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# SPERMATOZOA *

BY

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[WITH SPECIAL PLATE]

My researches on spermatozoa arose out of an interest in the early phases of reproduction, the fertilization by a spermatozoon of an unfertilized egg. Fertilization has been mainly studied in lower animals, notably the sea-urchin, because its eggs and spermatozoa can be obtained in vast quantities. In addition, the sea-urchin egg is transparent, so one can see quite well what is going on inside it. Although in higher animals such as man spermatozoa can be obtained by the million, human and mammalian eggs are awkward experimental material, both because they are produced in very small numbers and because they are difficult to obtain. It so happens that the general features of fertilization are fairly similar in sea-urchins and man; the fact, therefore, that we have to work a lot with lower animals does not greatly hinder our understanding of fertilization.

The unfertilized egg is a cell about the size of a small pin's head. In the animal kingdom spermatozoa usually collide with it by chance, though special mechanisms exist to ensure that the eggs and spermatozoa are liberated near each other. Sea-urchins, for example, crawl into shallow water near the shore at the breeding season, so that when they spawn, releasing their eggs or spermatozoa into the sea-water, there is quite a chance that they will be near each other. The spermatozoa are produced in fantastic numbers; for example, if all the spermatozoa produced in one breeding season by a single British sea-urchin were put end to end, they would nearly stretch round the world—20,000 miles (32,000 km.) to be precise. It is 24,000 miles (38,600 km.) round the world at the Equator. One of the many problems which has not been completely solved is why so many spermatozoa are produced relative to the number of eggs they have to fertilize. Russian scientists have put forward some rather odd theories to account for this disparity. They have suggested that, in addition to their normal function, spermatozoa fertilize cells lining the female reproductive tract, thereby conferring some benefit on the female. This is called somatic fertilization.

Returning to normal fertilization, when a spermatozoon collides with an egg, sticks to it, and starts to enter, the following things happen: first, a change takes place at the egg surface preventing other spermatozoa from refertilizing the egg. This phenomenon is called monospermy, or the block to polyspermy; with a few exceptions, monospermy is the rule. Of course, if two spermatozoa happen to collide in the right way with an egg, at so nearly the same time that the change in the egg surface is not complete, both may get in and fertilize the egg. That is dispermy or polyspermy. In the overwhelming number of cases such eggs soon die. There is, however, one boy in Sweden whom some people thought, wrongly I believe, might be the product of a dispermic egg—that is to say, two of his father's spermatozoa managed to get in and fertilize his mother's egg. This is why some people suspected this might be the case. The hereditary material, deoxyribonucleic acid (D.N.A.), is present in constant quantities in all the cells of human beings except two. These are eggs and spermatozoa, each of which contain half the D.N.A. present in the other cells of the body, so that when a spermatozoon and an egg come together at fertilization the normal amount of D.N.A. is restored. Ordinary cells in a human being contain 46 D.N.A.-carriers or chromosomes, so that human eggs and spermatozoa each contain 23 chromosomes. The cells in the body of the Swedish boy (who was abnormal in several respects) did not contain 46 but 69 chromosomes, which is 23 too many, the exact number present in the spermatozoon. There is, therefore, a possibility, though most people disbelieve it, that this boy was the product of a double fertilization, the only case known in the history of mankind.

But, as I said, this is exceedingly rare, and normally only one spermatozoon fertilizes an egg, others being prevented from entering by a change in the egg surface initiated by the first fertilizing spermatozoon.

Apart from initiating the block to polyspermy, the fertilizing spermatozoon has to hand over its hereditary material, D.N.A., to the egg, so that the offspring contains hereditary characteristics derived from both the mother and father. The spermatozoon also has another function and a most important one—to start the egg developing. Development can be initiated by a spermatozoon without the subsequent transfer of its D.N.A., and, in some cases, the development proceeds to the production of the adult, called in such circumstances gynogenetic. Parthenogenesis and gynogenesis are, evidently, similar phenomena. In the former, development is initiated by some physical or chemical stimulus; in the latter the stimulus is a spermatozoon which does not participate in the reactions following the initial, activating, stimulus.

Fascinating as these phenomena are, some five or six years ago I felt that it was going to be difficult, for the time being, to get much further in answering the question, "How does the spermatozoon fertilize the egg and initiate development?" or "What chemical, physical, or biochemical changes occur when an egg is fertilized?" I thought we had more or less come to a full stop for the time being, and that the subject had better be left for a few years until some clever person thought of a new way of tackling these questions. I therefore decided not to go on with my studies of fertilization, but to concentrate on one part of them, spermatozoa. They too are very fascinating. They are often said to look like microscopic tadpoles, consisting of a head and a tail with which they swim;

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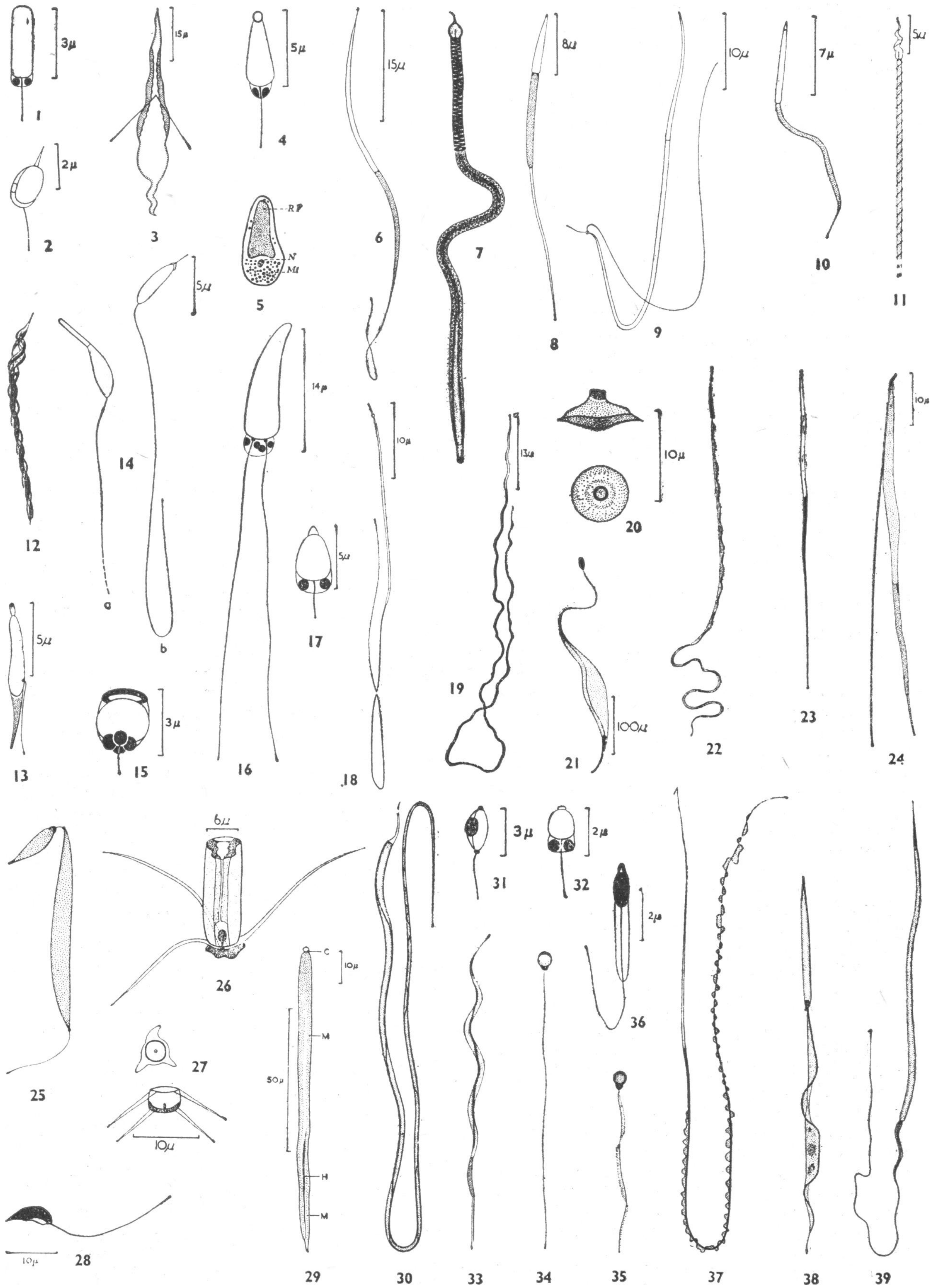


FIG. 1.—Examples of spermatozoa in the animal and plant kingdoms. (For key see opposite page.)

but if one takes a broader view and examines spermatozoa from different parts of the animal kingdom a considerable diversity of form is revealed. The animal kingdom is divided into about 22 major divisions, the phyla (Table I). Some of these divisions are rather coarse, because out of the million or so species of described animals, about 700,000 are insects, though in the Table, beard worms, the Pogonophora, of which there are only some 43 described species, appear to be more "important"—if that is the right word—than insects. We are only a tiny part of one of these phyla, about equal in "importance," from the point of view of the classification of the animal kingdom, to fleas.

### Sperm Morphology

It may be of interest to examine some examples (Fig. 1) of spermatozoa from different phyla of the animal kingdom and from plants, because, contrary to the belief of some people, many plants produce spermatozoa which fertilize eggs in the same way as human spermatozoa fertilize human eggs.

When thinking about these spermatozoa and the differences between them one cannot help asking such questions as, "What is the point of an undulating membrane?" "What is the point of having two tails?" "What is the point of not being able to move?" Similar questions arise when one examines the chemistry or biochemistry of semen, which consists of a liquid, seminal plasma, and spermatozoa suspended in it. If I am told the concentration of chloride, or of calcium, or of total nitrogen, or of citric acid, or of fructose in bull seminal plasma, I shall be able to predict the concentrations of the other constituents quite accurately, in spite of these five constituents being secreted by three separate glands. What is the point? I asked Professor Medawar, formerly of Birmingham University, whether it was possible that any of these peculiarities could be pointless. He replied that

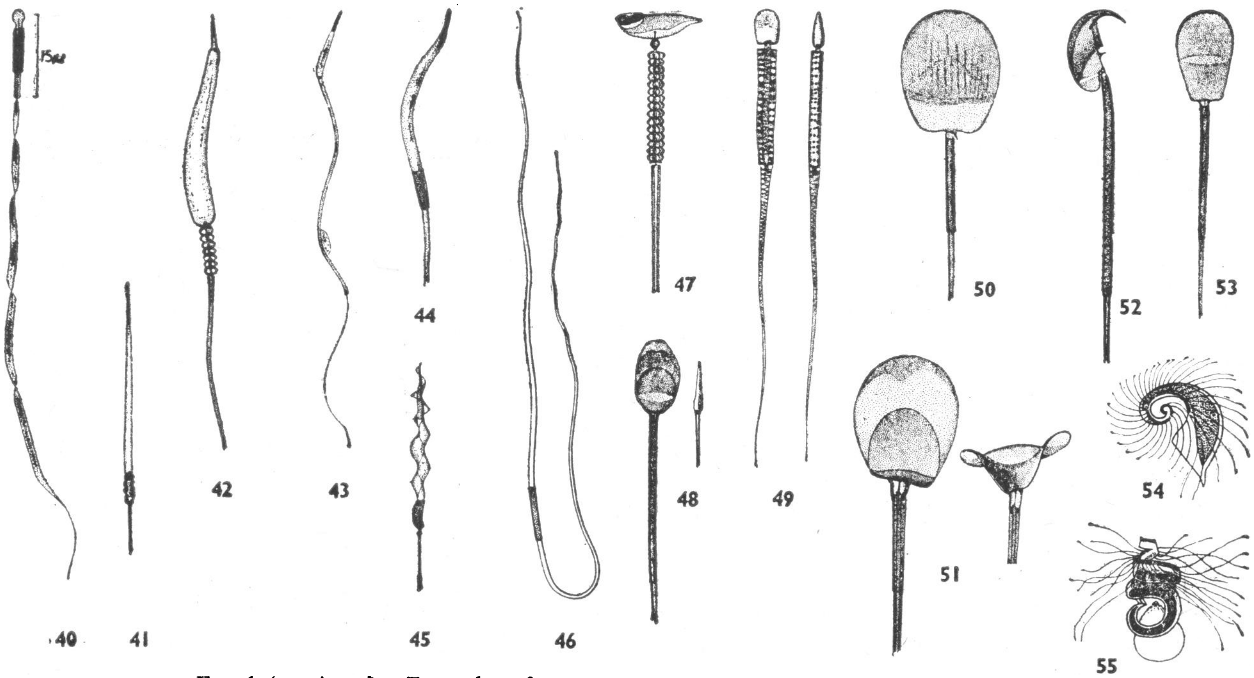


FIG. 1 (*continued*).—Examples of spermatozoa in the animal and plant kingdoms.

**Key to Fig. 1**

1 *Hydra vulgaris* (Cnidaria)
2 *Beroe cucumis* (Ctenophora)
3 *Macrostomum ruebushi* (Platyhelminthes)
4 *Cephalothrix* sp. (Nemertina)
5 *Ascaris* sp. (Nematoda)
6 *Loxosoma annelidicola* (Entoprocta)
7 *Plumatella fungosa* (Polyzoa)
8 *Diplosolen obelia* (Polyzoa)
9 *Phoronis pallida* (Phoronida)
10 *Nematomenia* sp. (Mollusca)
11 *Actaeon tornatilis* (Mollusca)
12 *Limax agrestis* (Mollusca)
13 *Loligo forbesi* (Mollusca)
14 *Bonellia viridis* (Echiuroidea)
15 *Echiurus echiurus* (Echiuroidea)
16 *Tomopteris helgolandica* (Annelida)
17 *Chaetopterus variopedatus* (Annelida)
18 *Erpobdella octoculata* (Annelida)
19 *Dinophilus* sp. (Annelida)
20 *Thyroglutus malayus* (Diplopoda)
21 *Thermobia domestica* (Insecta)
22 *Copris lunaris* (Insecta)
23 *Musca domestica* (Insecta)
24 *Parapodopsis cornuta* (Crustacea)
25 *Caprella aequilibra* (Crustacea)
26 *Homarus gammarus* (Crustacea)
27 *Cancer pagurus* (Crustacea)
28 *Plexippus paykulli* (Arachnida)
29 *Rhipicephalus sanguineus* (Arachnida)
30 *Sagitta bipunctata* (Chaetognatha)
31 *Ciona intestinalis* (Urochordata)
32 *Branchiostoma lanceolatum* (Cephalochordata)
33 *Chimaera monstrosa* (Bradyodonti)
34 *Clupea harengus* (Pisces)
35 *Esox lucius* (Pisces)
36 *Xiphophorus hellerii* (Pisces)
37 *Diemictylus viridescens* (Amphibia)
38 *Bufo bufo* (Amphibia)
39 *Rana esculenta* (Amphibia)
40 *Ichthyophis glutinosus* (Amphibia)
41 *Angius fragilis* (Reptilia)
42 *Testudo graeca* (Reptilia)
43 *Vipera berus* (Reptilia)
44 *Gallus gallus* (Aves)
45 *Corvus cornix* (Aves)
46 *Tachyglossus aculeatus* (Mammalia)
47 *Bettongia cuniculus* (Mammalia)
48 *Talpa europaea* (Mammalia)
49 *Pipistrellus pipistrellus* (Mammalia)
50 *Chaetophractus villosus* (Mammalia)
51 *Cynomys ludovicianus* (Mammalia)
52 *Mus musculus* (Mammalia)
53 *Cervus elaphus* (Mammalia)
54 *Equisetum arvense* (Pteridophyta)
55 *Pityrogramma sulphurea* (Pteridophyta)

Nos. 1, 2, 4, 6, 8–11, 13–19, 31, and 32 after Franzén (1955a–1958); 3 after Ferguson (1940); 5 after Panijel (1951); 7, 12, 30, 33, 37–39, 41, 42, and 44–53 after Retzius (1906–1909); 20 after Nath and Sharma (1952); 21 after Nath and Bhatia (1953); 22, 23, 34, 35, and 43 after Ballowitz (1890a–1917); 24 after Koltzoff (1908); 25 after Tuzet and Sanchez (1952); 26 and 27 after Bloch (1935); 28 and 29 after Sharma (1944, 1950); 36 after Vasisht (1954); 40 after Seshachar (1943); 54 and 55 after Belajeff (1898). Unless otherwise stated, all sperm heads are 3–10 μ long.

TABLE I.—*A Summarized Classification of Living Animals*
The approximate number of described species in each group is given in the second column
(After Rothschild, 1961)

| | |
|---|---|
| Phylum PROTOZOA | 30,000 |
| MESOZOA | 50 |
| PARAZOA | 4,200 |
| CNIDARIA | 9,600 |
| CTENOPHORA | 80 |
| PLATYHELMINTHES | 15,000 |
| NEMERTINA | 550 |
| ASCHELMINTHES | |
| Class Rotifera | 1,500 |
| Gastrotricha | 140 |
| Echinoderida | 100 |
| Priapulida | 5 |
| Nematomorpha | 250 |
| Nematoda | 10,000 |
| Phylum ACANTHOCEPHALA | 300 |
| ENTOPROCTA | 60 |
| POLYZOA | 4,000 |
| PHORONIDA | 15 |
| BRACHIOPODA | 260 |
| MOLLUSCA | 100,000 |
| SIPUNCULOIDEA | 275 |
| ECHIUROIDEA | 80 |
| ANNELIDA | 7,000 |
| ARTHROPODA | |
| Class Onychophora | 73 |
| Pauropoda, Diplopoda, Chilopoda, Symphyla | 9,400 |
| Insecta | 700,000 |
| Crustacea | 25,000 |
| Merostomata | 4 |
| Arachnida | 30,000 |
| Pycnogonida | 440 |
| Pentastomida | 60 |
| Tardigrada | 280 |
| Phylum CHAETOGNATHA | 50 |
| POGONOPHORA | 43 |
| ECHINODERMATA | 5,700 |
| CHORDATA | |
| Sub-phylum Hemichordata | 91 |
| Urochordata | 1,600 |
| Cephalochordata | 13 |
| Vertebrata | |
| Class Marsipobranchii, Selachii, Bradyodonti, Pisces | 23,000 |
| Amphibia | 2,000 |
| Reptilia | 5,000 |
| Aves | 8,590 |
| Mammalia | 4,500 |

selection pressure made this so unlikely as to be virtually out of the question. I put the same question to my colleague Dr. T. Mann at Cambridge. He said more or less the opposite.

These spermatozoa, from all over the animal and plant kingdoms, provoke the question, "Can one tell to which phylum, class, or order an animal belongs by examination of its spermatozoa ?" I don't think anyone to-day could give a categorical yes or no to this question, which is being examined at the moment in the class Aves, birds.

Some specialists on spermatozoa believe that the normal types can be divided into two classes (Fig. 2). Class 1, called primitive spermatozoa, are characterized by a small round or oval head and by a small middle-piece containing globular mitochondrial structures. Spermatozoa in this class are said to fertilize eggs outside the body of the female. In the second class, in which fertilization is internal, the head is larger or longer. The middle-piece is long, nearly double the length of the head, and the mitochondria are disposed in a helical tube or ribbon round it. I do not know if there are exceptions to this division into two classes; it would be interesting to find out. Even if the division is valid, a correlation between the difference in structure and in mode of reproduction has not yet been found.

So far, the head, which contains the hereditary material; the tail, which is the organ of locomotion; and the middle-piece have been mentioned. A spermatozoon has two other morphologically identifiable parts, the neck and the acrosome. The structure of the neck is poorly understood, but in human and bull spermatozoa a remarkable organelle, if that is the right word, is visible in it (Fig. 3). It looks like a pile of disks, every alternate one being opaque to electrons after osmic-acid fixation. No one has any idea what it is; it may be functionally connected in some way with the proximal centriole, which is thought to be the headquarters for the control of sperm movement, a complicated operation which will be discussed later.

The other structure, the acrosome, is situated at the anterior end of the head. It is concerned with the entrance of the spermatozoon into the egg or its passage through the membranes which often surround the unfertilized egg. Though the acrosome has for many years been the subject of painstaking and earnest studies,

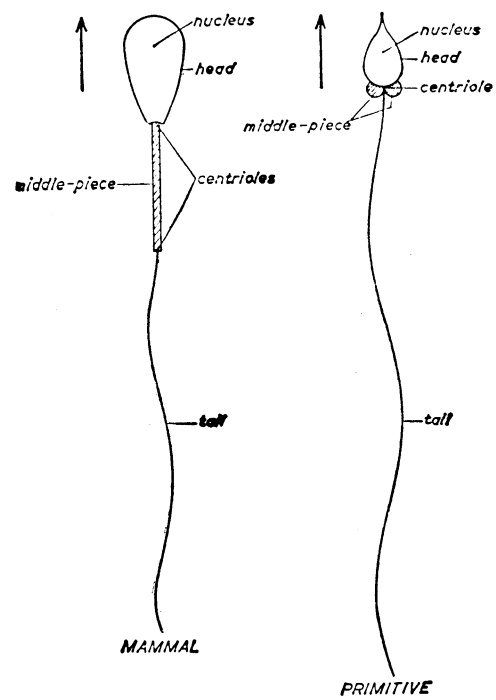


FIG. 2.—Diagrams of Class 1 (primitive) and Class 2 (mammal) spermatozoa.

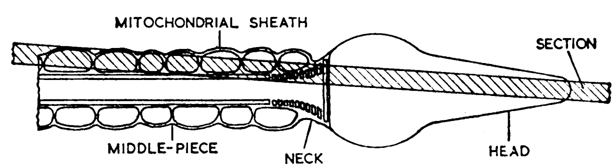


FIG. 3.—Diagram of human spermatozoon, longitudinal section. The hatched region is not relevant in this context.

particularly about its origins and development, it was not until the advent of the electron microscope that its ubiquity and functions were better understood. When spermatozoa, especially those in the primitive class, get near an egg, which means that they come under the influence of egg secretions, the acrosome reaction occurs. In the sea-urchin spermatozoon a granule is discharged from the acrosome (Special Plate, Fig. A). In other cases the acrosome explodes, opens, or greatly elongates (Fig. 4). In all these cases an enzyme is released from the acrosome and facilitates the passage of the spermatozoon through the cell membrane of the egg or the membranes bounding it. An analogous reaction may occur in mammalian spermatozoa, which also have an acrosome, when they undergo the ripening process known as capacitation. Rabbit and rodent spermatozoa

LORD ROTHSCHILD: SPERMATOZOA

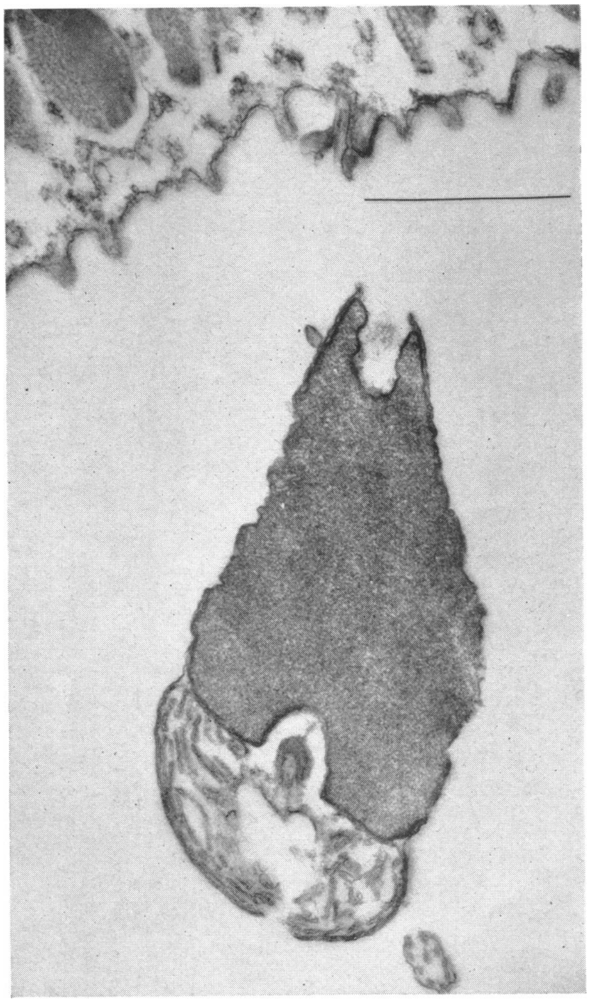

FIG. A.—Electron micrograph of longitudinal section of spermatozoon of *Strongylocentrotus droebachiensis* (sea-urchin) near egg surface of same species. The black line is 1 $\mu$ long. (Afzelius and Murray, 1957.)

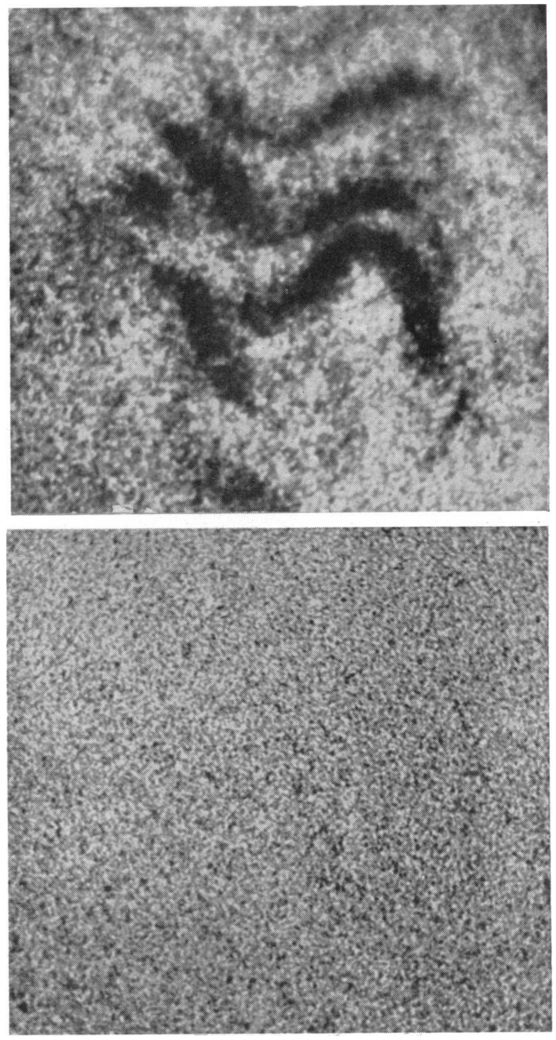

FIG. B.—Low-magnification view of active (top) and dead (bottom) bull spermatozoa in semen.

G. FORBES AND A. USHER: FATAL MYOCARDIAL SARCOIDOSIS

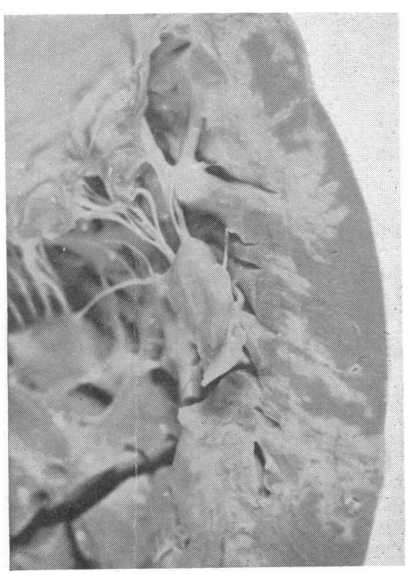

FIG. 1.—Showing granulomatous infiltration of ventricular wall involving papillary muscles.

FIG. 2.—Medium-power view of a typical field from the interventricular septum. Note the extensive fibrosis with islands of epithelioid cells and numerous multinucleate giant cells. (H. and E. ×32.)

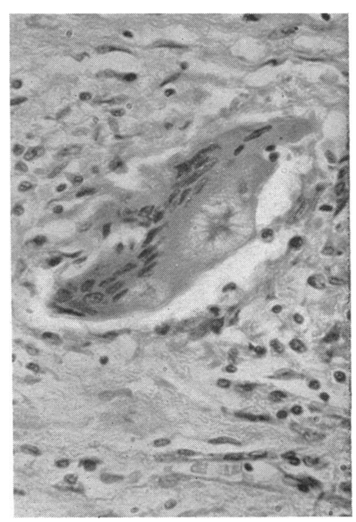

FIG. 3.—Multinucleate giant cell containing large asteroid inclusion body. A second smaller asteroid may be seen in the lower part of this cell. (H. and E. ×105.)

need some four to six hours' life after ejaculation before they can fertilize eggs. This is called capacitation. It used to be thought that this four to six hours of ripening had to be spent in the female reproductive tract. But in 1958 Noyes, Walton, and Adams injected newly

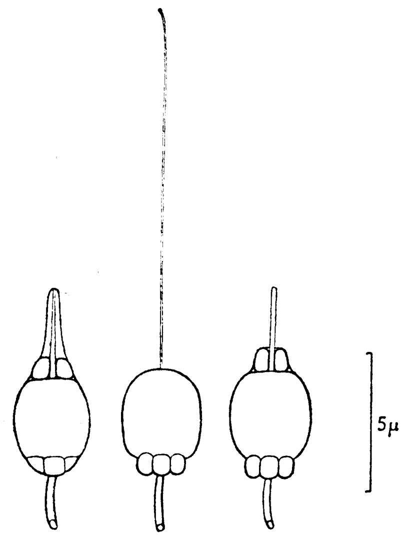


FIG. 4.—Diagram of spermatozoon of *Mytilus edulis*. Left, unreacted; right, partially reacted; centre, after acrosomal reaction. (After Dan and Wada, 1955.)

ejaculated rabbit spermatozoa into the anterior chamber of the eye of a male rabbit and found that, after the appropriate period of time, the spermatozoa were capacitated and could fertilize rabbit eggs. There is some evidence that the acrosome of rodent spermatozoa contains the enzyme hyaluronidase, which facilitates the passage of spermatozoa between the cells which surround unfertilized eggs, and that capacitation involves the breakdown of the acrosome.

### X and Y Spermatozoa

Male mammals produce two sorts of spermatozoa, with different amounts of D.N.A. in their heads, called X and Y spermatozoa. If an X spermatozoon fertilizes an egg the offspring is female; but if a Y spermatozoon fertilizes an egg the offspring is male. In birds the situation is reversed, there being two different sorts of eggs and one sort of spermatozoon. In mammals X and Y spermatozoa are produced in approximately equal numbers, so that the chance of the offspring being male or female is about half, as it is that a tossed coin will come up heads or tails. Actually, the odds in human beings are 106 to 100 in favour of a live male child. But, assuming the chances are equal, as they nearly are, the probability that a married couple will have a series of consecutive male or female children is as shown in

LEGENDS TO SPECIAL PLATE: L. WOLMAN

FIG. 1.—Cystic laminar necrosis of left insular cortex. (Mallory's P.T.A.H. stain. ×11.)

FIG. 2.—Gliosis of superficial part of frontal cortex forming wall of cyst. (H. and E. ×170.)

FIG. 3.—Numerous small cysts in middle cortical laminae of posterior insula. (H. and E. ×114.)

FIG. 4.—More intact cortex of frontal lobe showing band of gliosis replacing middle laminae. (Holzer. ×11.)

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Table II. There is therefore nothing very odd about a married couple having three or even four male or female children in succession, though people seem curiously loath to accept this situation and anxious, for some reason, to believe that some men produce

TABLE II.—*Probability of Consecutive Male or Female Children*

| Consecutive Male or Female Children | Probability |
|---|---|
| 1 | 1/2 |
| 2 | 1/4 |
| 3 | 1/8 |
| 4 | 1/16 |
| 5 | 1/32 |
| 6 | 1/64 |

predominatingly X or predominatingly Y spermatozoa, or that some women selectively kill off male or female embryos at a very early stage after fertilization; so much so that before the second world war a doctor is reputed to have started a clinic at Monte Carlo to help people have children of the sex they desired. Married couples went to him and received treatment which varied according to whether they wanted a male or female child. If the treatment was successful the couple paid the doctor £100; if it was not successful the doctor received no payment, so that everyone was satisfied, particularly the doctor, for the following reason. As the chances of producing a male or a female child are about equal, the doctor's "treatment" produced a child of the required sex in about half the total number of consultations. The doctor therefore made on the average £50 per consultation.

Some effort has, naturally, been expended in trying to separate X and Y spermatozoa, first, because such a separation would be of great scientific interest; secondly, because it could be exploited to gratify the wishes of prospective parents; and, thirdly, because of the economic importance of being able to control the sex of cattle, poultry, and other domestic farm animals, Leaving aside such wild ideas as that an alkaline environment might favour the conception of males or an acid one that of females, four methods have been used to try to identify or separate X and Y spermatozoa.

One of these involves a special type of centrifugation, it being probable that there is, at any rate, a minute difference between the sizes or masses of X and Y spermatozoa, because they contain different amounts of D.N.A. Claims that a separation by centrifugation has been achieved should not at present be accepted.

A second method of separating X and Y spermatozoa, and one which has received considerable attention in recent years, involves the hypothesis that the surfaces of X spermatozoa are negatively charged and therefore migrate in an electric field to the anode, whereas the surfaces of Y spermatozoa are positively charged and therefore migrate to the cathode in an electric field. The most recent claim that X and Y spermatozoa can be separated by virtue of their electrokinetic properties, though by no means the first, was in 1957. The description of these experiments was incomplete; moreover, the statistical treatment of the results is open to criticism. Consequently, the evidence for the hypothesis that X and Y spermatozoa have zeta potentials of opposite signs is far from proved, and more recently two independent groups of workers have reported that no such differences can be found in various species of mammalian spermatozoa.

A third way of separating X and Y spermatozoa depends on presumptive antigenic differences between them. Spermatozoa contain antigens against which specific antibodies can be made. Female rabbits have, for example, been injected intravenously and subcutaneously with 10–30 million spermatozoa. The idea underlying this experiment was that Y chromosomes, being foreign to the body of the female rabbit, might give rise to anti-Y antibodies which, at the time of a subsequent insemination, would inactivate or kill the Y spermatozoa in the semen in the female genital tract. The experiment was a failure in the sense that the sex ratio of rabbits born after this experiment did not differ significantly from normal; that is to say, the ratio male/female was 100/105. Other more sophisticated methods of separating X and Y spermatozoa by immunological methods have been suggested, and these deserve to be followed up. In the meantime one must conclude that the immunological approach has not so far been successful.

The fourth method of identifying, not separating, X and Y spermatozoa concerns the idea that there might be a difference in size between the two types. Claims that the spermatozoa of an individual mammal fall into two main groups, or, more technically, that there is a bimodal size distribution among the spermatozoa, have been made in the past; but to date there is no evidence that any such size differences exist.

In 1960 human sperm heads were reported to fall into two distinct populations, without intermediate types, as regards the shape of the head. These claims were fallacious.

To sum up, therefore, there is at present no evidence of morphological, physicochemical, or immunological differences between X and Y spermatozoa, though it is certain that there is a chemical difference between them. It may be that this chemical difference is too small to be tracked down by any known technique; on the other hand, it may be that someone will have a brainwave and achieve separation or identification by a method of which we have not so far thought.

## Sperm Movement

The speed at which spermatozoa swim makes it difficult to see any details of their movement down the microscope with the naked eye. There are two ways of slowing up spermatozoa so that one can see how they swim; the first is by high-speed cinematography, and the second by making the fluid medium in which the spermatozoa are suspended more viscous. In both the former and the latter case bull spermatozoa can be seen to swim forward by passing two-dimensional waves of bending from the front to the back ends of their tails when the preparation involves the use of a cover-slip on a drop of sperm suspension. It is these bending waves which propel the spermatozoa forward. The amplitude of the waves does not decrease towards the end of the tail; this means that the energy needed to produce them is fed in all along the tail, which is not just waved to and fro at the front end. There is some biochemical confirmation of this, as the enzyme adenosine triphosphatase, which we shall see later is concerned with sperm movement, is found all along the tail and not only at the front end. Until the advent of the electron microscope, and in particular the examination under it of ultra-thin sections, there was no chance of knowing what structures within the sperm tail, which is about 0.3 $\mu$ in radius, cause these bending waves. Ultra-thin sections of the sperm tail reveal a remarkable submicroscopic structure which is undoubtedly responsible for them. In essence, this structure consists of nine fibrils, arranged in a circular array, with two more fibrils at the centre. The fibrils run straight along the whole length of the tail without any twists or spirals. The simplest hypothesis to explain how the fibrils produce the waves of bending is that they shorten or contract like muscles, in a particular order, both in space and time. That is to say, a wave of shortening, followed by relaxation, passes down each of the nine outer fibrils at different times during the bending cycle. There must also be compression elements in the tail, because the contracting fibrils have to do their work against a relatively rigid or incompressible structure; and it is reasonable to suppose that this rigid structure or "backbone" is the central pair of fibrils. Unfortunately, we cannot watch the fibrils contracting and relaxing, for two reasons. First, being only 250 Å. in diameter, they probably cannot be seen with the light microscope. Secondly, to see them at all, one would have to disrupt the cell membrane of the sperm tail, which completely upsets the metabolism and normal organization of the tail. I said that the fibrils *probably* cannot be seen with the light microscope. There is, however, a remote chance of observing them under dark-ground illumination, to which the normal rules of transmitted light microscopy do not apply, and with the recently invented optical mazer which produces a light pulse of extreme brilliance, its intensity per unit area being 10,000 times that of the sun anywhere on earth. Experiments using an optical mazer as a light source are in progress at the moment. Even if enough light is available to see the fibrils, the sperm tail must still be disrupted to expose them. This involves the procedure called extraction, to which I shall revert later on.

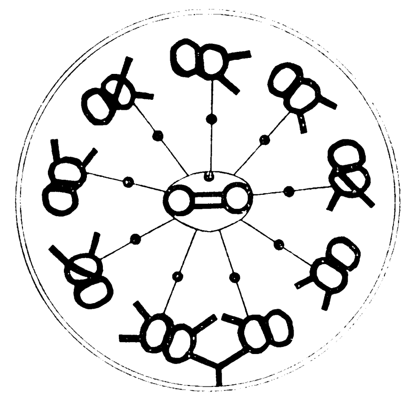

Fig. 5.—Diagram of transverse section of a cilium, an organ similar to a flagellum. (After Gibbons, 1961.)

Refinements in preparative techniques and in electron microscopy itself have revealed an ever-increasing submicroscopic structural complexity in the sperm tail, as can be seen in Fig. 5. One might make the superficially reasonable assumption that these structures have some purpose and are necessary for sperm movement—and the sperm tail is only concerned with movement. But if this assumption is reasonable, how is it that flagellated bacteria swim in apparently the same way as spermatozoa, though their tails or flagella are simple tubes, only 120 Å. in width, without any internal structure at all? This difference between the propulsive organs of bacteria and spermatozoa is remarkable and, to me, scarcely credible. The contradiction, if that is the right word, can be resolved only by an analysis of the movements of bacterial flagella similar to that which has been made of bull and sea-urchin sperm tails. Considering the size of bacterial flagella, such an analysis is easier to discuss than to do.

## Wave Formation

Dense suspensions of spermatozoa exhibit a phenomenon known as wave formation, which is the periodic aggregation of the spermatozoa into groups which disintegrate and re-form in a random way throughout the suspension (Special Plate, Fig. B). The phenomenon only occurs when the suspension is dense—that is to say, when the number of spermatozoa per millilitre is high and when the spermatozoa are very active. The causes of wave formation are imperfectly understood, but, as it is correlated with sperm density and activity, it might be a measure of the fertilizing capacity of the suspension. Wave formation cannot itself be measured, but it causes or is associated with changes in the electrical properties of the suspension which can be. When an alternating electric current, sufficiently small not to affect or harm spermatozoa, is passed through a dilute suspension or one containing dead spermatozoa, the alternating current resistance or electric impedance is constant. If, however, the suspension is dense and the spermatozoa are active, the impedance varies up to 100 or so times a minute (Fig. 6). As in the case of wave formation, the size and frequency of the impedance changes are proportional to sperm density and activity. The impedance change frequency of bull semen is quite a good index of its fertilizing capacity—as good, I think, as any of the other methods of assessment, such as rate of fructolysis, methylene-blue reduction time, or scoring by eye. Human semen does not exhibit impedance changes, because the number of spermatozoa per millilitre is too low, being about one-tenth of that in bull semen. It would be interesting to see whether human semen exhibits wave formation and impedance changes after concentration of the spermatozoa by centrifugation to 1,000 million per ml., the average value in bull semen.

### Stirring the Medium

When bull semen is examined under the microscope the impression is gained that the whole suspension is in a state of turbulence and is being vigorously stirred. Even at low magnification the microscope may deceive one because it magnifies distance but not time. A spermatozoon swims at only just over a foot an hour. How much, in fact, do spermatozoa stir the medium in which they swim? A few years ago I was interested in this question because I was doing some experiments on bull spermatozoa in the absence of oxygen. Their container was in communication with the air through a narrow tube, and I wanted to know whether oxygen would diffuse from the air at its normal very slow rate down this tube, or whether the spermatozoa stirred the medium sufficiently to accelerate normal diffusion to a significant extent. I thought it best to put this question to two specialists in fluid dynamics, who both came to the conclusion that bull sperm tails would have little effect on the diffusion coefficient of oxygen in water. They might, in fact, cause an increase of about 13%. About a month ago I put a suspension of bull spermatozoa into each of two differential manometers and shook one manometer in the usual way at 100 cycles per minute and left the other one stationary. To my surprise the oxygen uptake of both suspensions was the same. If the same experiment is done with a suspension of yeast, the unshaken suspension respires at a much lower rate than the shaken one. Such experiments can be used to determine the effective diffusion coefficient of oxygen in water being stirred by sperm tails. So far from causing an increase of 13%, it is not difficult to show that the tails cause an increase of more than 600%. This result shows that a suspension of spermatozoa, even when diluted, as in such experiments, to an extent which precludes wave formation occurring, cannot be considered as an assemblage of spermatozoa each of which behaves as it would if it were on its own. The most probable explanation of the discrepancy between theory and practice is that there is a degree of order in a sperm suspension—they are not just like gas molecules moving at random.

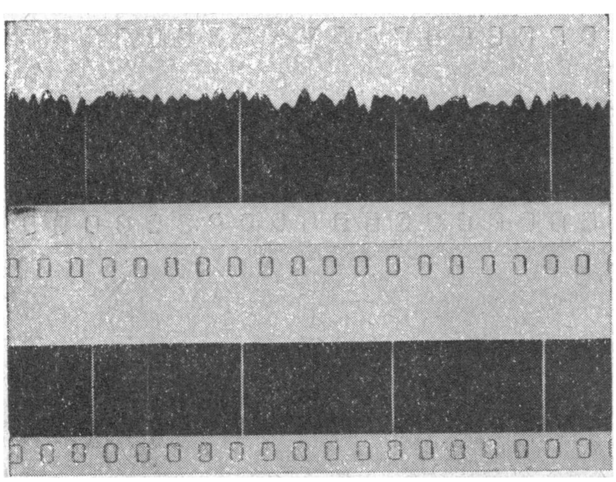

FIG. 6.—Impedance changes in ram semen (top) diluted 1:1 with Ringer solution, 37° C. The same semen (bottom) containing dead spermatozoa. The white vertical lines are 30 seconds apart.

*(To be concluded next week)*

# CLOSED ABDOMINAL INJURY

BY

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At a time when the accident services of the country have come under national review it seemed appropriate to study the cases of abdominal trauma treated in this hospital in recent years.

The peacetime experience in abdominal traumatic surgery of any one general surgeon, excepting those in specialist accident units, must of necessity be limited. With increasing mechanization in industry, density and speed of road traffic, and an ever-present and healthy adventuresomeness in youth, however, this experience is likely to be increased.

Although the literature abounds with records of recovery after operation for massive trauma and reviews of series of cases of injury to a single viscus, it seems more than likely that many failures in diagnosis and treatment may fail to reach the record books, and there are few published records of personal series of unselected cases of abdominal trauma.

While the injured abdomen may present lesser problems in diagnosis and treatment to the older surgeon, perhaps with an extensive wartime experience to draw upon, it is commonly the less experienced surgeon who is confronted with the immediate problem of the abdominally injured patient. His is clearly a heavy responsibility.

The diagnosis of the patient with an intra-abdominal injury is not always the simple matter standard textbooks suggest. Unlike disease, trauma has a total disregard for artificially created systems, and multiplicity of injury is common. Associated head injury, perhaps with conscious level seriously depressed or even absent, a not uncommon association with an alcoholic state,