

ELECTRON MICROSCOPIC STUDIES OF SPERMATOOZA

II. THE MORPHOLOGY OF THE HUMAN SPERMATOZOON

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Summary

Suitable washing techniques, which do not appreciably affect sperm motility, and enzymic digestion, have made it possible to give a clear picture of the finer structures in the human spermatozoon, using the electron microscope.

The axial filament, which arises from the anterior distal centriole, consists of nine or possibly eleven fibrils, which have a maximum diameter of about 500 Å, and taper gradually towards the tip of the tail. The proximal regions of the fibrils, immediately adjacent to and within the anterior distal centriole, consist of a number of granules, about 600×400 Å, longitudinally aligned. These granules are presumably concerned in the protein synthesis which is responsible for the growth of the axial filament during spermiogenesis.

The axial filament is surrounded in the mid-piece of the sperm by a broad helically-wound cord or spireme, which terminates, after 12-15 turns, at the annular posterior distal centriole.

In the sperm tail, the axial filament is encased in a strong sheath, the major component of which is a closely-wound helical cord about 200 Å in diameter, ending abruptly about 7-10 μ from the distal extremity of the axial filament. In marked contrast to the behaviour of bull sperm, this naked tip of the axial filament does not readily fray into the component fibrils.

The tail contains two fibrils which appear to be less susceptible to pepsin than the remainder. This result seems to imply some functional differentiation, and the mechanism of sperm locomotion is discussed in the light of the structural detail revealed.

I. INTRODUCTION

In recent years a number of reports on the electron microscopy of spermatozoa have appeared in the literature. These include studies on bull and towl sperm (Baylor, Nalbandov, and Clark 1943), fowl sperm (Grigg and Hodge 1949), bull sperm (Bretschneider and Van Iterson 1947) and *Arbacia* sperm (Harvey and Anderson 1943). Schmitt (1944) has discussed the ultra-structure of sperm tails in the light of the electron microscopical and optical evidence.

The human spermatozoon, however, has received little attention from electron microscopists, possibly because it does not lend itself so easily to direct methods of examination. Only two reports have appeared to date. Seymour and Benmosche (1941) described the general appearance of the human spermatozoon and noted that the mid-piece was apparently segmented. Reed

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and Reed (1948) examined spermatozoa from 38 young healthy subjects. They found that the galea capitis and brush-branching of the tail commonly observed in the bull sperm were characteristically absent in the human spermatozoon, and claimed that there was evidence for a spiral formation within the mid-piece. This resembles the finding of Bretschneider and Van Iterson (1947) that there is a helically-wound cord in the mid-piece of the bull sperm.

In the work reported here, the application of enzymic digestion techniques has enabled the finer structural details to be elucidated more fully than in the past. These methods have already been used to advantage in studies of the fowl spermatozoon (Grigg and Hodge 1949).

II. MATERIALS AND METHODS

The relatively high proportion of colloidal and other extraneous material present in fresh human semen rendered it unsuitable for the mounting of specimens for electron microscopic (E.M.) examination without further treatment. Dilution with distilled water and washing by centrifugation was a useful technique in separating the spermatozoa from the colloidal material also present in the semen, but, in view of the drastic effects of distilled water on fowl spermatozoa (Grigg and Hodge 1949), there is necessity for caution in the interpretation of the results obtained by this method. The work on fowl spermatozoa has made it clear that the safest preparative procedures for spermatozoa are, in general, those in which the motility is not impaired by the treatment. The motility is thus a convenient index of the structural integrity of the spermatozoa being treated. Suitably clean suspensions of human spermatozoa were easily obtained by the procedure outlined below, and one could be certain that the spermatozoa were free from any distortion or structural alteration, since the motility was not appreciably impaired at any stage of the washing procedure.

Samples of fresh semen were diluted with 15-20 volumes of Tyrode solution and agitated to ensure homogeneous dispersion. There was no apparent decrease in motility arising from the dilution, a result which is in marked contrast to the rapid cessation of all movement which occurs if the semen is diluted with distilled water. Thermal shock effects were guarded against in all manipulations by the avoidance of sudden temperature changes. The spermatozoa were spun down in an angle centrifuge at 1000-2000 r.p.m. and resuspended in fresh Tyrode solution after discarding the supernatant liquid. The centrifugation and resuspension was repeated three or four times in order to free the sperm from as much contaminating material as possible, the motility being checked after each operational sequence. After five centrifugations, the majority of the spermatozoa were still highly active, and any loss in motility could be attributed to the mechanical effect of centrifugation. The adequacy

of the procedure is indicated by the observation that many of the spermatozoa in a thrice-washed suspension were still active after 48 hours storage at room temperature.

The spermatozoa could now be mounted by allowing a drop of the suspension to dry on a conventional specimen screen covered by a collodion film. However, this procedure resulted in the formation of numerous salt crystals, so that there was some danger of distortion. There was also the possibility of structural changes due to the increasing hypertonicity during evaporation of the drop to dryness. Although salt crystals were easily removable by washing the screen in distilled water, this involved the possibility of drastic alterations as a result of exposing the spermatozoa to a hypotonic medium. These dangers were effectively overcome by adding a small volume of 10 per cent. formalin to the final washed suspension to bring the concentration of formalin to about 0.5 per cent. All movement ceased immediately and suspensions were then left overnight to ensure complete fixation, spun down and resuspended in distilled water. One or two washings sufficed to obtain a salt-free suspension from which specimens for examination in the electron microscope were easily prepared. Formalin-fixed spermatozoa were free from the disruptive effects of distilled water. The above technique of washing in suitable isotonic media, adding formalin, and finally washing in distilled water seems to be generally applicable to biological materials which it is desired to obtain free from the structural alterations resulting from hypo- or hypertonicity of the suspending medium.

Tryptic* and peptic digestion was carried out on the final washed suspensions in distilled water. Several washings were necessary to remove all traces of free formalin. The spermatozoa were spun down, resuspended in a suitable buffer solution (pH 3 for pepsin, pH 8 for trypsin), and a few crystals of the enzyme added. With pepsin, 30 minutes at 37°C. was sufficient to break down most of the spermatozoa to a state suitable for examination. For trypsin much longer periods were necessary (several days). Enzymic action was stopped after the required incubation period by the addition of formalin, and the material either mounted immediately or after further washing with distilled water.

The well-known technique of staining specimens with phosphotungstic or phosphomolybdic acid was often employed as a means of increasing image contrast, as was the shadow-casting technique of Williams and Wyckoff (1946). Platinum was used exclusively as the shadowing metal in preference to gold, which tends to migrate and coagulate under the influence of a high-intensity electron beam. In all shadow-cast specimens, the shadow-casting was carried out so that the ratio of shadow length to object height was about 4:1.

The electron microscope used in the present investigation was an R.C.A. Type EMU. The instrument was fitted with an objective aperture and was calibrated for magnification by the method of Farrant and Hodge (1948).

* The enzymes used in the investigation were "Difco" pepsin and "B.D.H." trypsin.

III. RESULTS

(a) General Appearance

Plate 1, Figures 1 and 2, illustrates the outline of spermatozoa after the Tyrode-formalin treatment described above. The sperm head varies both in size and shape, but is usually ovoid in outline and $3\text{--}4\text{ }\mu$ long. Although some of this variation in appearance is due to individual differences, much of it is the result of the manner in which the sperm lie on the supporting film. That many of the sperm heads do not lie flat on the film but project upwards at various angles has been demonstrated by shadow-casting. The sperm head is attached to the mid-piece and tail by a short region ($<1\text{ }\mu$) which may be termed the neck. This region corresponds to the articular strands described by Bretschneider and Van Iterson (1947) in bull sperm. The neck is immediately followed by the mid-piece, which is $0.6\text{--}0.7\text{ }\mu$ wide and $5\text{--}6\text{ }\mu$ long, and often shows internal structure, which will be considered in detail later. The mid-piece is followed by the tail proper, which is about $0.5\text{ }\mu$ wide at the tail-mid-piece junction and tapers gradually until a point about $7\text{--}10\text{ }\mu$ from the extreme end is reached. At this point the width decreases abruptly and remains fairly constant up to the tip (Plate 1, Figs. 2 and 4; Plate 2, Fig. 6). Plate 2, Figure 6, shows that this break in outline corresponds with the termination of the helically-wound cord of the tail sheath. The naked tip of the tail ($7\text{--}10\text{ }\mu$ in length) is usually intact and shows no sign of fraying. This is in agreement with the observation of Reed and Reed (1948) that there is no brush branching of the tail in this region. Occasionally, however, fraying does occur as a result of "osmotic shock" (Plate 2, Fig. 5).

None of the sperm examined showed the presence of the galea capitis, which is normally present in bull sperm, nor was there any sign of the crater-like notch on the vertex of the head, which Seymour and Benmosche (1941) suggested was possibly some form of suction apparatus to facilitate penetration of the ovum.

The overall lengths of the spermatozoa were between 50 and $65\text{ }\mu$. Here again, as for the sperm head, there was a considerable range of individual variation. A number of sperm had cytoplasmic beads attached at various points, but most frequently on the mid-piece close to the head. These beads varied in size up to something approaching the dimensions of the sperm head. Their presence did not seem to affect the motility of the spermatozoa as seen in hanging-drop preparations. Although a few spermatozoa were observed with small heads and other possibly abnormal features, the description of such abnormalities is beyond the scope of the present paper, which is intended only as a basis of reference for future work on the development and pathology of spermatozoa. It is believed that the features described here are those of normal spermatozoa.

(b) The Sperm Head

The profile of the sperm head is shown in Plate 1, Figure 3, which was taken when the supporting film ruptured and curled over. The thickest part of the head is about 1μ . It will be seen that the anterior region of the head is thin, and tapers towards the anterior extremity. The thinness of the head here explains why there is often a region which is partially transparent to 50 kilovolt electrons. The high density of the material in the head is consistent with the belief that it consists mainly of nuclear material. It seems reasonable to suppose that Plate 1, Figures 1 and 2, presents fairly good representations of the appearance of the spermatozoa in their natural state, provided that some allowance is made for the moderate degree of flattening arising from the dehydration necessarily imposed by electron microscopic examination. Dawson and MacFarlane (1948) and Farrant and O'Connor (1949) have discussed the dimensional changes resulting from drying, under various conditions, of the larger animal viruses. Their results appear to indicate that fixation, in general, has a beneficial effect in minimizing the partial collapse which occurs on dehydration of biological material.

Pepsin appears to have little effect on the material of the sperm head (Plate 2, Fig. 7; Plate 5, Fig. 14). The heads are swollen by trypsin and often show transparent areas. Occasionally they burst and the material within is extruded, but it has not yet been possible to demonstrate the chromatin fibrils which are clearly visible in fowl sperm heads after similar treatment (Grigg and Hodge 1949). Swelling of the head, similar to that observed in trypsin-treated samples, was also observed when spermatozoa, after repeated washing in Tyrode solution, were spun down and resuspended in distilled water.

(c) Mid-Piece and Tail

These two structures seem to be differentiated regions of a more general structure which might be termed the locomotor unit. The justification for considering them together lies in the observation that the axial filament runs continuously throughout both structures from the rear of the head to the tip of the tail, an organization which implies a physiological as well as a structural continuity.

Plate 2, Figure 7; Plate 3, Figure 8; Plate 4; Plate 5; Plate 6; and Plate 7 illustrate the internal structure revealed by treatment with pepsin at pH 3. The axial filament evidently consists of a number of fine fibrils (Plate 4; Plate 5; and Plate 6, Fig. 15) and extends continuously throughout the mid-piece and tail. In the mid-piece region, the axial filament appears to consist of nine fibrils (Plate 5, Fig. 13; Plate 6, Fig. 15), none of which are differentiated in appearance or resistance to peptic digestion from the remainder. The interpretation of the results for the tail region is complicated by the occurrence of two dense fibrils which appear to be intimately associated with the helical cord of the tail sheath (Plate 4, Fig. 12; Plate 7, Fig. 18). Unfortunately it has not been

possible to determine whether these two fibrils are additional to the nine already demonstrated, or whether they indicate some differentiation in the tail region of two of the nine fibrils; that is, whether the tail contains a total of eleven or nine fibrils respectively. It is of interest to note in this connection that Grigg and Hodge (1949) have demonstrated a total of eleven fibrils in the fowl sperm tail in which the membranous tail sheath is easily disrupted by distilled water. Two of these fibrils are clearly differentiated from the remaining nine on the basis of their relative susceptibility to distilled water and peptic digestion. In the human spermatozoon the presence of a helical cord in the tail sheath prevents fraying of the tail in distilled water, but it seems likely that there is a similar differentiation among the tail fibrils.

The axial filament is surrounded in the mid-piece by a helical structure (Plate 2, Fig. 7; Plate 3, Figs. 8 and 9), which has often been referred to in the literature as the spireme, and is believed to be derived from the mitochondria which migrate to this region during spermiogenesis. Plate 4, Figures 11 and 12, shows the mid-piece and tail in spermatozoa which have suffered extensive peptic digestion. The latter Figure demonstrates clearly that the spireme breaks down into a number of elongated bodies, which in the intact spermatozoon are presumably joined end to end to form a continuous helical cord. It is of interest to note that in the fowl spermatozoon the mitochondrial granules are apparently arranged to give a true segmentation, and there is no helical winding in the mid-piece or tail (Grigg and Hodge 1949). Plate 3, Figure 10, illustrates the helical arrangement in the mid-piece of the bull sperm. The three fine filaments, which stain densely with phosphomolybdic acid, appear to be components of the broad helical cord described by Bretschneider and Van Iterson (1947). Similar fine filaments have been observed in the mid-piece of the human spermatozoon, particularly on the original plates, but were not sufficiently clear for reproduction in this paper. Since helical structures have also been observed in the mid-piece of ram and marsupial sperm (Hodge, unpublished data), the evidence available at present seems to indicate that helical structures are characteristically present in the mid-piece of mammalian spermatozoa.

The fibrils of the axial filament are surrounded in the anterior portion of the tail proper by a strong sheath, the major component of which is a helically-wound cord about 200 Å in diameter. This helical winding may be seen in untreated sperm (Plate 1 and Plate 2, Figs. 5 and 6), but is most clearly visible in preparations subjected to peptic digestion (Plate 6, Fig. 16; Plate 7, Fig. 17). It commences at the tail-mid-piece junction (Plate 2, Fig. 7) and terminates at a point 7-10 μ from the extreme tip of the tail (Plate 2, Fig. 6). This helical cord has also been demonstrated in bull sperm (Bretschneider and Van Iterson 1947) and in marsupial sperm (Hodge, unpublished data). It is not present in avian sperm (Grigg and Hodge 1949) or in *Arbacia* sperm (Harvey and Anderson 1943). It seems reasonable, therefore, to suppose tentatively that it is a characteristic feature of mammalian sperm, although more extensive

investigation will be necessary before this view can be definitely accepted. The presence of the helical cord affords an explanation of the failure of mammalian sperm tails to fray into fibrils when placed in distilled water. This phenomenon occurs easily with fowl and squid sperm, which have only a membranous tail sheath, easily ruptured by "osmotic shock."

The failure of the naked tip of the human sperm tail to fray as does the tip in bull sperm seems capable of two explanations. The axial filament itself may be surrounded by a relatively tough membrane or the fibrils may be effectively cemented together by an inter-fibrillar matrix material. Such a matrix material has been demonstrated in the fowl sperm, but evidently fails in some degree to prevent separation of the fibrils, since the tails fray easily in distilled water.

There is little to suggest why the helical winding should end abruptly, leaving about 8-10 μ of naked axial filament. It seems possible that there is here a functional analogy with such locomotor organs as the fish tail, where as is well known, the "flexibility" increases steadily as the extremity of the tail is approached. A consideration of the hydrodynamic principles involved shows that such a variation in "flexibility" is essential if the propulsive organ is to work at maximum efficiency. This variation is apparently partially achieved in the sperm by the tapering of the tail from the tail-mid-piece junction. That the propulsive movements of the sperm tail are essentially similar to those of the fish tail is easily seen in hanging-drop preparations in which the sperm have lost most of their initial vigorous activity.

The helical cord itself shows signs of a characteristic fine structure (Plate 7, Fig. 17), which has however been obscured to some extent by the drastic procedures required to free the helical cord from the axial filament. The functional nature of this cord is obscure. That it is not essential for locomotion is indicated by its absence in many other types of sperm. It would seem to be primarily a structural feature, but may possibly contribute in some degree towards efficiency of propulsion.

The fibrils of the axial filament arise from a composite body (Plate 5, Fig. 13, Plate 6, Fig. 15) which will be termed the anterior distal centriole in accordance with the nomenclature adopted for the fowl spermatozoon (Grigg and Hodge 1949). The anterior distal centriole is located at the rear extremity of the sperm head, and according to classical observations on spermiogenesis is immediately adjacent to the proximal centriole in the mature sperm. The axial filament is believed to develop from the anterior distal centriole during spermiogenesis. None of the electron microscope evidence is at variance with this belief, but a systematic study of spermiogenesis with this instrument would be necessary to confirm it.

The fibrils of the axial filament are about 500 Å wide in the vicinity of the anterior distal centriole and taper gradually to a relatively uniform diameter in the tail proper. The anterior extremity of each fibril consists of several longitudinally aligned granules about 600×400 Å (Plate 7, Fig. 18). These

small granules are possibly concerned in the production of the fibrils during spermiogenesis. The anterior distal centriole seems to consist almost exclusively of them.

The tail fibrils sometimes exhibit what appears to be a periodic cross-striation, the axial period being about 100 Å. This structure appears to be similar to that observed by Hall, Jakus, and Schmitt (1945) in smooth molluscan muscle, but peptic digestion obscured the structure to such a degree that reproduction of the micrographs was impossible. However, a structure such as this is not unlikely, since all evidence to date suggests that these fibrils must be contractile elements responsible for sperm locomotion. The thinness of the fibrils in the region beyond the mid-piece in pepsin-treated sperm (Plate 4, Fig. 11) suggests that they are composite structures, consisting of an outer easily digested layer surrounding an inner more resistant core, and moreover, that there is some differentiation between the part of each fibril contained within the mid-piece and that part within the tail itself, at least with respect to their resistance to enzymic attack. This may well be a reflection of some functional difference. A similar diminution in diameter of the tail fibrils has also been observed in fowl sperm after enzymic digestion (Grigg and Hodge 1949).

The possible roles of the two well-defined fibrils seen in Plate 4, Figure 12, and Plate 7, Figure 18, are of considerable interest. These fibrils appear to be relatively insusceptible to the action of pepsin as compared with the other fibrils in the tail, a phenomenon which suggests that there may also be a functional differentiation between the two types of fibrils. Any theory regarding their function must of necessity at this stage be purely speculative, but it seems worthwhile to point out that if the fibrils of the axial filament are contractile elements responsible for sperm locomotion, then the characteristically "sinusoidal" flexure of the sperm tail during motion must be induced by localized contraction of small lengths of the fibrils in a regular time sequence pattern. The "sinusoidal" configuration of the tail cannot be explained by a sequence of contractions in which the whole length of each fibril is simultaneously involved, and it becomes apparent that only a fraction of any given fibril can be contracted at any given instant. If this is so, a "sinusoidal" flexure can only be achieved in two ways:

- (a) The contraction of a fibril may pass along its length in the form of a wave of contraction. If then waves of contraction are initiated in the various fibrils in some definite order and with a time-lag between the initiation of each pulse, a "sinusoidal" flexure could be obtained.
- (b) If the two differentiated fibrils (Plate 4, Fig. 12; Plate 7, Fig. 18) are regarded as "neural" fibrils, capable of transmitting impulses, then the localized contraction of the contractile fibrils may occur only in those regions in intimate contact with the "neural" fibrils. Thus if the "neural" fibrils cross over one another several times in the length of the tail and alternately transmit impulses in a regular time sequence, the tail must assume a "sinusoidal" configuration at any given instant.

Although the two differentiated fibrils were often observed to cross over one another, there was no apparent regularity and the observation may well have been fortuitous. The observation that the tail fibrils appear to be composite structures, consisting of a relatively resistant core and a less resistant sheath (see Plate 4, Fig. 11 and Plate 7, Fig. 18) seems to favour the notion of waves of contraction. Indeed this is the simplest possible explanation of the functioning of the axial filament, but leaves unexplained the structural complexity of the tail as a whole.

IV. ACKNOWLEDGMENT

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APPENDIX I

LIST OF PREPARATIVE TREATMENTS

(a) Fresh semen diluted with 15-20 volumes of Tyrode solution, centrifuged, and resuspended 3 X in Tyrode solution, formalin added, stored 24 hours at room temperature, centrifuged and resuspended 2 X in distilled water.

(b) Fresh semen diluted with 15-20 volumes of Tyrode solution, centrifuged, and resuspended 2 X in isotonic saline and 2 X in distilled water to produce "osmotic shock."

(c) Initial treatment as in (a), then acidified to pH 3 with HCl, pepsin added, incubated at 37°C., or 20°C. for 10, 20, or 30 minutes. (See captions to electron micrographs for time and temperature of incubation). Reaction was usually stopped with formalin and the samples centrifuged and resuspended 2 X in distilled water before mounting.

(d) Initial treatment as in (a), then resuspended in McIlvaine buffer at pH 8, trypsin added, incubated at 37°C. for 67 hours, reaction stopped with formalin, centrifuged and resuspended 2 X in distilled water before mounting.

EXPLANATION OF PLATES 1-7

Abbreviations used in electron micrographs.—h., sperm head; m., mid-piece; t., sperm tail; n., neck of sperm; a.f., axial filament; sp., spireme; a.d.c., anterior distal centriole; p.d.c. posterior distal centriole; t.s., tail sheath; t.h., termination of helical component of tail sheath; f., fibrils of axial filament; r.f., resistant fibrils; g., granules in fibrils of axial filament near anterior distal centriole.

PLATE 1

- Fig. 1.—Human sperm treated as in (a) (see Appendix I for details of preparative treatments), shadowed with platinum, showing general appearance of head, mid-piece, and tail.
Fig. 2.—Complete human spermatozoon, treatment (a), shadowed with platinum.
Fig. 3.—Human sperm head, treatment (b), unstained, showing profile as seen after rupture and curling of the supporting film.
Fig. 4.—Human sperm, treatment (a), shadowed with platinum, showing typical appearance of the intact tail.

PLATE 2

- Fig. 5.—Human sperm, treatment (b), unstained, showing tail and portion of mid-piece. Note fraying of the axial filament as a result of "osmotic shock."
Fig. 6.—Human sperm, treatment (a), stained with phosphomolybdic acid, illustrating the helical component of the tail sheath and its abrupt termination, leaving a length of the axial filament exposed.
Fig. 7.—Human sperm, treatment (c), incubated with pepsin for 20 minutes at 20°C., stained with phosphomolybdic acid, showing the broad helical structure within the mid-piece and the fine helical component of the tail sheath.

PLATE 3

- Fig. 8.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., shadowed with platinum. Note helical structure in mid-piece and tail.
Fig. 9.—Human sperm, treatment (d) with trypsin, stained with phosphomolybdic acid. Note the fibrils of the axial filament running through the mid-piece and tail, and the helical structure in the mid-piece.
Fig. 10.—Bull sperm transported in yolk-citrate medium, centrifuged, and resuspended 6 X in Tyrode solution, formalin added, stored 24 hours at room temperature, centrifuged, and resuspended 2 X in distilled water, stained with phosphomolybdic acid, showing portion of mid-piece. Note the three densely-staining fibrils arranged in helical fashion around the fibrils of the axial filament.

PLATE 4

- Fig. 11.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., stained with phosphomolybdic acid, illustrating the relative resistance of those portions of the fibrils contained within the mid-piece. Note also the granular appearance (g.) of the fibrils near the anterior distal centriole.

- Fig. 12.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., stained with phosphomolybdic acid, showing disorganization of the helical structure in the mid-piece into a number of elongated granules and the two resistant fibrils in the tail. Note also the remains of the helical winding of the tail sheath.

PLATE 5

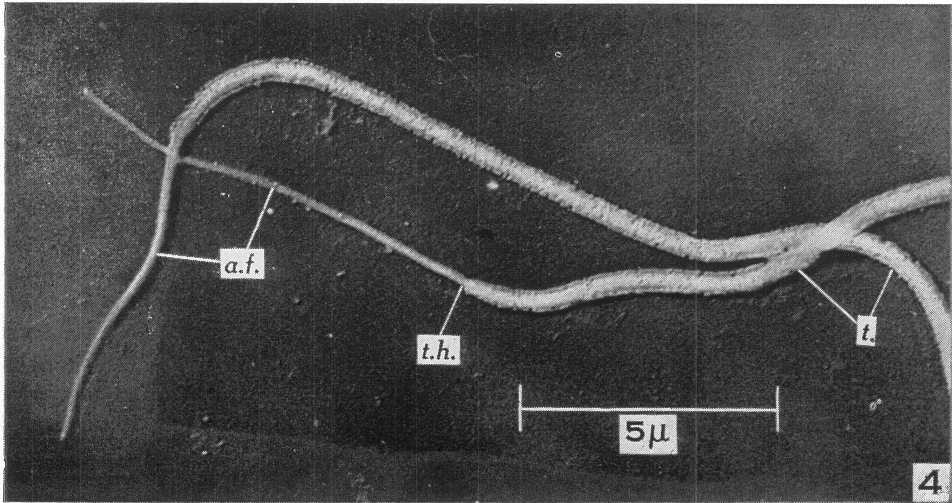
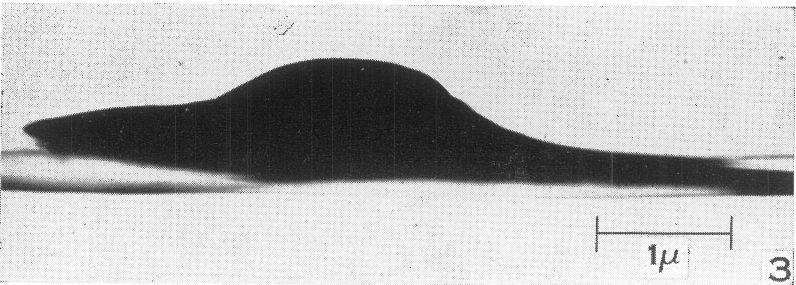
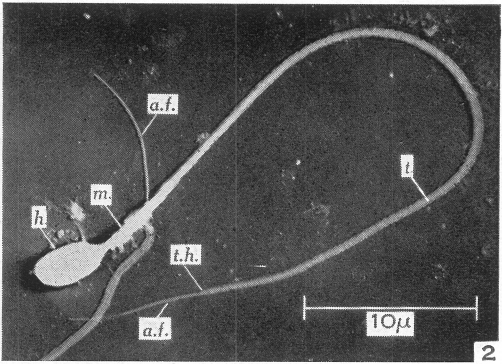
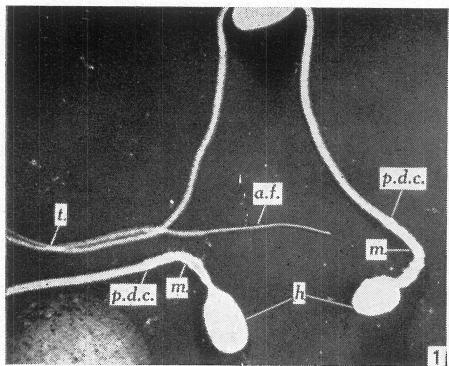
- Fig. 13.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., shadowed with platinum, showing anterior distal centriole and fibrils of the axial filament.
- Fig. 14.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., stained with phosphomolybdic acid. Note fibrils arising from the anterior distal centriole. Mid-piece has been entirely removed except for the axial filament.

PLATE 6

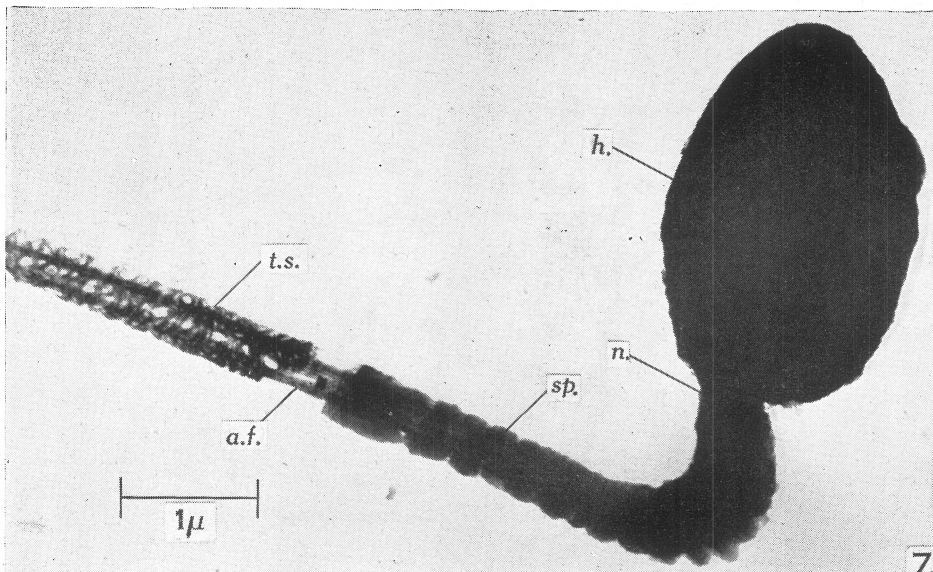
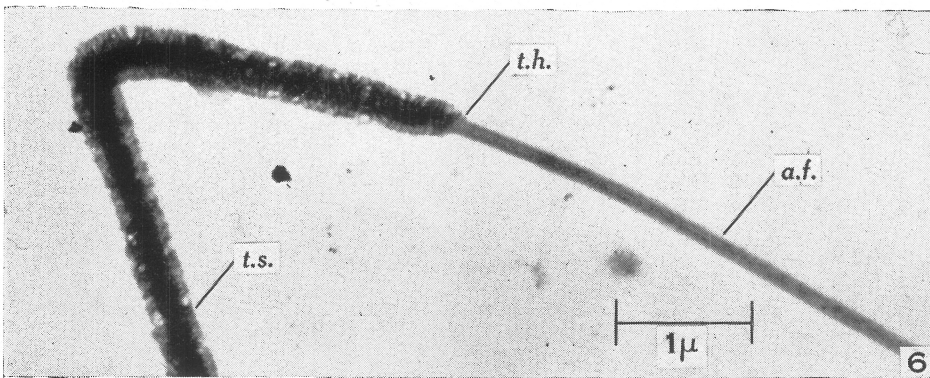
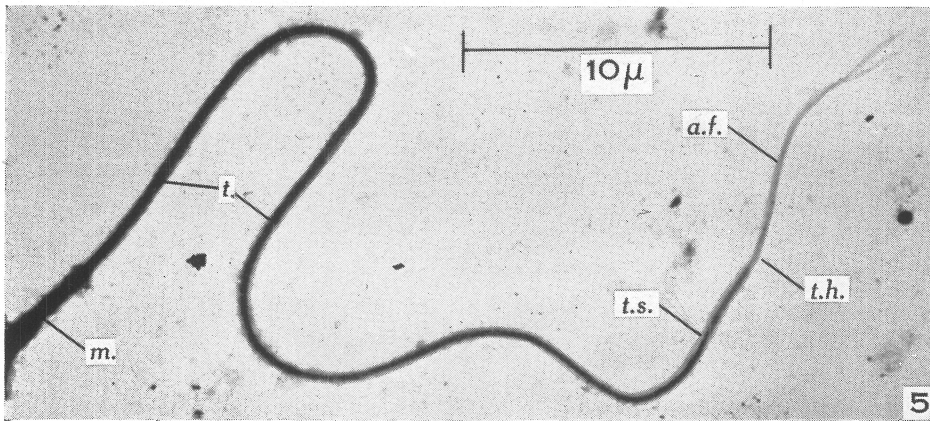
- Fig. 15.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., shadowed with platinum, showing nine fibrils of the axial filament arising from the anterior distal centriole and passing into the tail sheath.
- Fig. 16.—Human sperm, treatment (c), incubated with pepsin for 10 minutes at 20°C., stained with phosphomolybdic acid, showing in more detail the helical component of the tail sheath.

PLATE 7

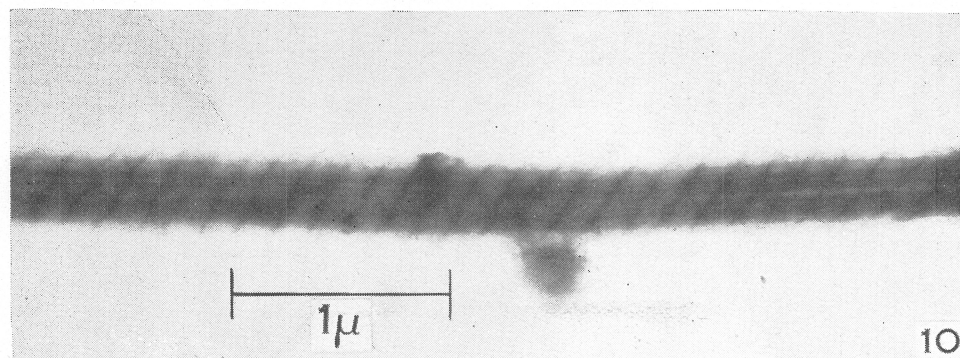
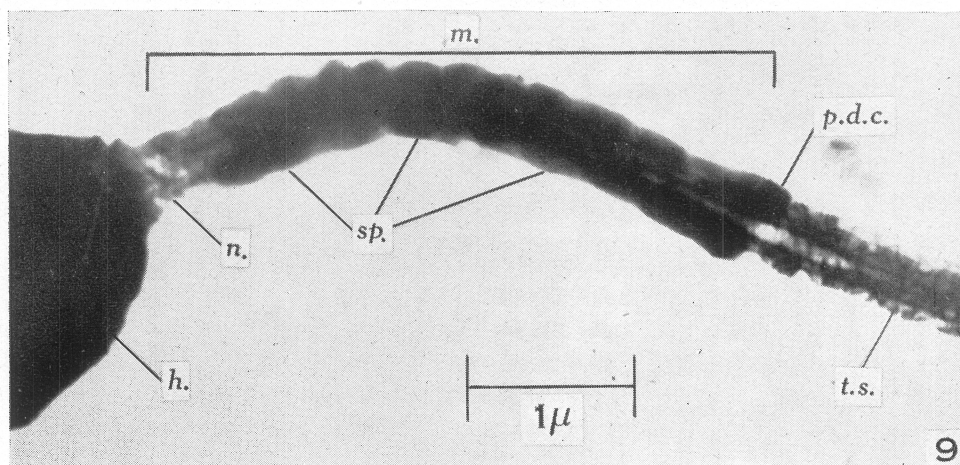
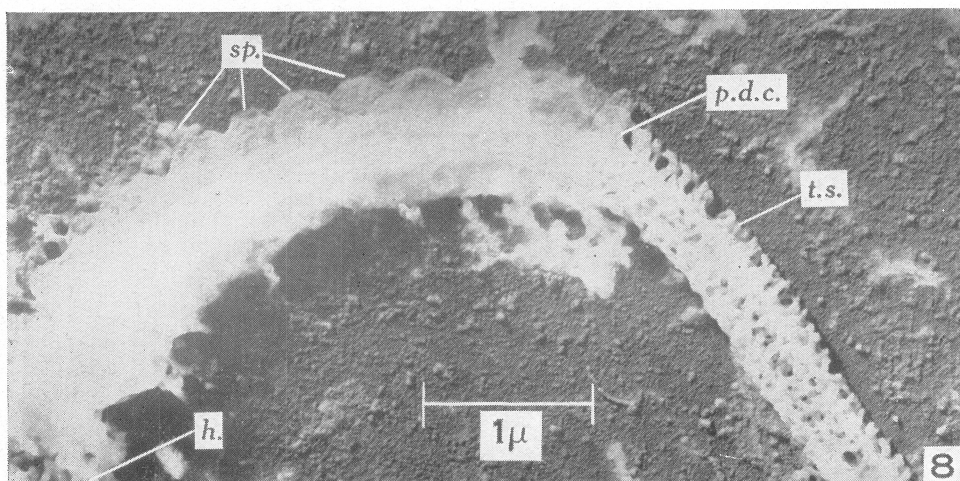
- Fig. 17.—Human sperm, treatment as in Plate 6, Figure 16, stained with phosphomolybdic acid, small portion of the helically-wound component of the tail sheath. Note the fine structure of the helical cord.
- Fig. 18.—Human sperm, treatment (c), incubated with pepsin for 30 minutes at 37°C., stained with phosphomolybdic acid, showing the fibrils of the axial filament, granules (g.) adjacent to the anterior distal centriole, and the two resistant fibrils (r.f.).

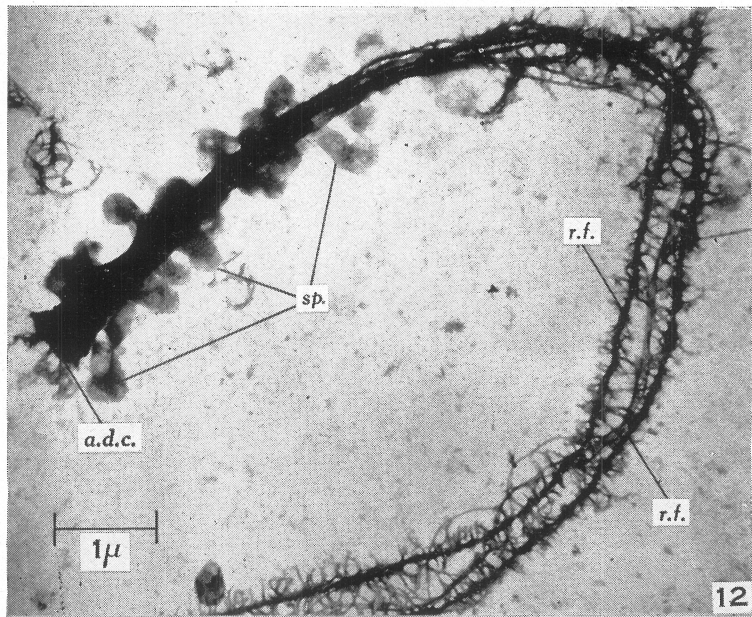
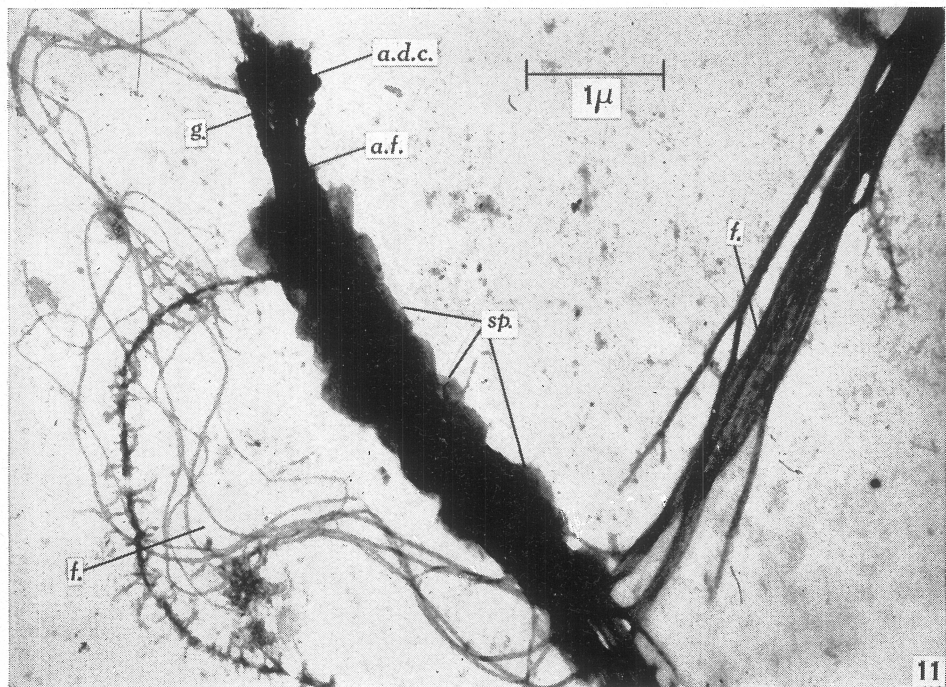


HODGE.—ELECTRON MICROSCOPIC STUDIES OF SPERMATOOA

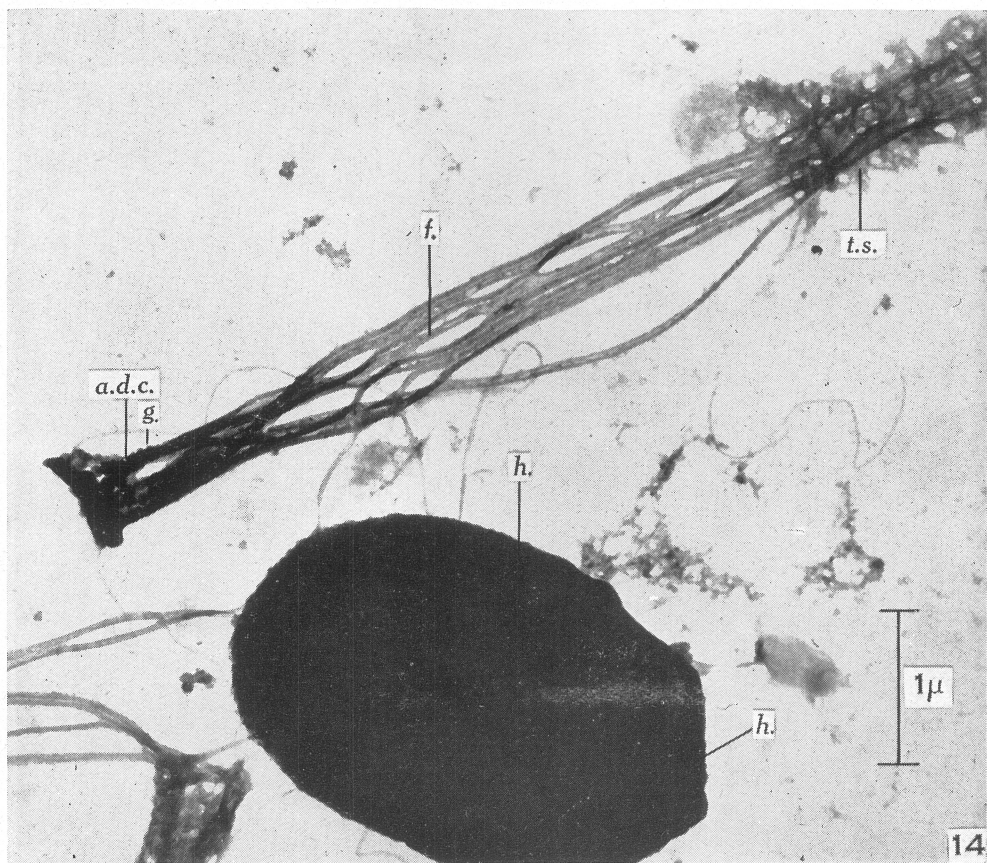
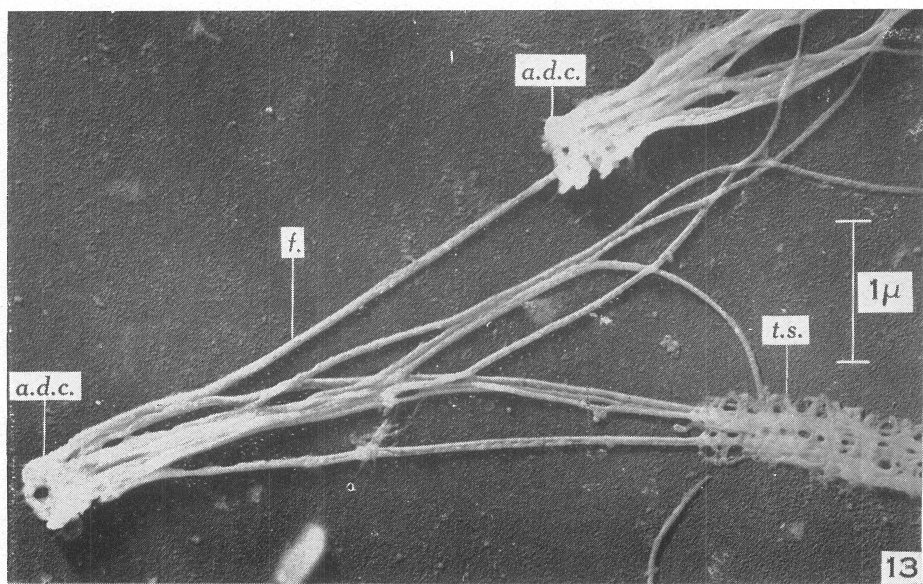


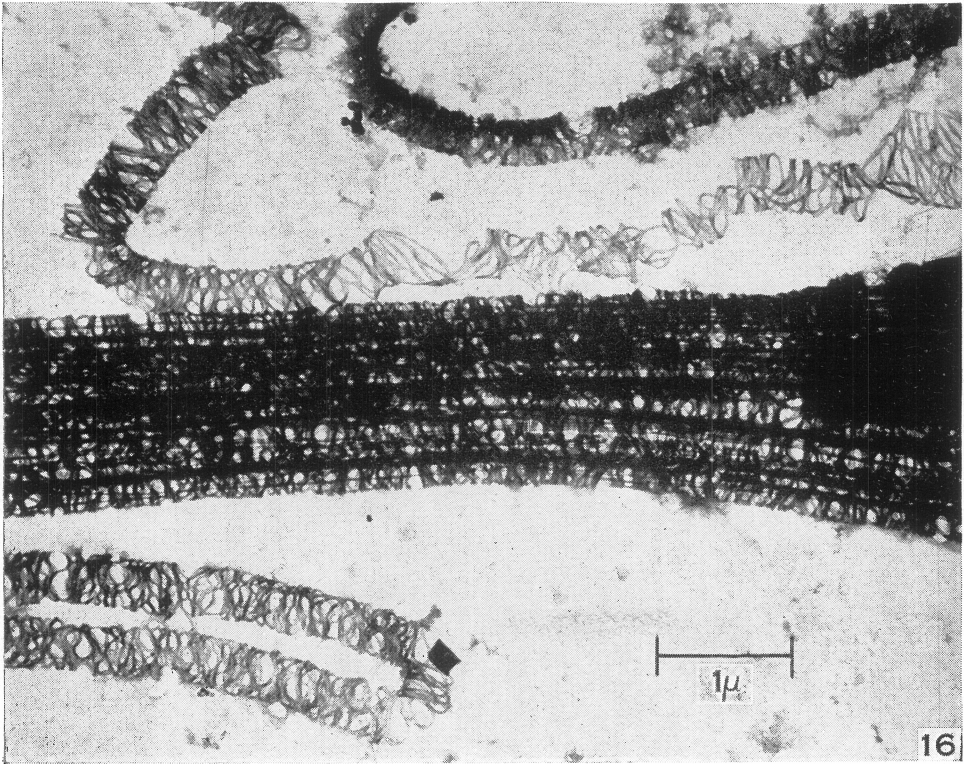
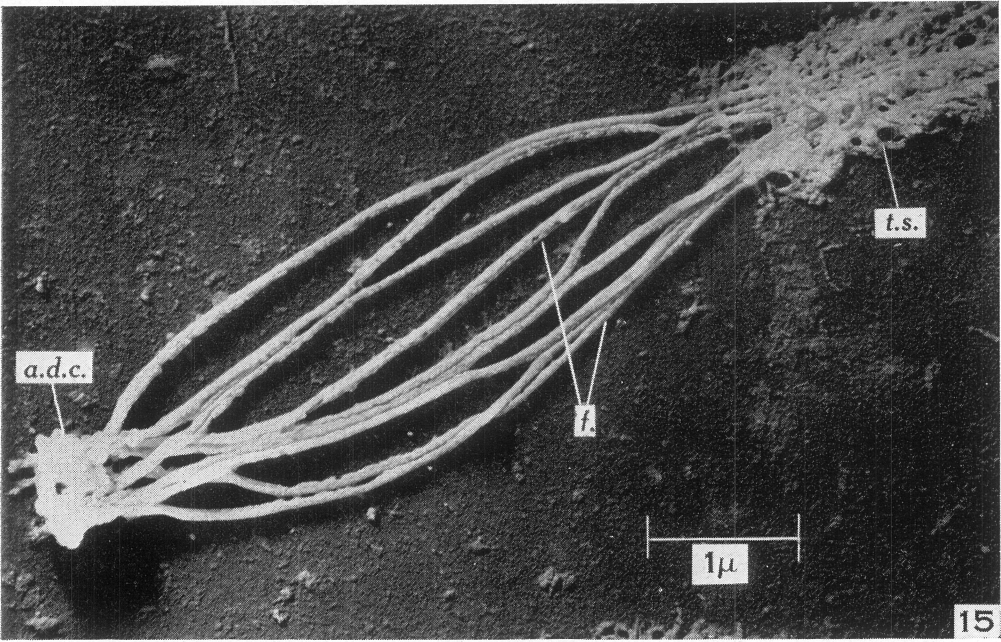
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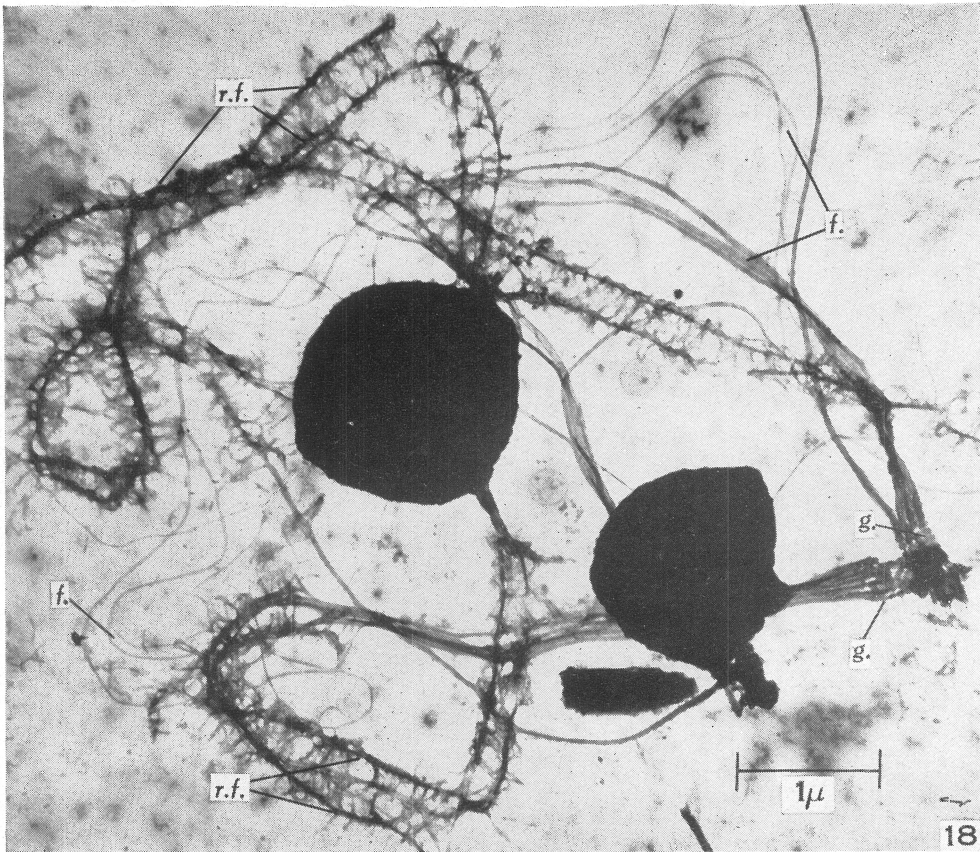
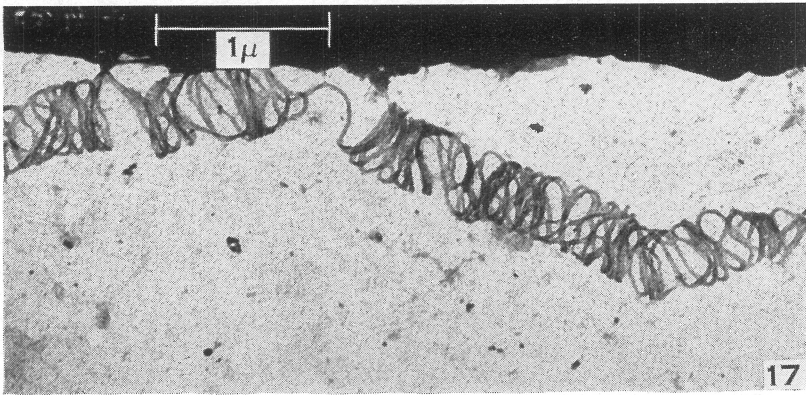




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