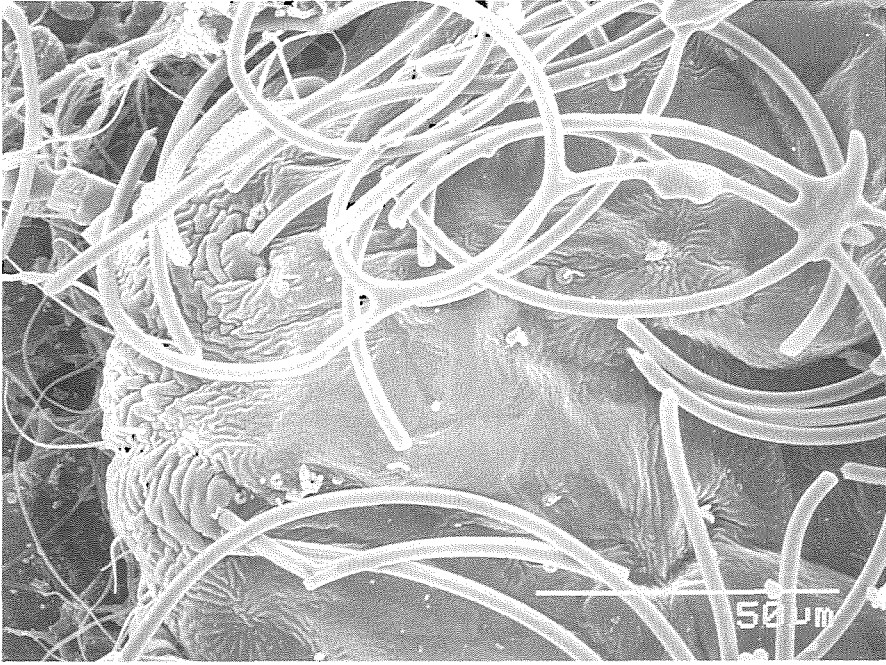
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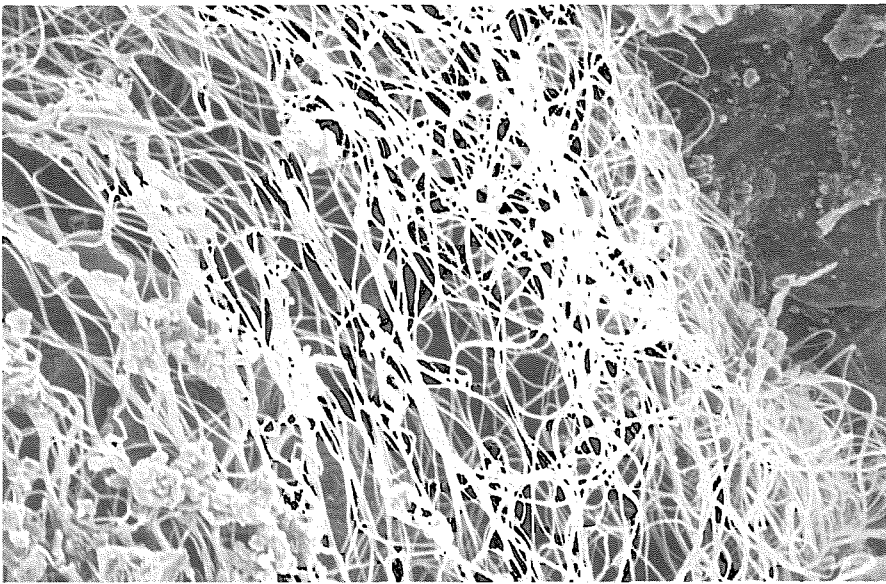
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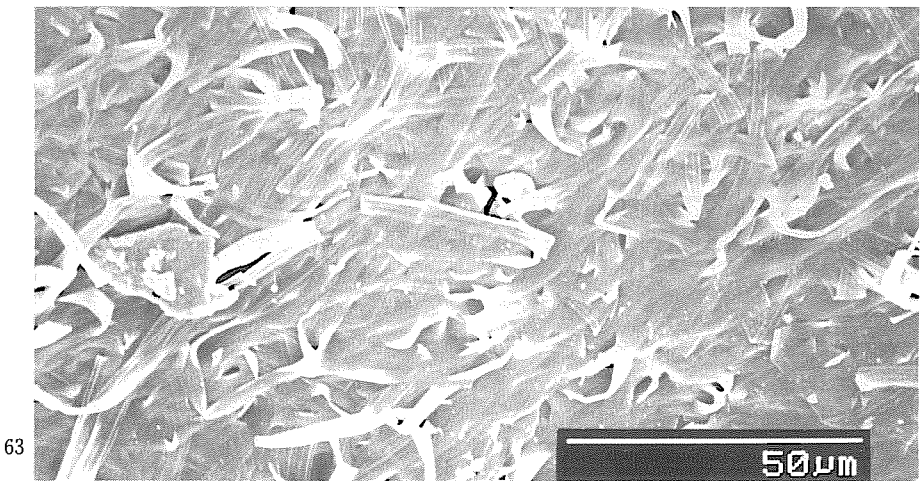
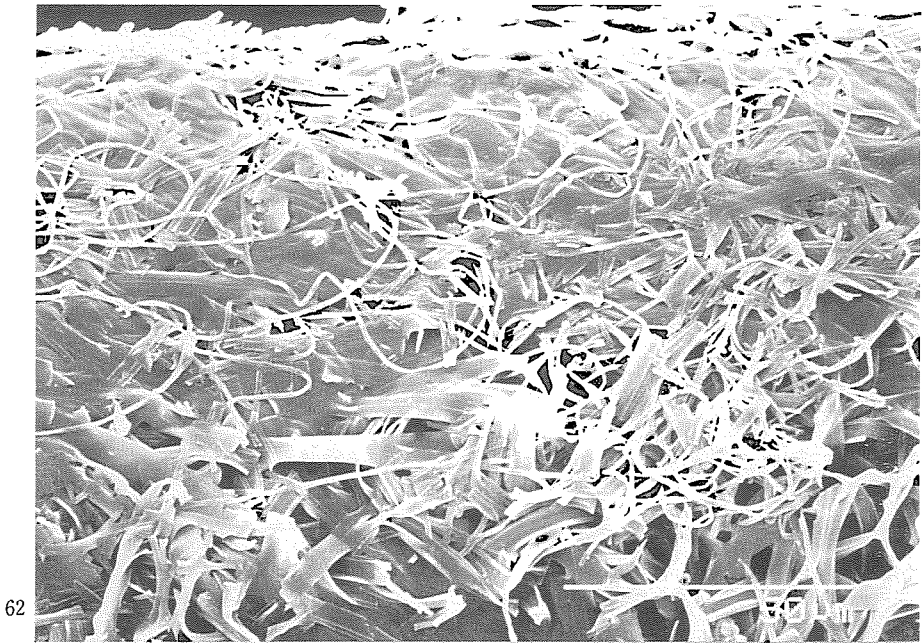
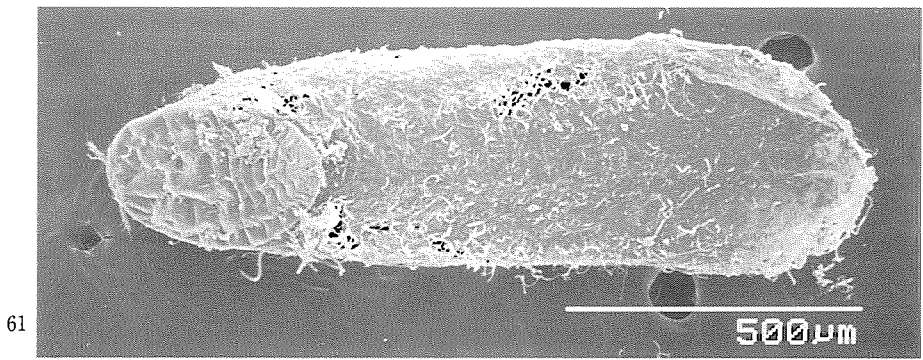
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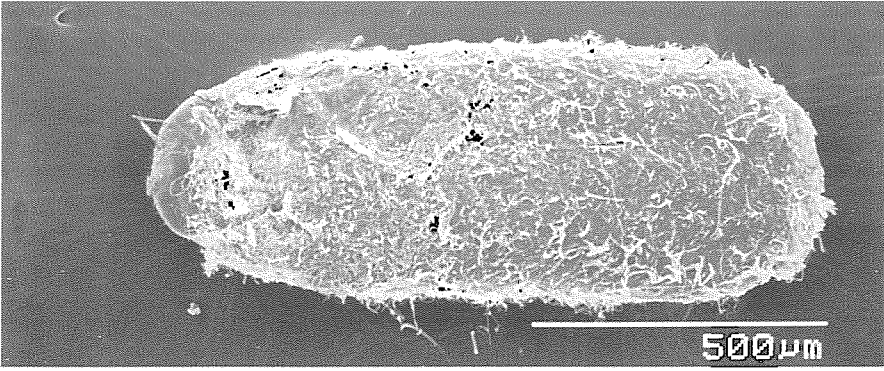


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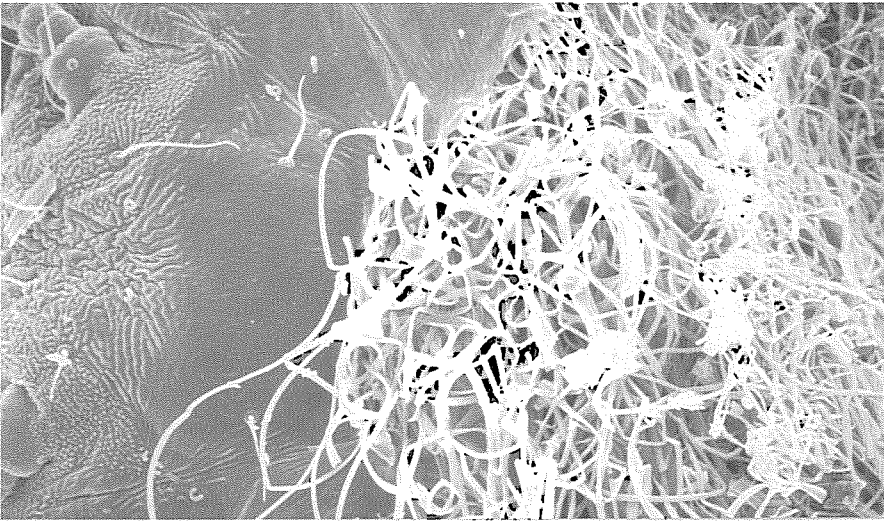


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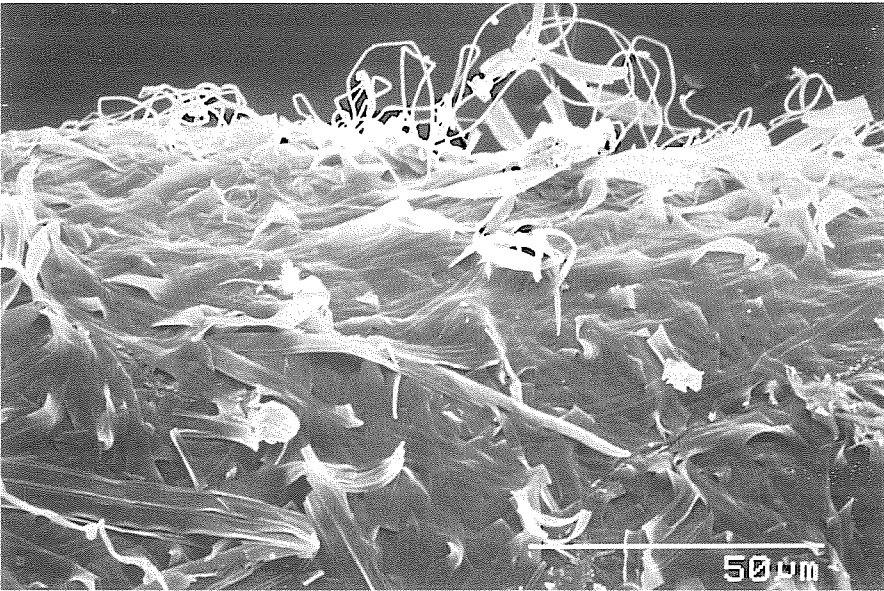




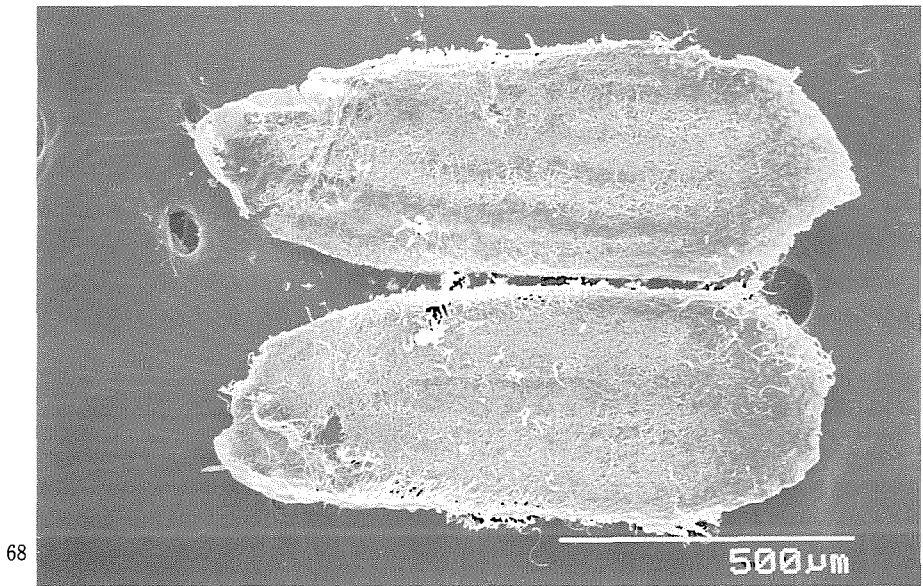
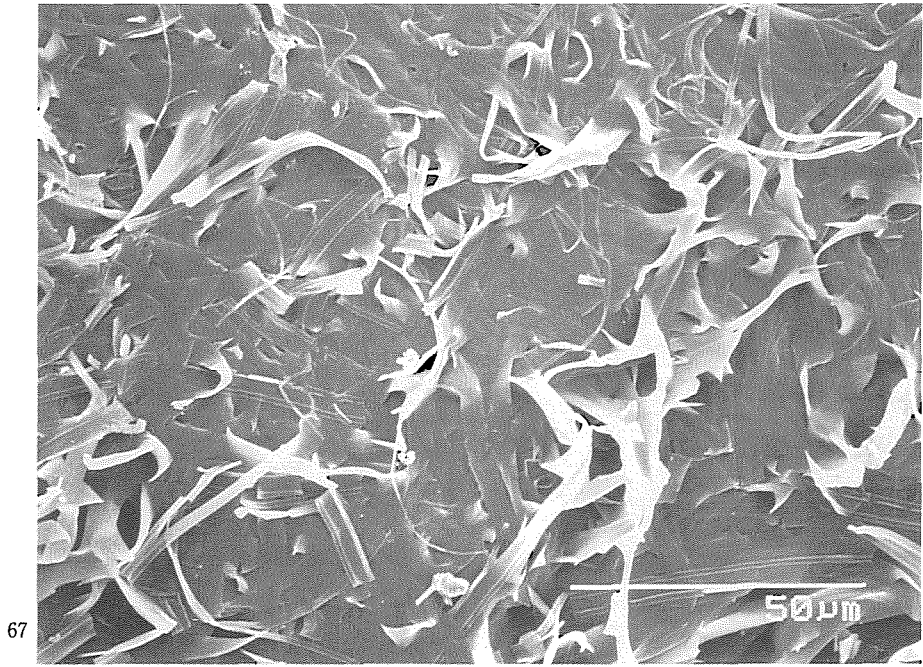
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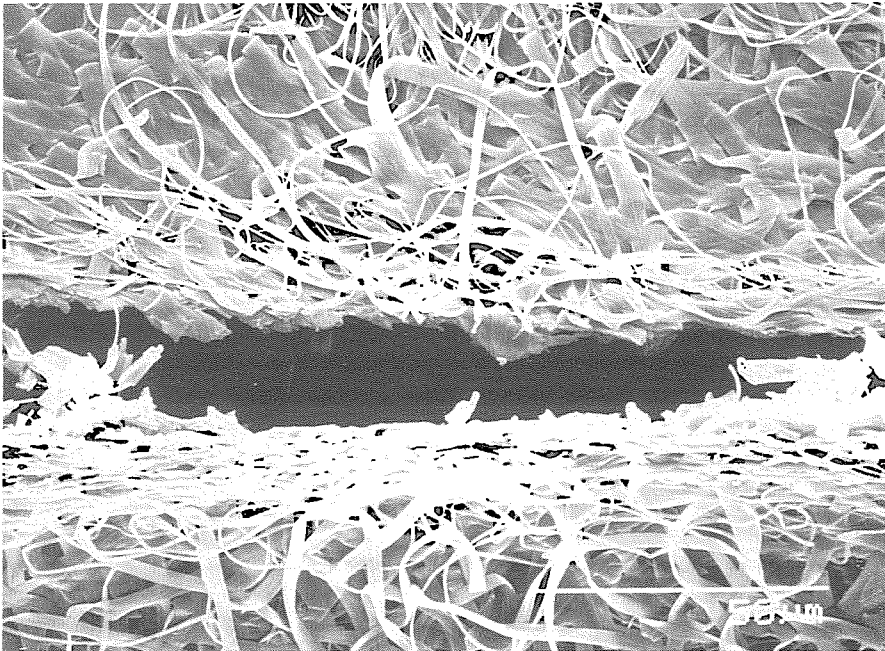


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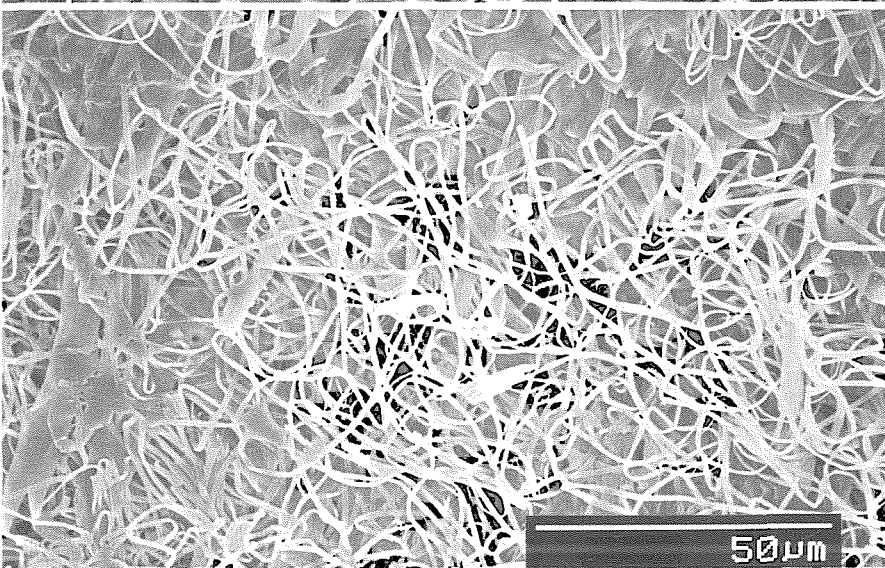


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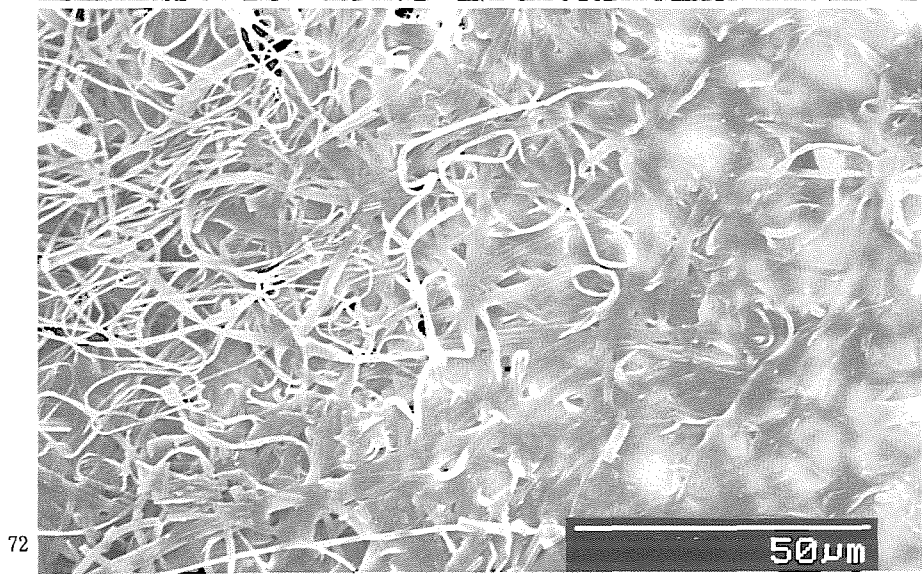
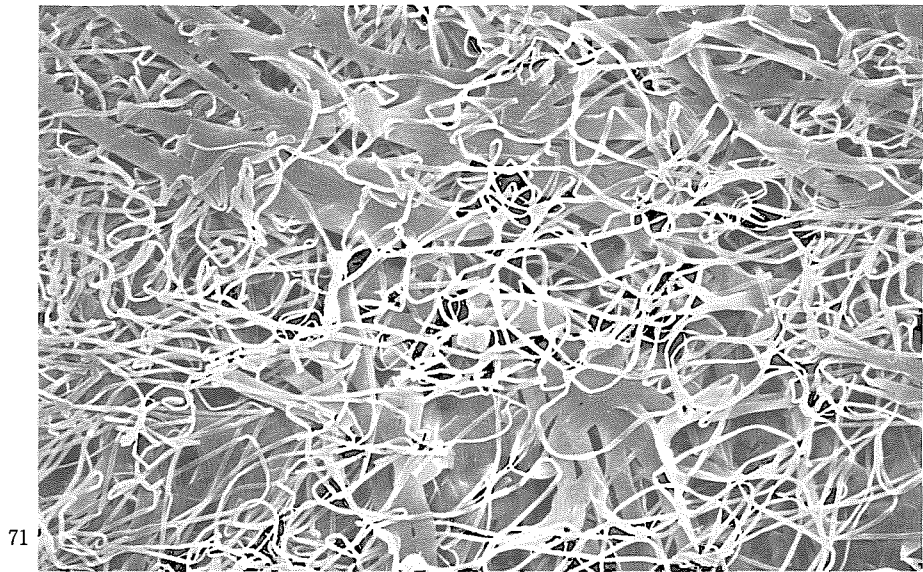


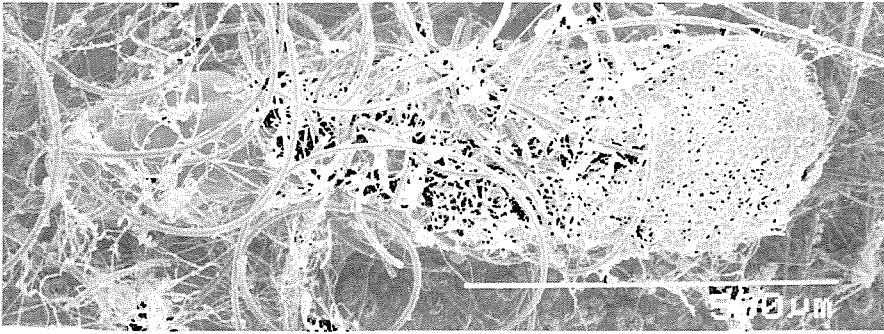


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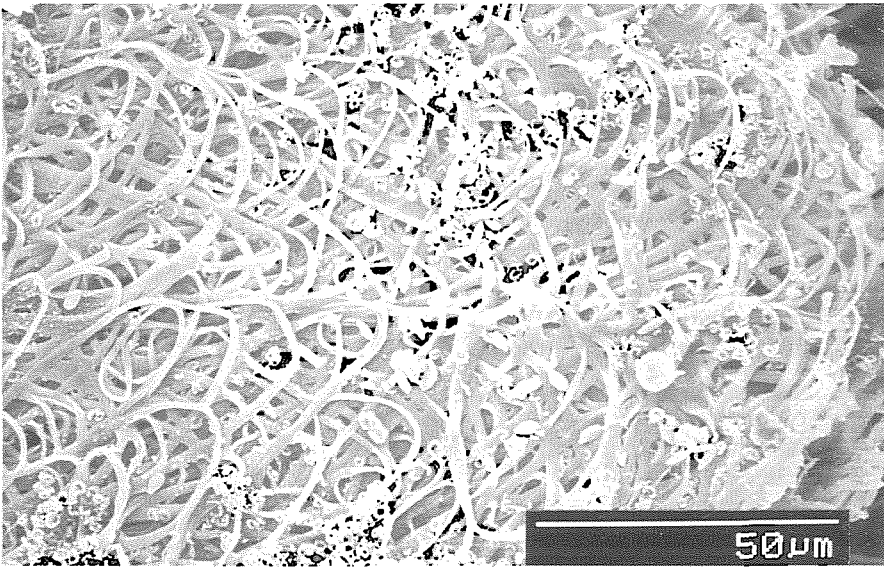


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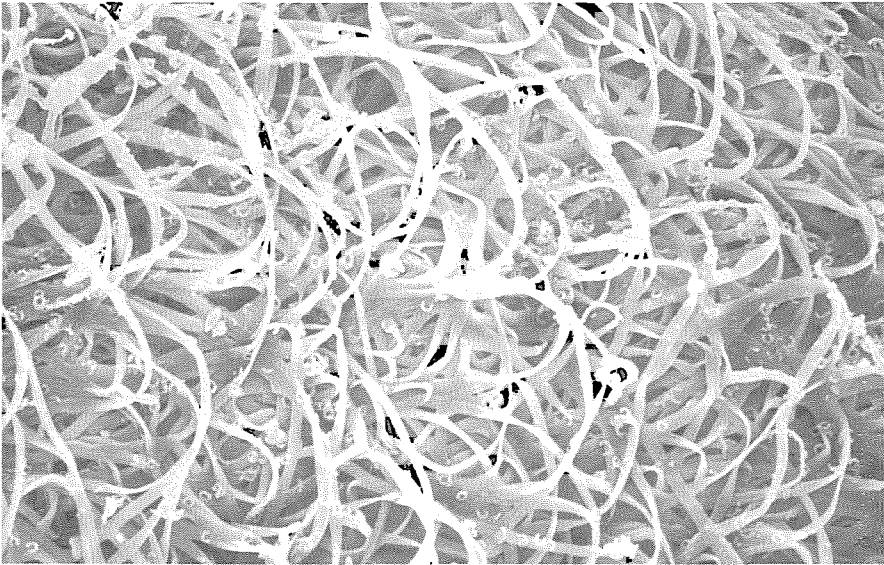




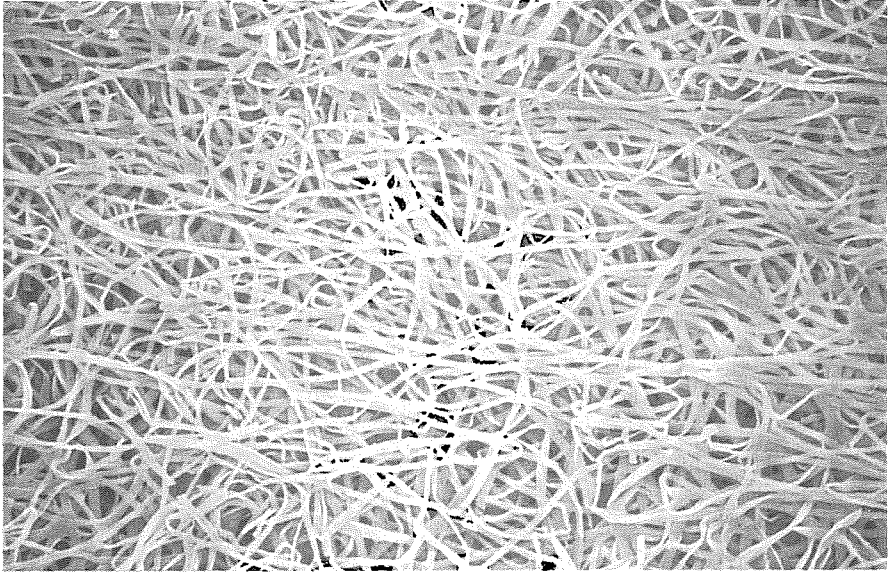
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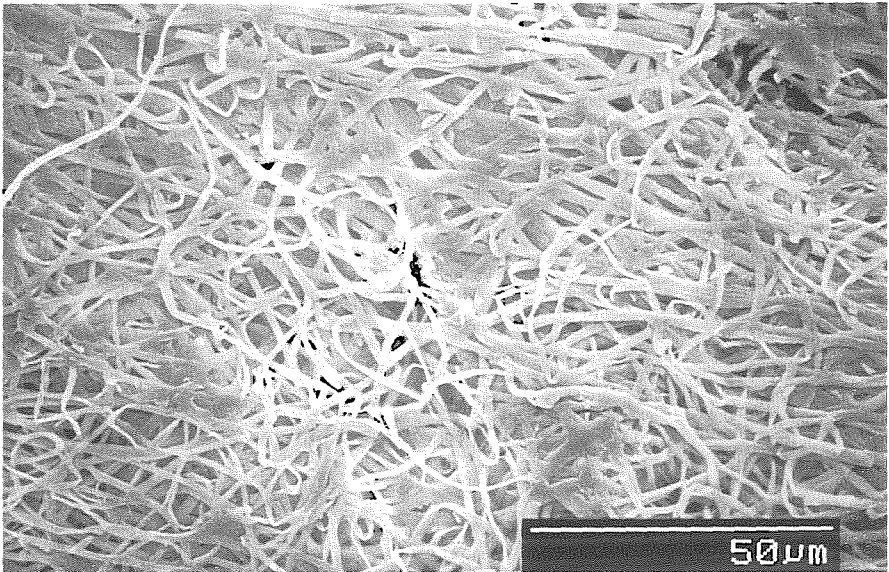
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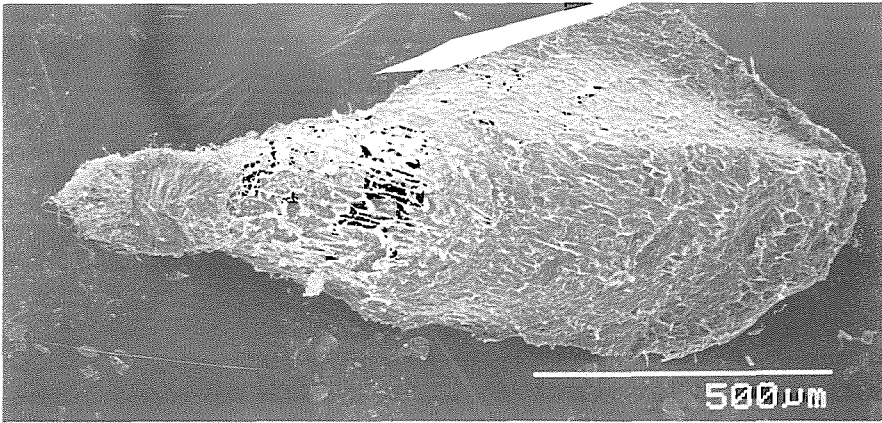
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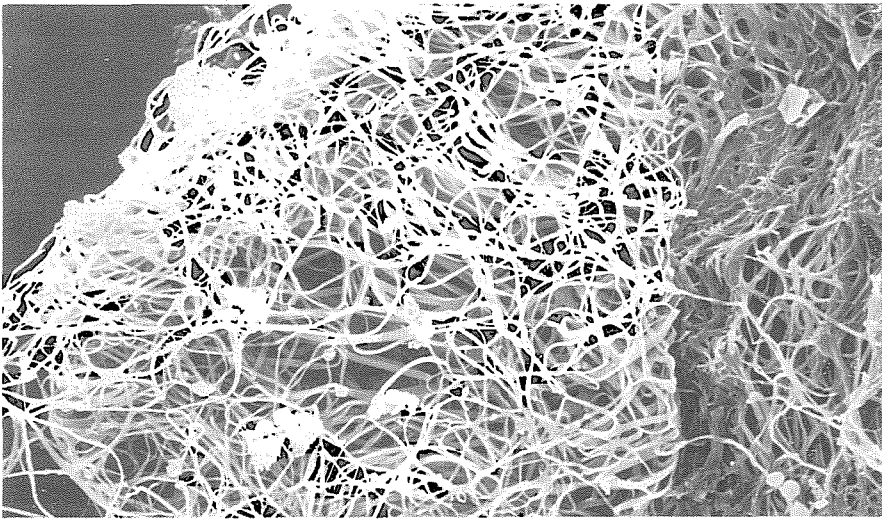
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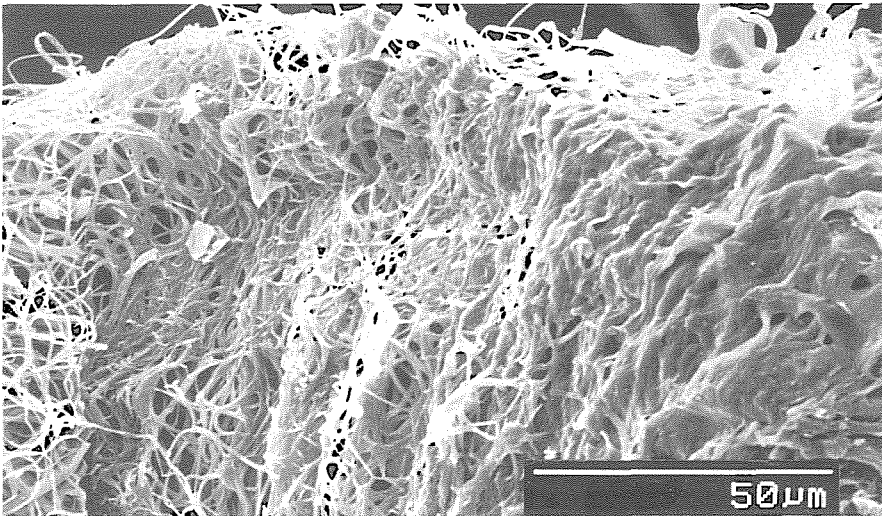
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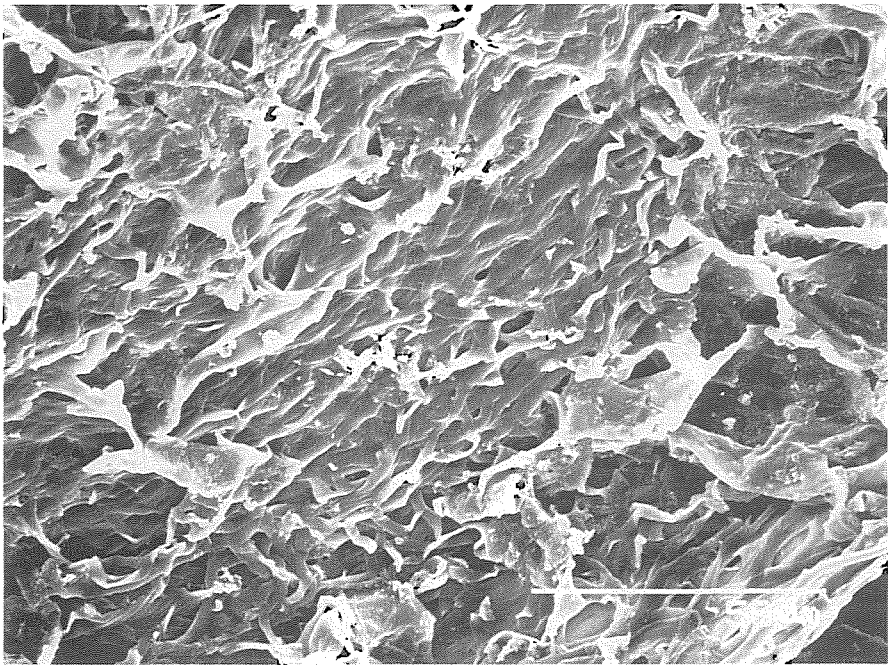
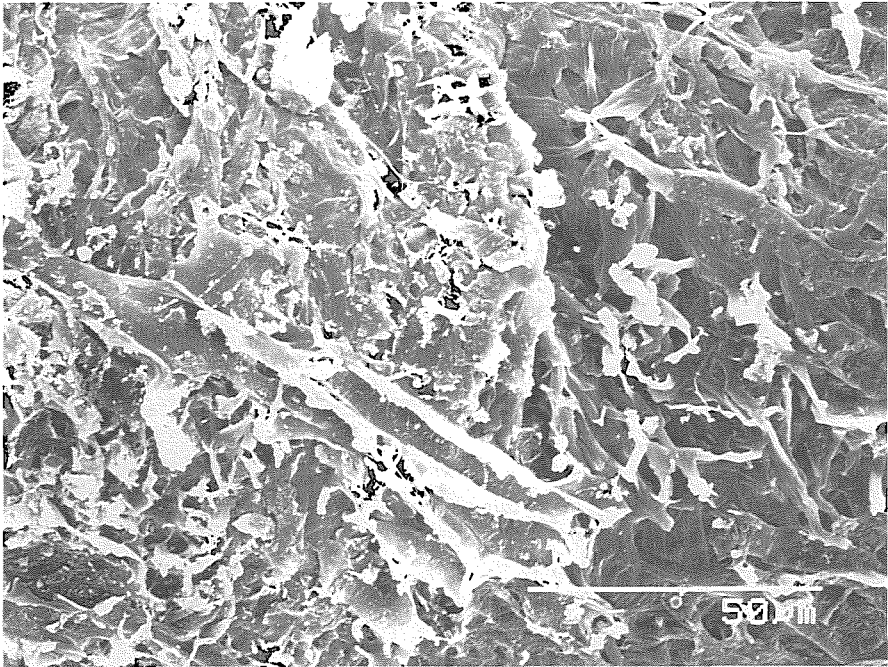
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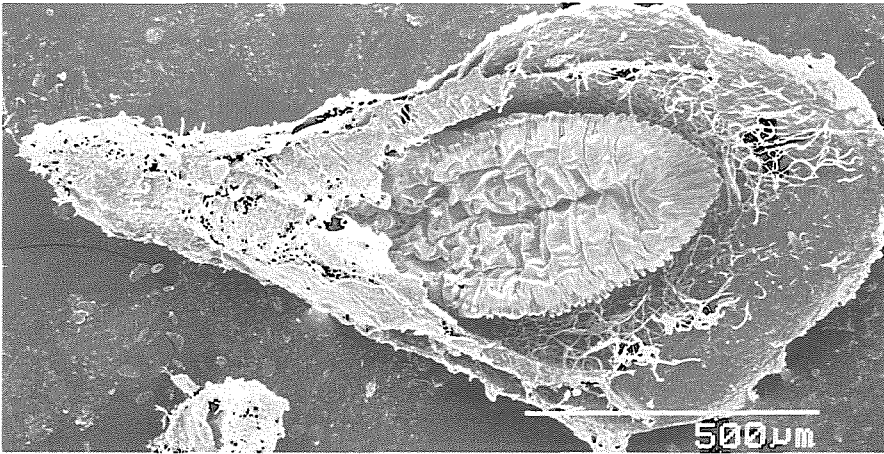


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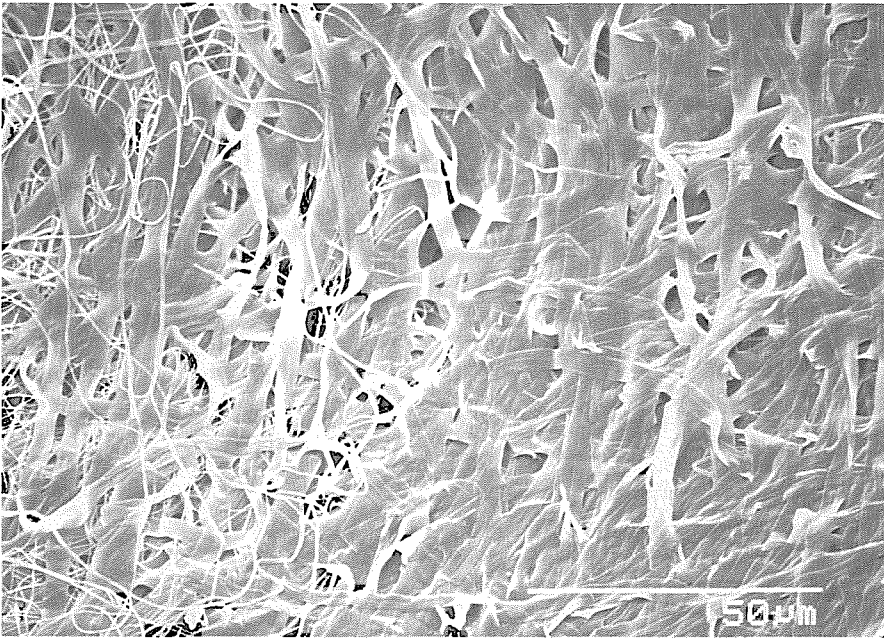


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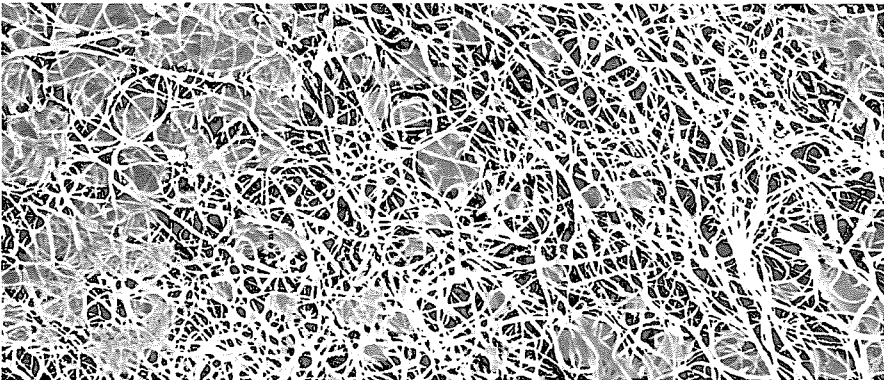




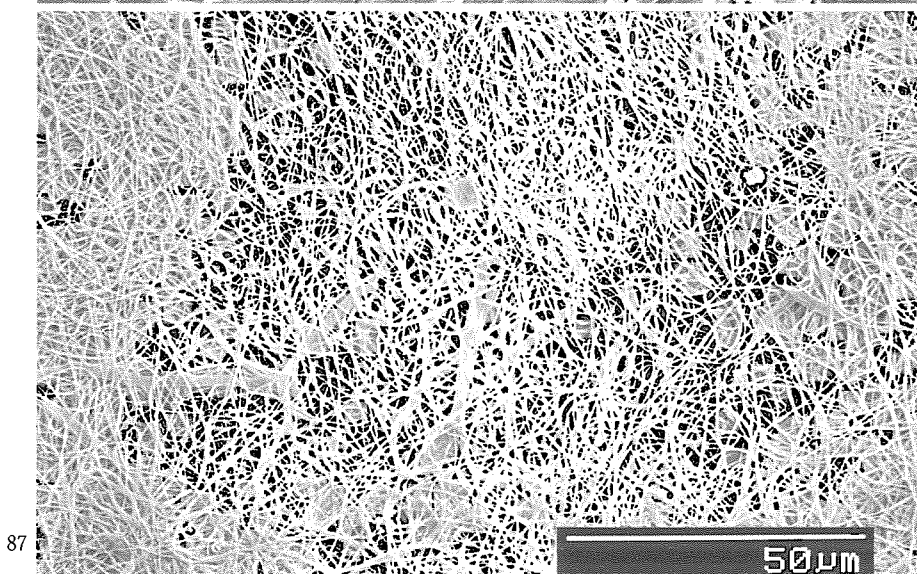
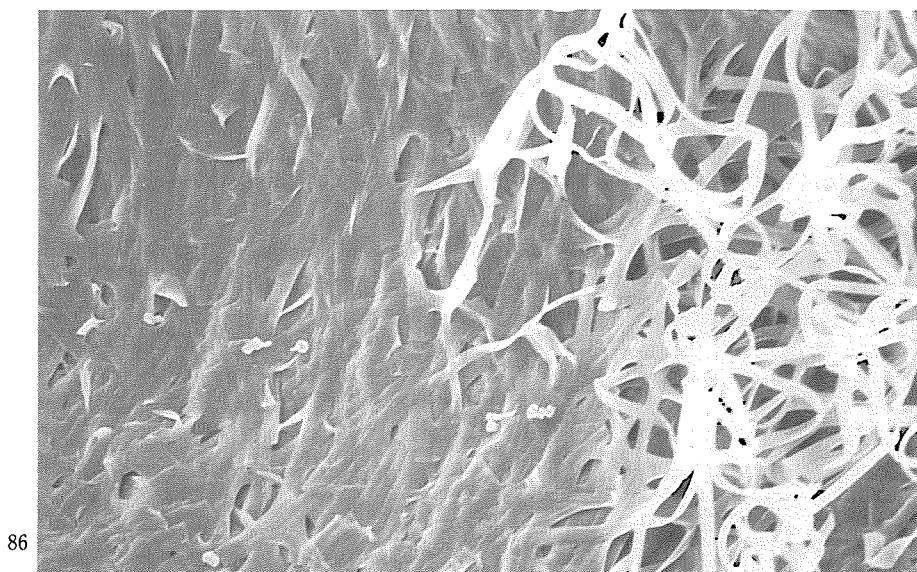
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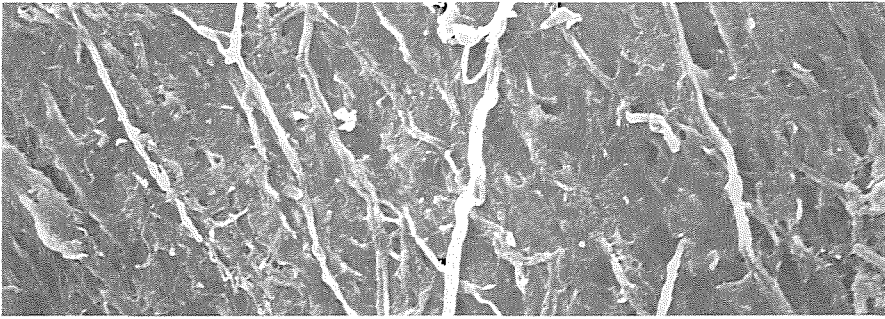


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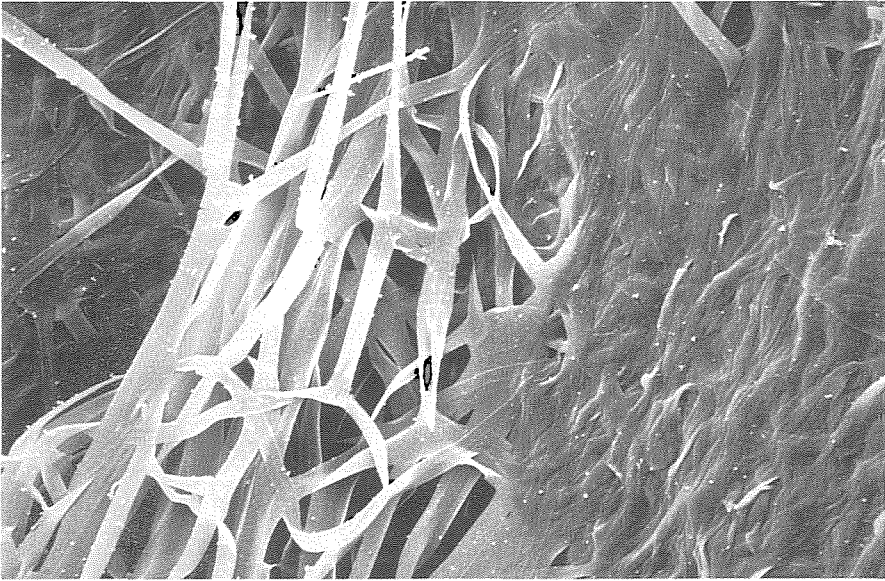


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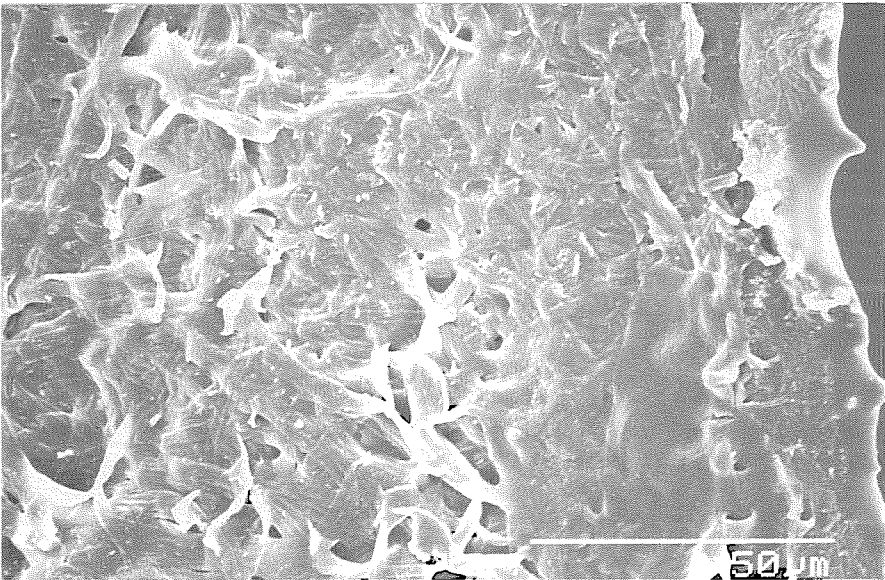




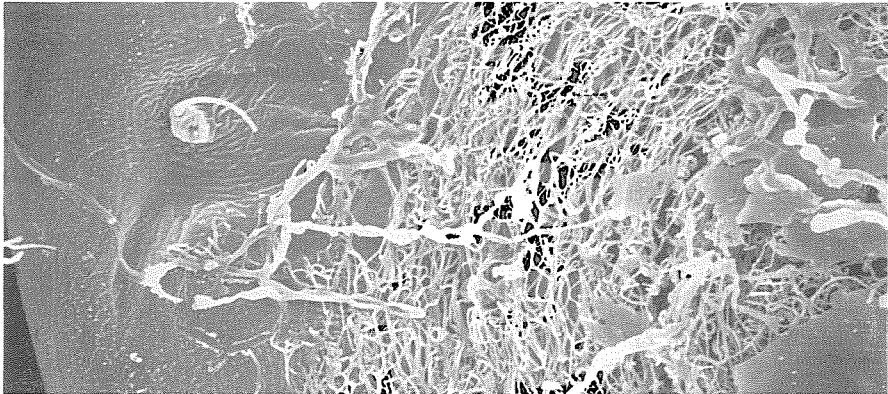
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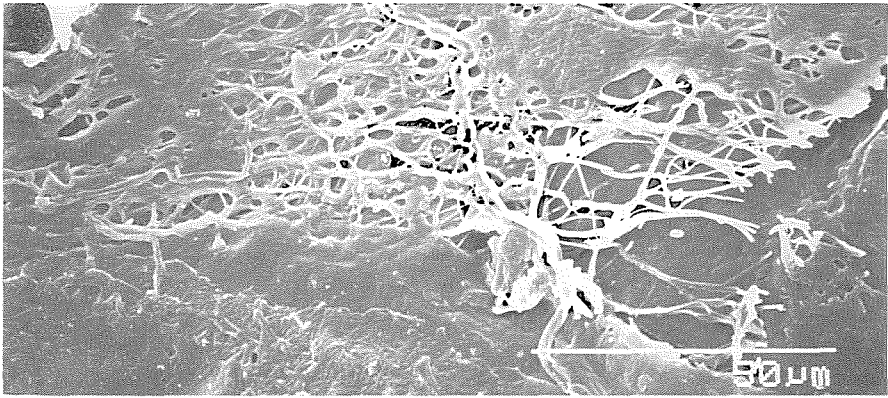
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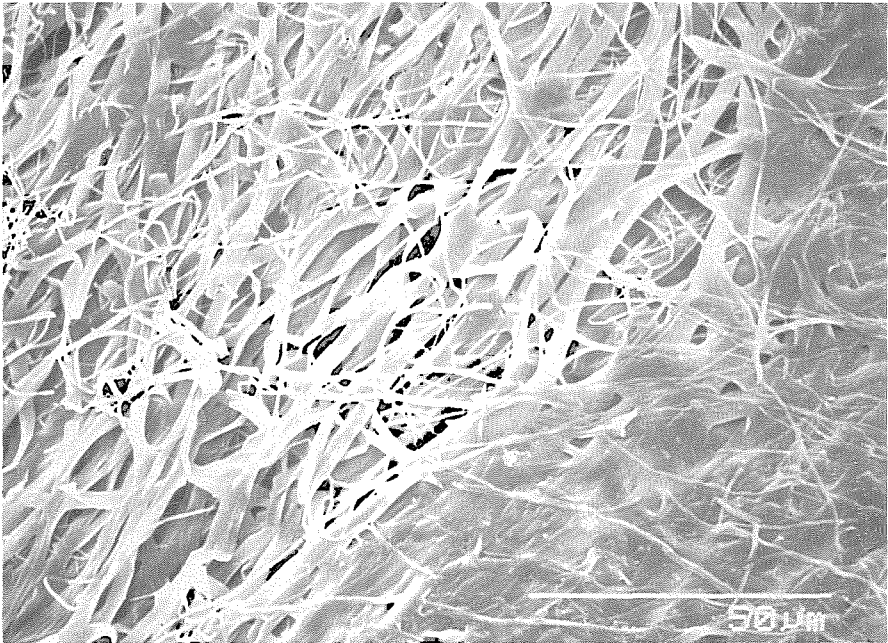
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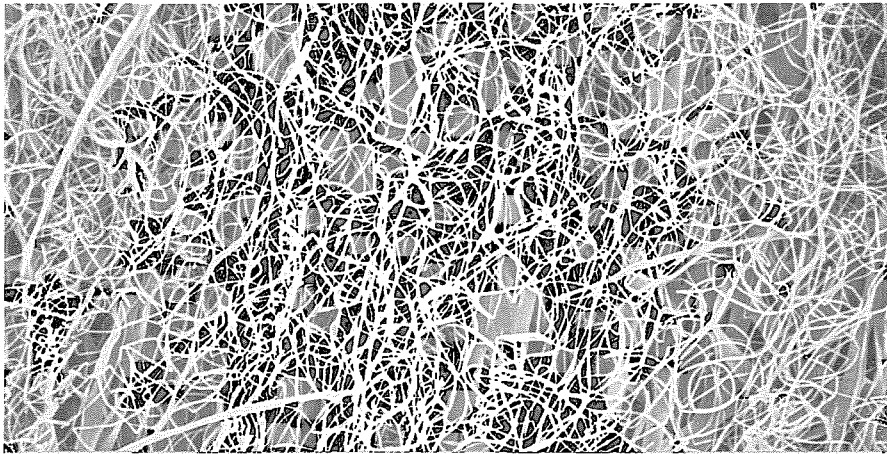
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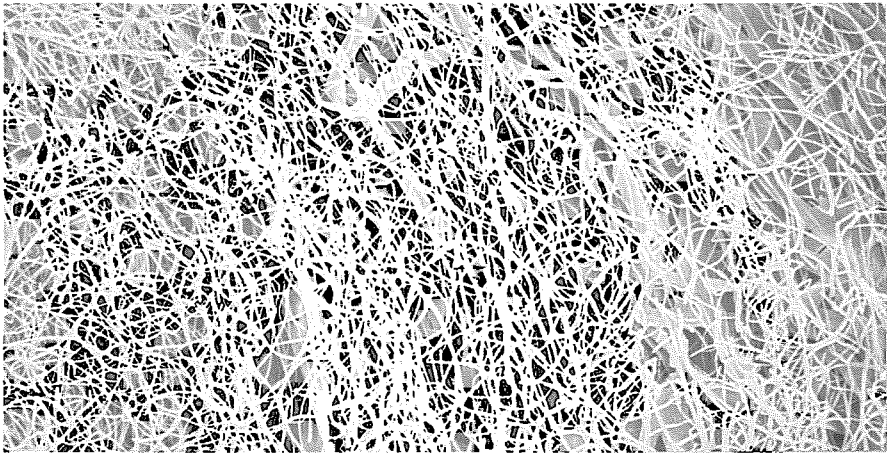
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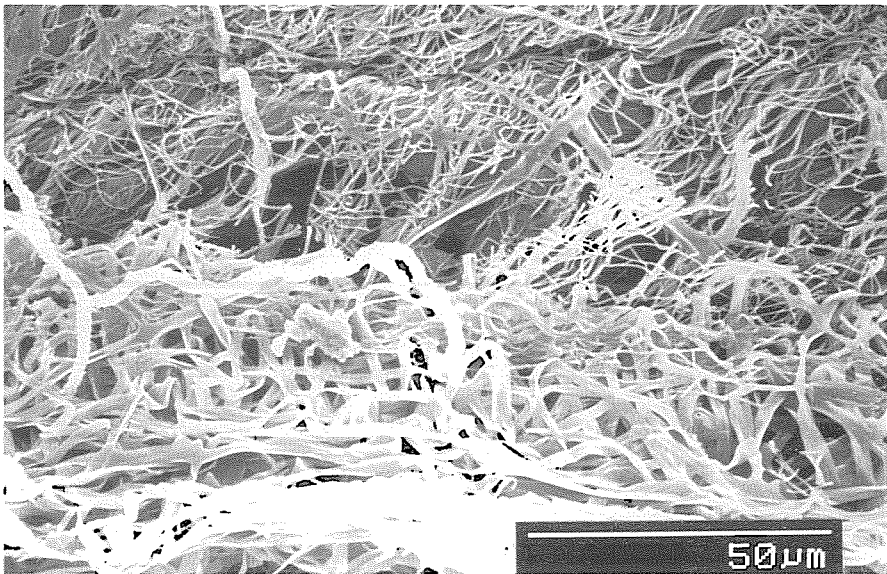
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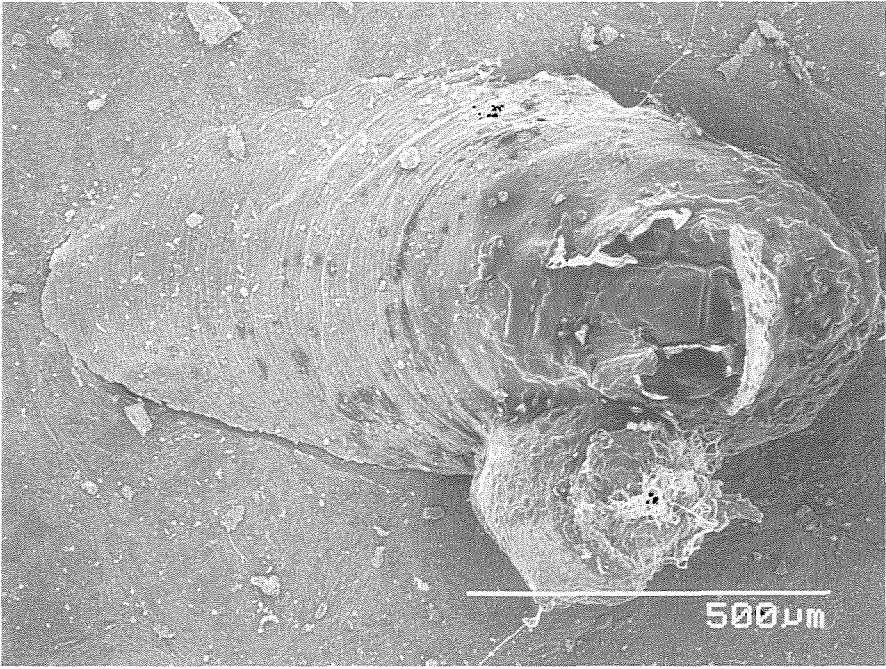
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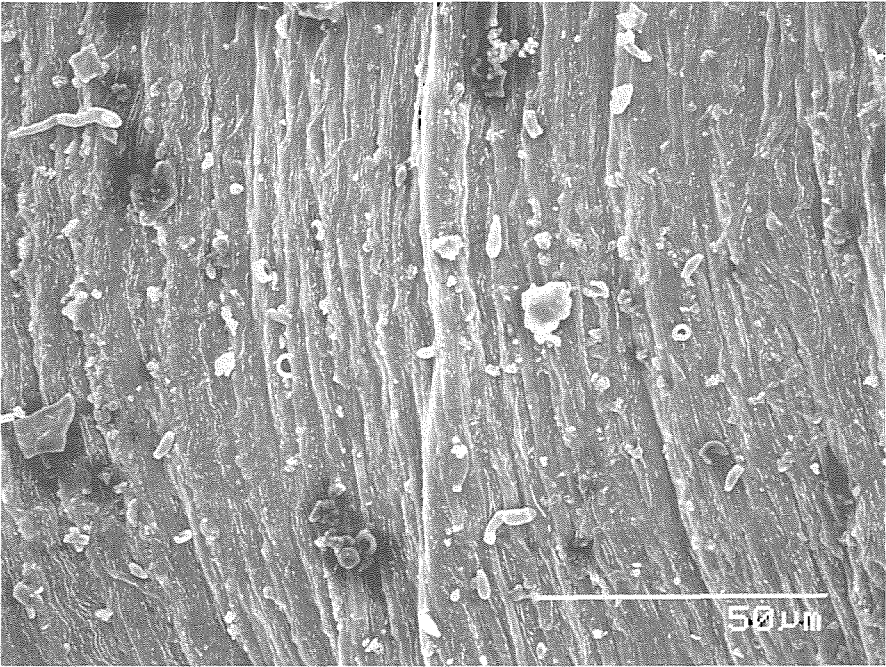
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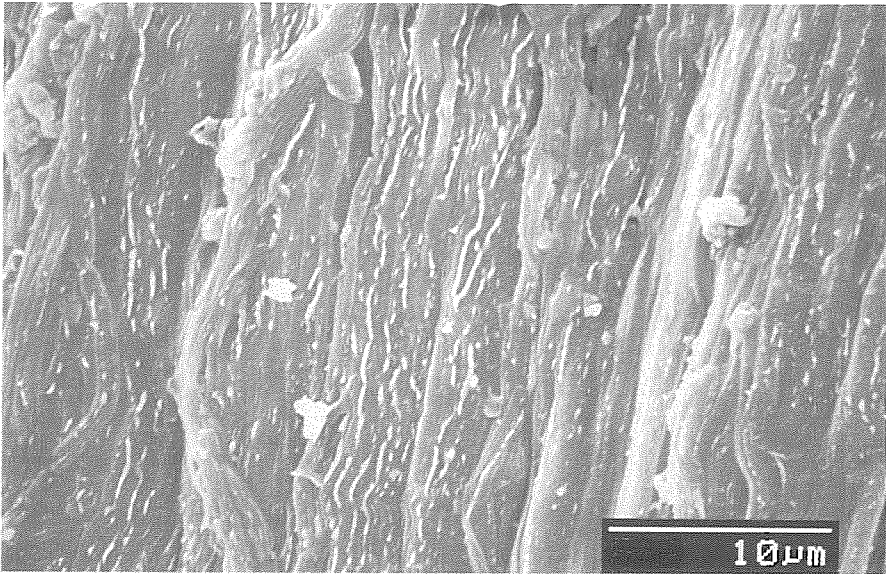
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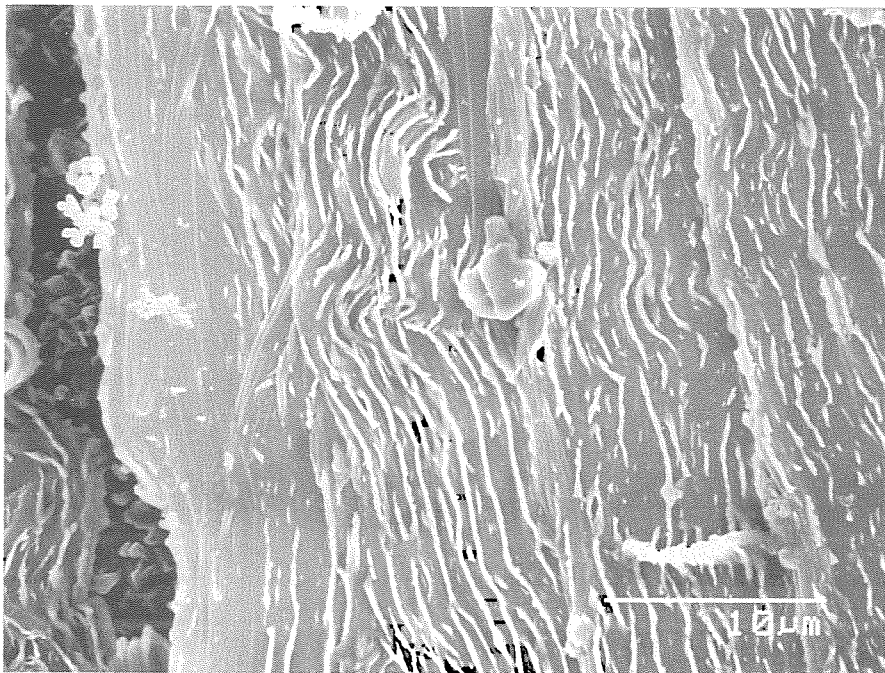
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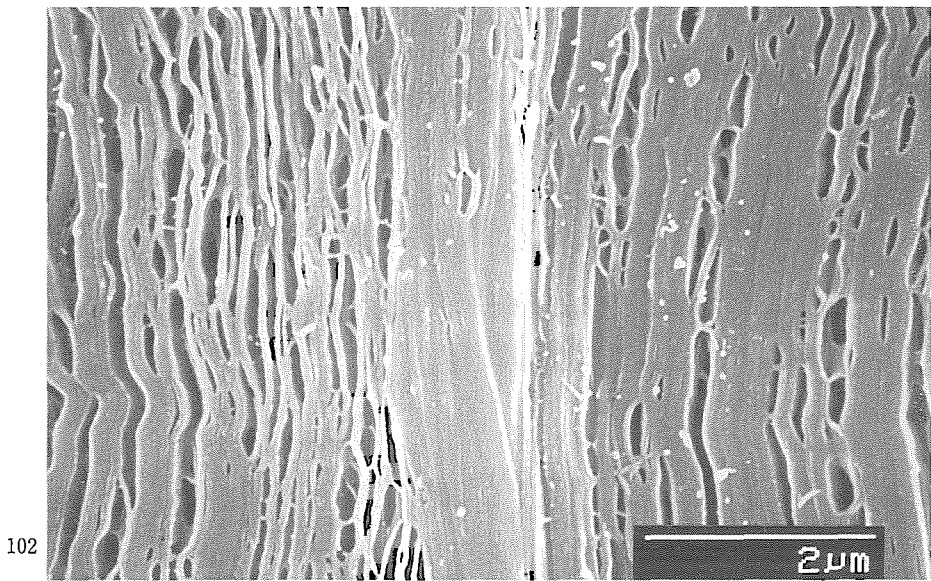
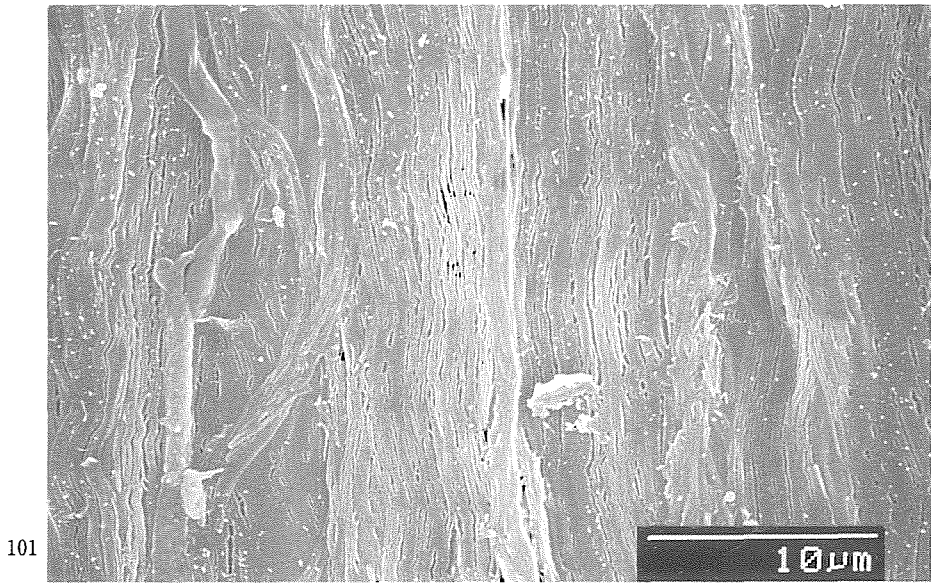
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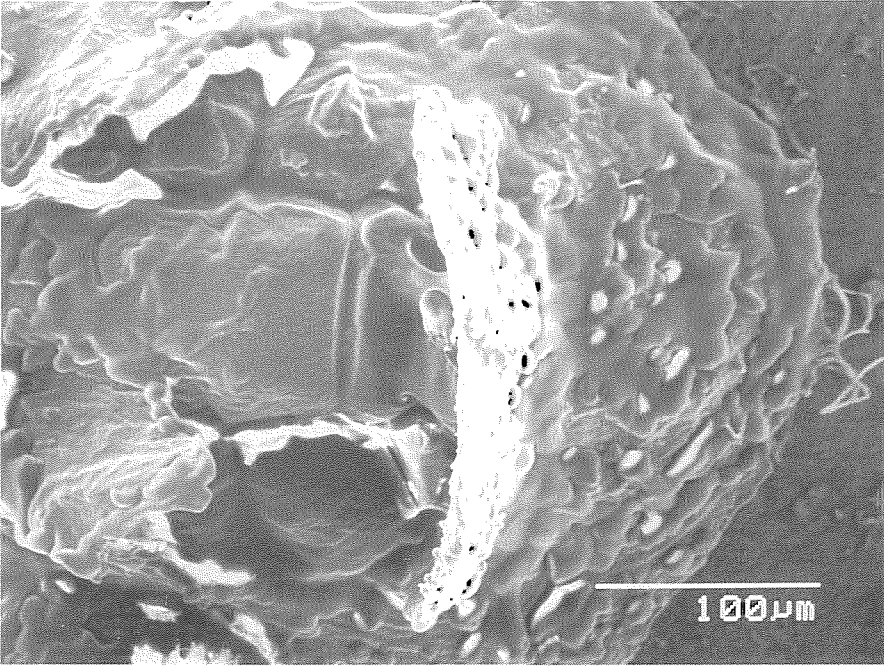


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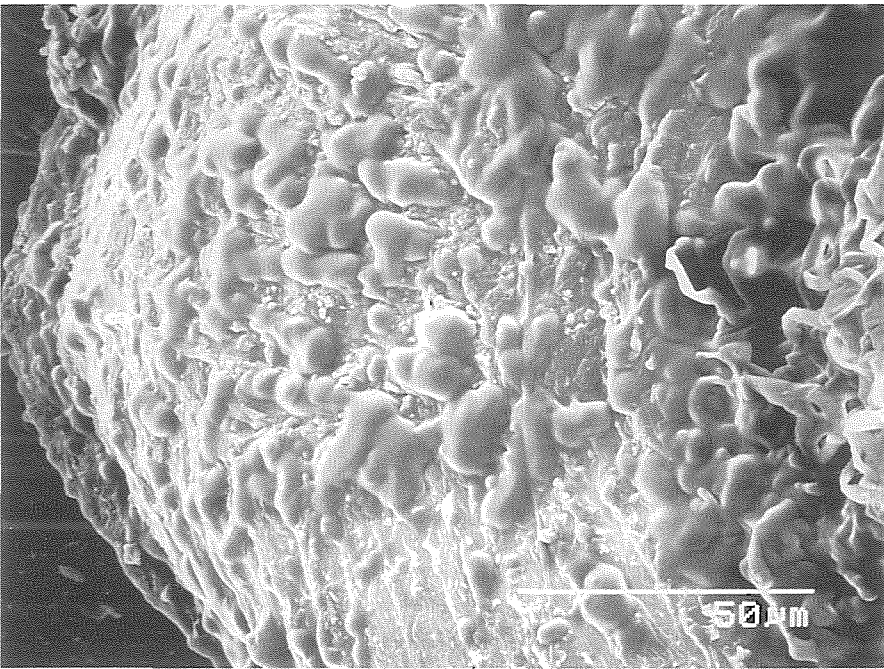


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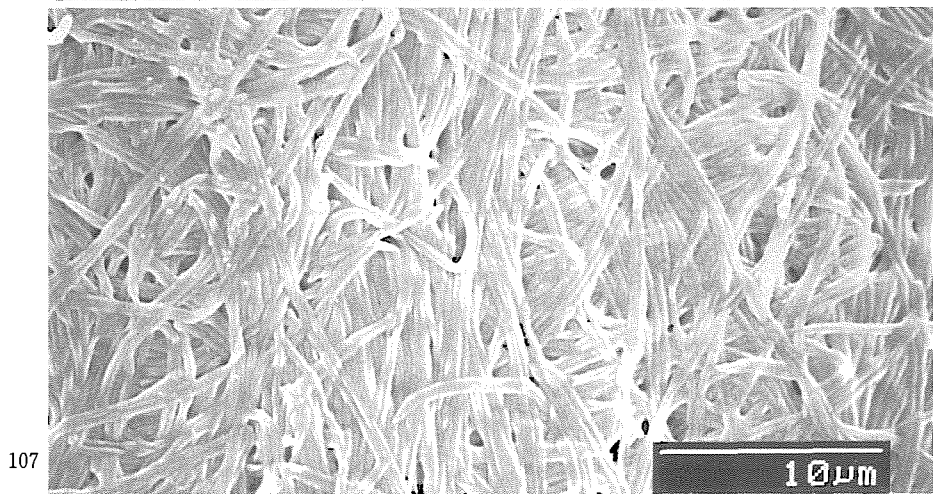
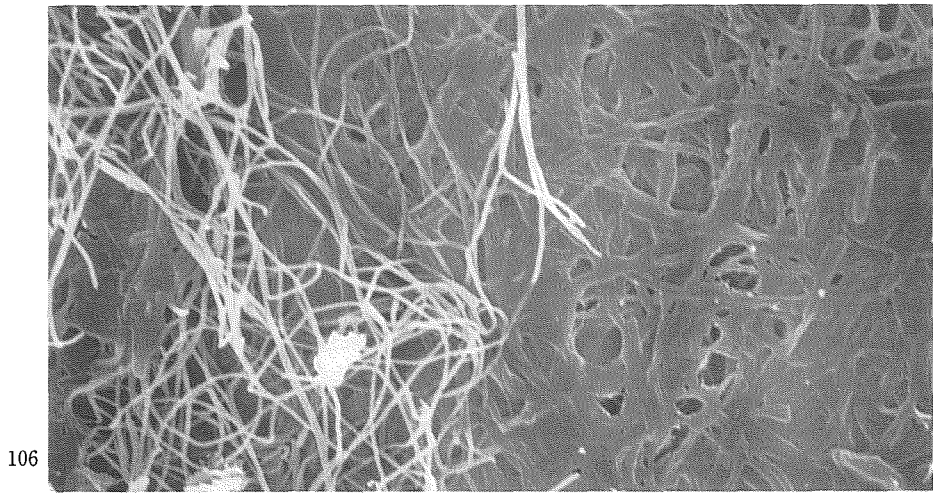
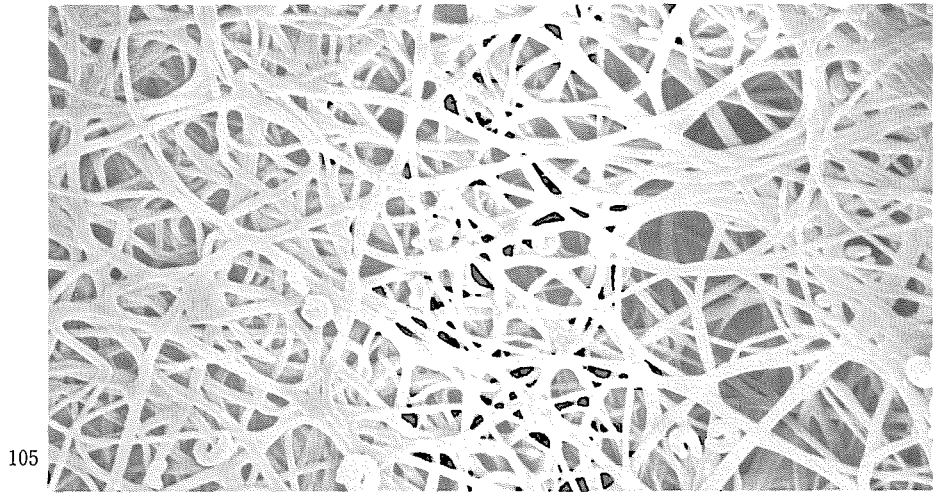


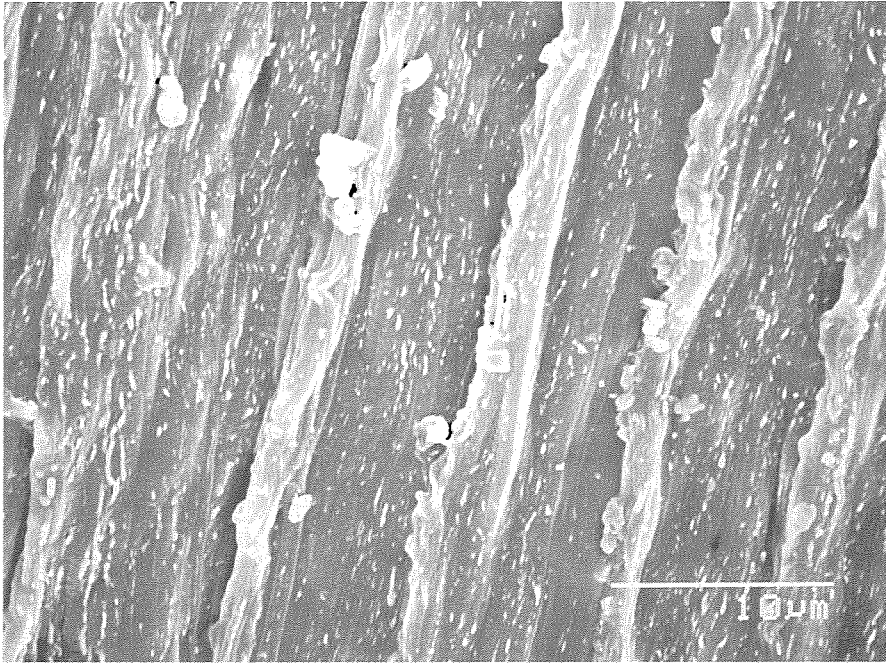


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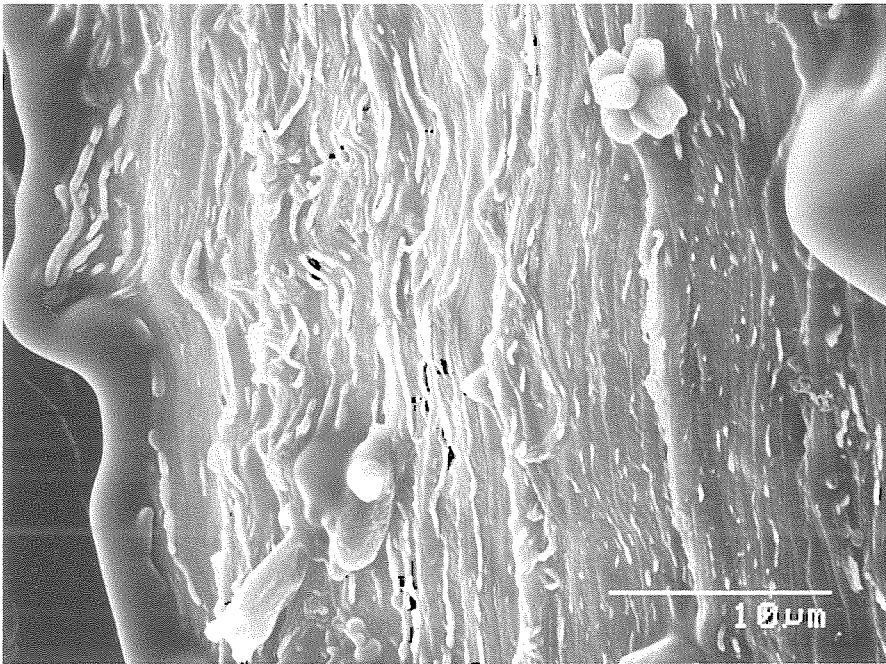


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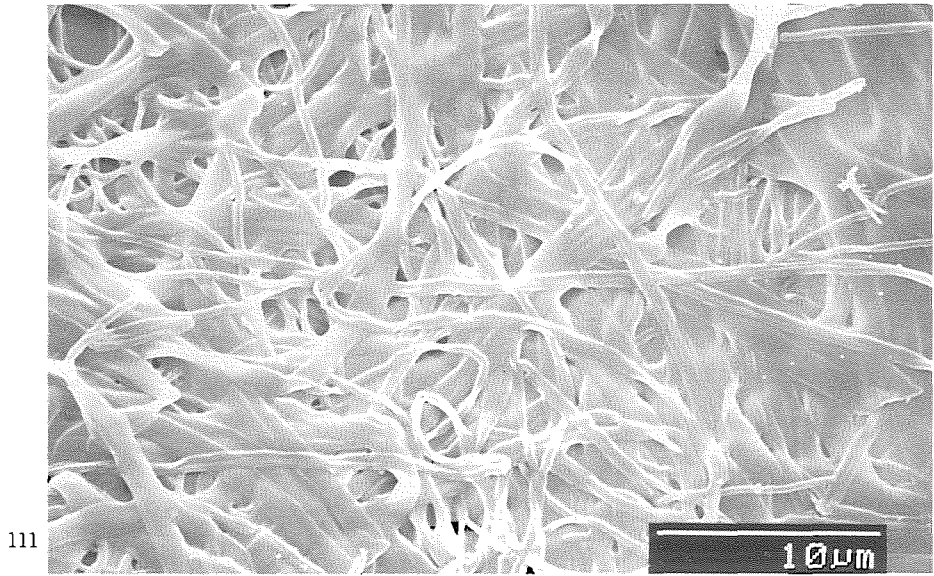
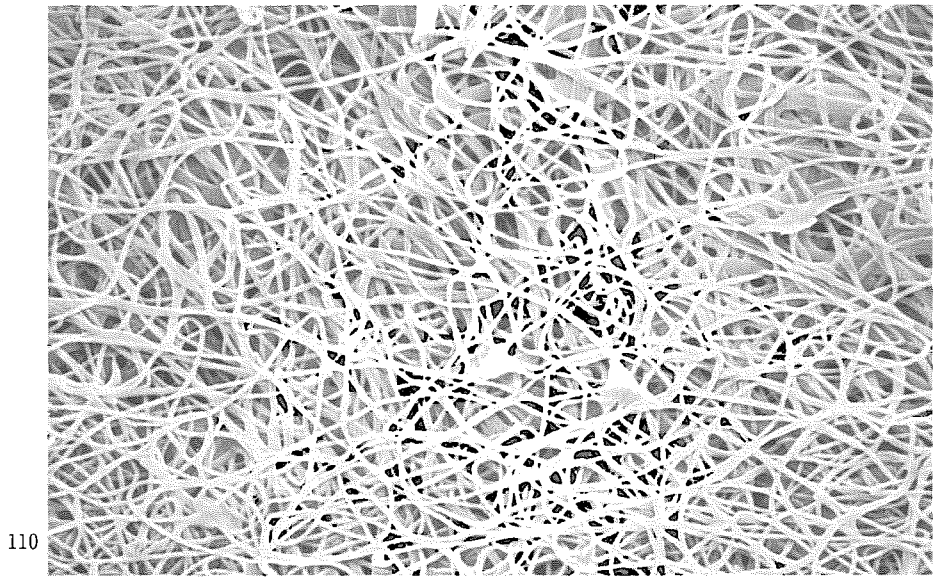


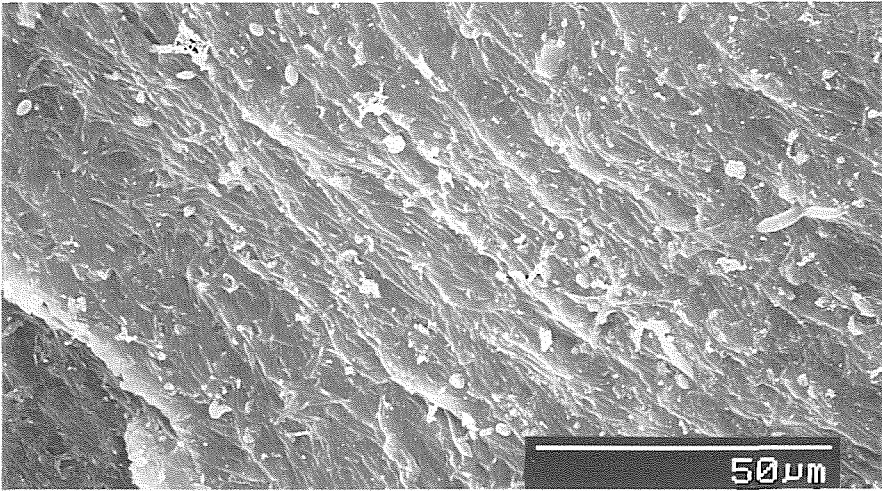


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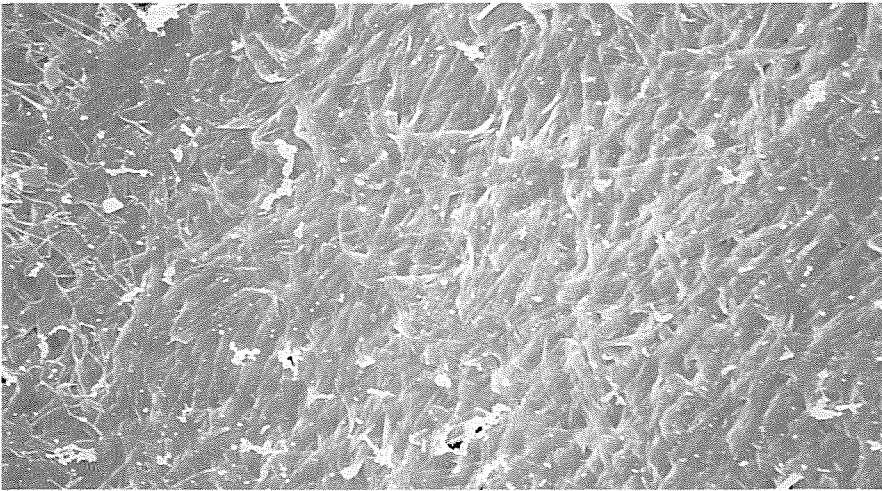


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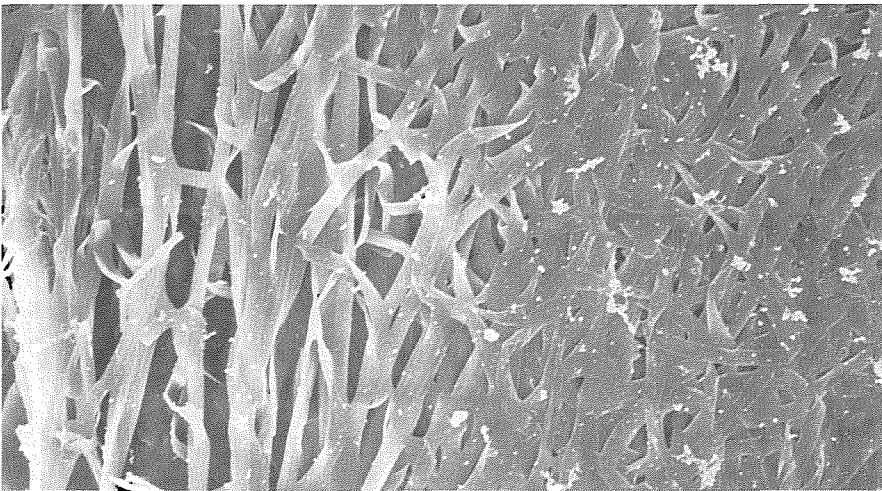




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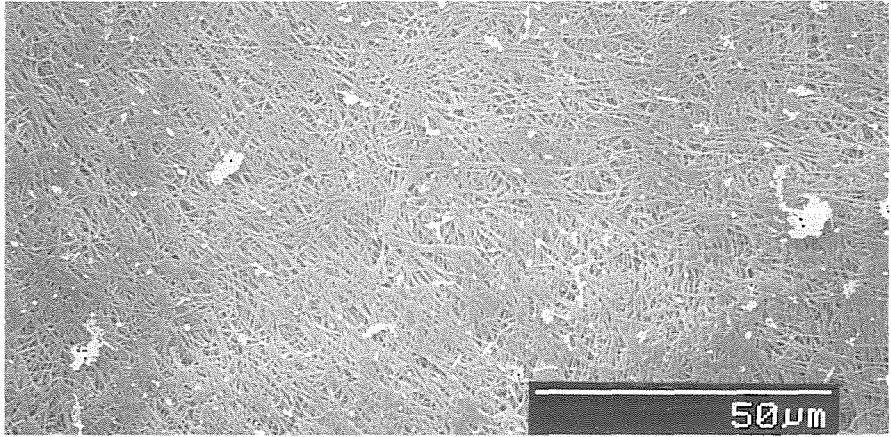


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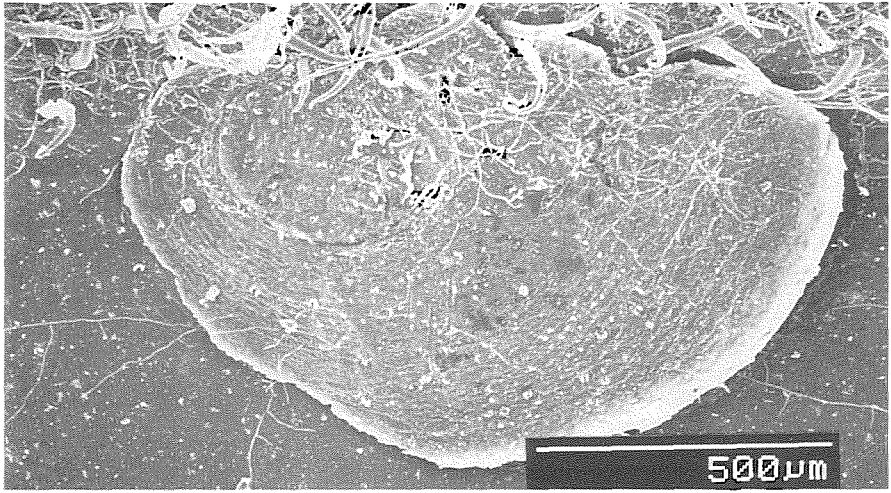


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