

## CHAPTER III

### THE GERM-CELLS

“Not all the progeny of the primary impregnated germ-cells are required for the formation of the body in all animals; certain of the derivative germ-cells may remain unchanged and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren; so included, any derivative germ-cell may commence and repeat the same processes of growth by imbibition and of propagation by spontaneous fission as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual.”

RICHARD OWEN.<sup>1</sup>

“Es theilt sich demgemäss das befruchtete Ei in das Zellenmaterial des Individuums und in die Zellen für die Erhaltung der Art.”

M. NUSSBAUM.<sup>2</sup>

THE germ from which every living form arises is a single cell, derived by the division of a parent-cell of the preceding generation. In the unicellular plants and animals this fact appears in its simplest form as the fission of the entire parent-body to form two new and separate individuals like itself. In all the multicellular types the cells of the body sooner or later become differentiated into two groups, which as a matter of practical convenience may be sharply distinguished from one another. These are, to use Weismann's terms: (1) the *somatic cells*, which are differentiated into various tissues by which the functions of individual life are performed and which collectively form the “body,” and (2) the *germ-cells*, which are of minor significance for the individual life and are destined to give rise to new individuals by detachment from the body. It must, however, be borne in mind that the distinction between germ-cells and somatic cells is not absolute, as some naturalists have maintained, but only relative. The cells of both groups have a common origin in the parent germ-cell; both arise through mitotic cell-division during the cleavage of the ovum or in the later stages of development; both have essentially the same structure and both *may* have the same power of development, for there are many cases in which a small fragment of the body consisting of only a few somatic cells, perhaps only of one, may give rise by regeneration to a complete body. The distinction between somatic and germ-cells is an expression of the

<sup>1</sup> *Parthenogenesis*, p. 3, 1849.

<sup>2</sup> *Arch. Mik. Anat.*, XVIII., p. 112, 1880.

physiological division of labour; and while it is no doubt the most fundamental and important differentiation in the multicellular body, it is nevertheless to be regarded as differing only in degree, not in kind, from the distinctions between the various kinds of somatic cells.

In the lowest multicellular forms, such as *Volvox* (Fig. 57), the differentiation appears in a very clear form. Here the body consists of a hollow sphere, the walls of which consist of two kinds of cells. The very numerous smaller cells are devoted to the functions of nutri-

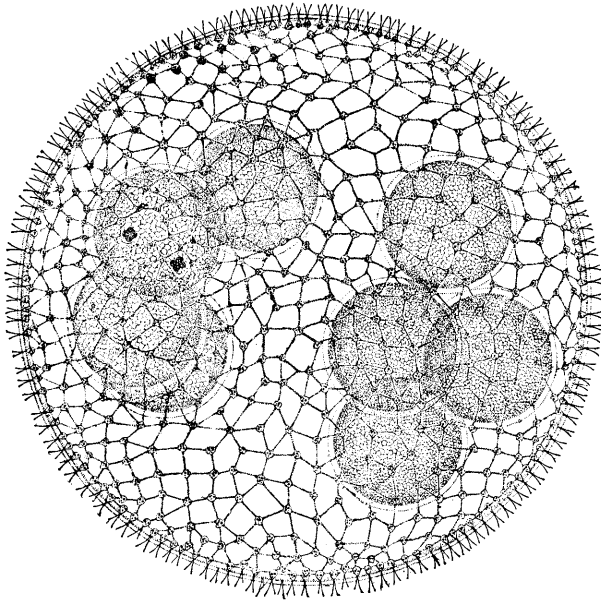


Fig. 57. — *Volvox*, showing the small ciliated somatic cells and eight large germ-cells (drawn from life by J. H. EMERTON).

tion and locomotion, and sooner or later die. A number, usually eight, of larger cells are set aside as germ-cells, each of which by progressive fission may form a new individual like the parent. In this case the germ-cells are simply scattered about among the somatic cells, and no special sexual organs exist. In all the higher types the germ-cells are more or less definitely aggregated in groups, supported and nourished by somatic cells specially set apart for that purpose and forming distinct sexual organs, the *ovaries* and *spermaries* or their equivalents. Within these organs the germ-cells are carried, protected, and nourished; and here they undergo various differentiations to prepare them for their future functions.

In the earlier stages of embryological development the progenitors of the germ-cells are exactly alike in the two sexes and are indistin-

guishable from the surrounding somatic cells. As development proceeds, they are first differentiated from the somatic cells and then diverge very widely in the two sexes, undergoing remarkable transformations of structure to fit them for their specific functions. The structural difference thus brought about between the germ-cells is, however, only the result of physiological division of labour. The female germ-cell, or ovum, supplies most of the material for the body of the embryo and stores the food by which it is nourished. It is therefore very large, contains a great amount of cytoplasm more or less laden with food-matter (*yolk* or *deutoplasm*), and in many cases becomes surrounded by membranes or other envelopes for the protection of the developing embryo. On the whole, therefore, the early life of the ovum is devoted to the accumulation of cytoplasm and the storage of potential energy, and its nutritive processes are largely constructive or anabolic. On the other hand, the male germ-cell or spermatozoön contributes to the mass of the embryo only a very small amount of substance, comprising as a rule only a single nucleus and a very small quantity of cytoplasm. It is thus relieved from the drudgery of making and storing food and providing protection for the embryo, and is provided with only sufficient cytoplasm to form a locomotor apparatus, usually in the form of one or more cilia, by which it seeks the ovum. It is therefore very small, performs active movements, and its metabolism is characterized by the predominance of the destructive or katabolic processes by which the energy necessary for these movements is set free.<sup>1</sup> When finally matured, therefore, the ovum and spermatozoön have no external resemblance; and while Schwann recognized, though somewhat doubtfully, the fact that the ovum is a cell, it was not until many years afterward that the spermatozoön was proved to be of the same nature.

#### A. THE OVUM

The animal egg (Figs. 58–59) is a huge spheroidal cell, sometimes naked, but more commonly surrounded by one or more membranes which may be perforated by a minute opening, the *micropyle*, through which the spermatozoön enters (Fig. 63). It contains an enormous nucleus known as the *germinal vesicle*, within which is a very conspicuous nucleolus known to the earlier observers as the *germinal spot*. In many eggs the latter is single, but in other forms many

<sup>1</sup> The metabolic contrast between the germ-cells has been fully discussed in a most suggestive manner by Geddes and Thompson in their work on the *Evolution of Sex*; and these authors regard this contrast as but a particular manifestation of a metabolic contrast characteristic of the sexes in general.

nucleoli are present, and they are sometimes of more than one kind, as in tissue-cells.<sup>1</sup> In many forms no centrosome or attraction-sphere is found in the egg until the initial stages in the formation of the polar bodies, though Mertens ('93) describes a centrosome and attraction-sphere in the young ovarian eggs of a number of vertebrates (Fig. 79), while Platner ('89) and Stauffacher ('93) find what they believe to be centrosomes in much later stages of *Aulostomum* and *Cyclas*, lying outside the nuclear membrane. Beside these cases should be placed those described by Balbiani, Munson, Nemec, and others in which a body closely resembling an attraction-sphere is identified as a "yolk-nucleus" or "vitelline body," as described at page 158. In none of these cases is the identification of this body wholly satisfactory, nor is it known to have any connection with the polar mitoses. Most observers find no centrosome until the prophases of the first polar mitosis. Its origin is still problematical, some observers believing it to arise *de novo* in the cytoplasm (Mead), others concluding that it is of nuclear origin (Mathews, Van der Stricht, Rückert), still others that it persists in the cytoplasm hidden among the granules. In any case it is again lost to view after formation of the polar bodies, to be replaced by the cleavage-centrosomes which arise in connection with the spermatozoön (p. 187).

The egg-cytoplasm almost always contains a certain amount of nutritive matter, the *yolk* or *deutoplasm*, in the form of liquid drops, solid spheres or other bodies suspended in the meshwork and varying greatly in different cases in respect to amount, distribution, form, and chemical composition.

### I. *The Nucleus*

The nucleus or germinal vesicle occupies at first a central or nearly central position, though it shows in some cases a distinct eccentricity even in its earliest stages. As the growth of the egg proceeds, the eccentricity often becomes more marked, and the nucleus may thus come to lie very near the periphery. In some cases, however, the peripheral movement of the germinal vesicle occurs only a very short time before the final stages of maturation, which may coincide with the time of fertilization. Its form is typically that of a spherical sac, surrounded by a very distinct membrane (Fig. 58); but during the growth of the egg it may become irregular or even amoeboid (Fig. 77), and, as Korschelt has shown in the case of insect-eggs, may move through the cytoplasm toward the source of food. Its structure is

<sup>1</sup> Häcker ('95, p. 249) has called attention to the fact that the nucleolus is as a rule single in small eggs containing relatively little deutoplasm (coelenterates, echinoderms, many annelids, and some copepods), while it is multiple in large eggs heavily laden with deutoplasm (lower vertebrates, insects, many crustacea).

on the whole that of a typical cell-nucleus, but is subject to very great variation, not only in different animals, but also in different stages of ovarian growth. Sometimes, as in the echinoderm ovum, the chromatin forms a beautiful and regular reticulum consisting of numerous chromatin-granules suspended in a network of linin (Fig. 58). In other cases, no true reticular stage exists, the nucleus containing throughout the whole period of its growth the separate daughter-chromosomes of the preceding division (copepods, selachians, Amphibia),<sup>1</sup>

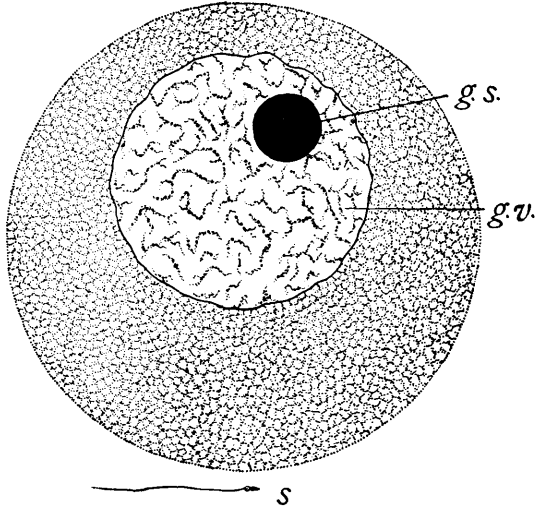


Fig. 58. — Ovarian egg of the sea-urchin, *Toxopneustes* ( $\times 750$ ).

*g.v.* Nucleus or germinal vesicle, containing an irregular discontinuous network of chromatin; *g.s.* nucleolus or germinal spot, intensely stained with hæmatoxylin. The naked cell-body consists of a very regular alveolar meshwork, scattered through which are numerous minute granules or microsomes. (Cf. Figs. 11, 12.) Below, at *s*, is an entire spermatozoon shown at the same enlargement (both middle-piece and flagellum are slightly exaggerated in size).

and these chromosomes may undergo the most extraordinary changes of form, bulk, and staining-reaction during the growth of the egg.<sup>2</sup> It is a very interesting and important fact that during the growth and maturation of the ovum a large part of the chromatin of the germinal vesicle may be lost, either by passing out bodily into the cytoplasm, by conversion into supernumerary or accessory nucleoli which finally degenerate, or by being cast out and degenerating at the time the polar bodies are formed (Figs. 97, 128).

The nucleolus of the egg-cell is, as elsewhere, a variable quantity and is still imperfectly understood. It often attains an enormous development, forming the "Keimfleck" or "germinal spot" of the

<sup>1</sup> p. 273.

<sup>2</sup> p. 338.

early observers. There are some cases (*e.g.* echinoderm eggs) in which it is always a single large spherical body (Fig. 58), and this condition appears to be characteristic of the very young ovarian eggs of most animals. As a rule, however, the number of nucleoli increases with the growth of the ovum, until, in such forms as Amphibia and reptiles, they may be numbered by hundreds.

In a large number of cases the nucleoli are of two quite distinct types, which Flemming has distinguished as the "principal nucleolus"

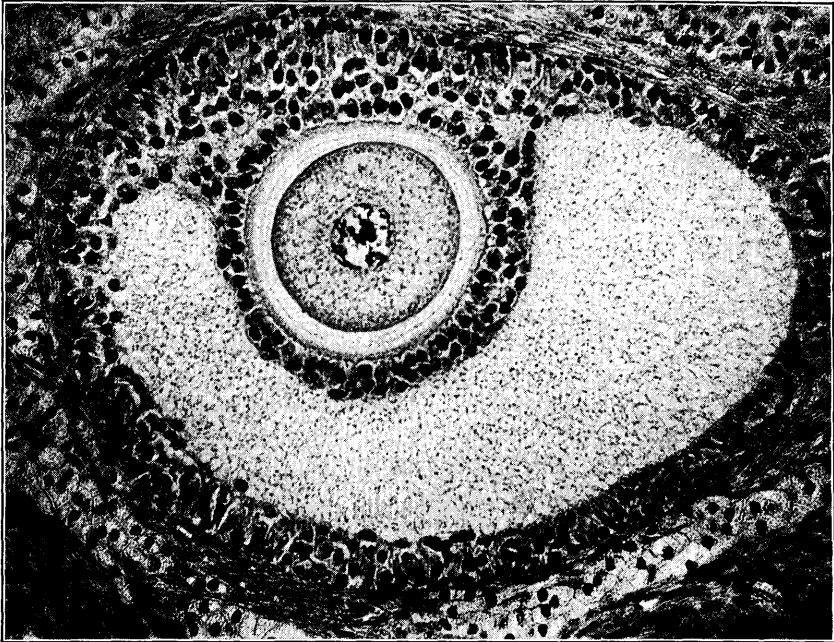


Fig. 59.—Ovum of the cat, within the ovary, directly reproduced from a photograph of a preparation by DAHLGREN. [Enlarged 235 diameters.] The ovum lies in the Graafian follicle within the *discus proligerus*, the latter forming the immediate follicular investment (*corona radiata*) of the egg. Within the *corona* is the clear *zona pellucida* or egg-membrane. (*Cf.* Fig. 92.)

(*Hauptnucleolus*) and "accessory nucleoli" (*Nebennucleoli*). These differ widely in staining-reaction; but it does not yet clearly appear whether they definitely correspond to the plasmosomes and karyosomes of tissue-cells (p. 34). The principal nucleolus, which alone is present in such eggs as those of echinoderms, often stains deeply with chromatin-stains, yet differs more or less widely from the chromatin-network,<sup>1</sup> and in some cases at least it does not contribute

<sup>1</sup> *Cf.* List, '96, Montgomery, '98, 2, and Obst., '99.

to the formation of chromosomes. It cannot therefore be directly compared to the net-knots or karyosomes of tissue-cells. This nucleolus is often vacuolated and sometimes assumes the form of a hollow vesicle. It is rarely double or multiple. The accessory nucleoli, on the other hand, are in general coloured by plasma-stains, thus resembling the plasmosomes of tissue-cells; they are often multiple, and as a rule they arise secondarily during the growth of the egg (Fig. 61). The accessory nucleoli often have no connection with the principal; but in some mollusks and annelids an accessory and a principal nucleolus are closely united to form a single compound body (Figs. 60, 61). The numerous nucleoli of the amphibian or reptilian egg appear to be of the "accessory" type. The singular inconstancy of the nucleolus is evidenced by the fact that even closely related species may differ in this regard. Thus, in *Cyclops brevicornis*, according to Häcker, the very young ovum contains a single intensely chromatic nucleolus; at a later period a number of paler accessory nucleoli appear; and still later the principal nucleolus disappears, leaving only the accessory ones. In *C. strenuus*, on the other hand, there is throughout but a single nucleolus.

The physiological meaning of the nucleoli is still involved in doubt. Many cases are, however, certainly known in which the nucleolus plays no part in the later development of the nucleus, being cast out or degenerating *in situ* at the time the polar bodies are formed. It is, for example, cast out bodily in the medusa *Æquorea* (Häcker) and in various annelids and echinoderms, afterward lying for some time as a "metanucleus" in the egg-cytoplasm before degenerating. In these cases the chromosomes are formed in the germinal vesicle independently of the nucleoli (Fig. 125), which degenerate *in situ* when the membrane of the germinal vesicle disappears. In such cases it seems quite certain that the nucleoli do not contribute to the formation of the chromosomes, and that their substance represents passive material which is of no further direct use. Hence we can hardly doubt the conclusion of Häcker, that the nucleoli of the germ-cells are, in some cases at least, accumulations of by-products of the nuclear action, derived from the chromatin either by direct transformation of its substance, or as chemical cleavage-products or secretions. It will be shown in Chapter V. that in some cases a large part of the chromatic reticulum is cast out, and degenerates at the time the polar bodies are formed. The immense growth of the chromatin during the ovarian development is probably correlated in some way with the intense constructive activity of the cytoplasm (p. 339); and when this latter process has ceased a large part of the chromatin-substance, having fulfilled its functions, is cast aside. It seems not improbable that the nucleoli are tributary to the same general process, perhaps

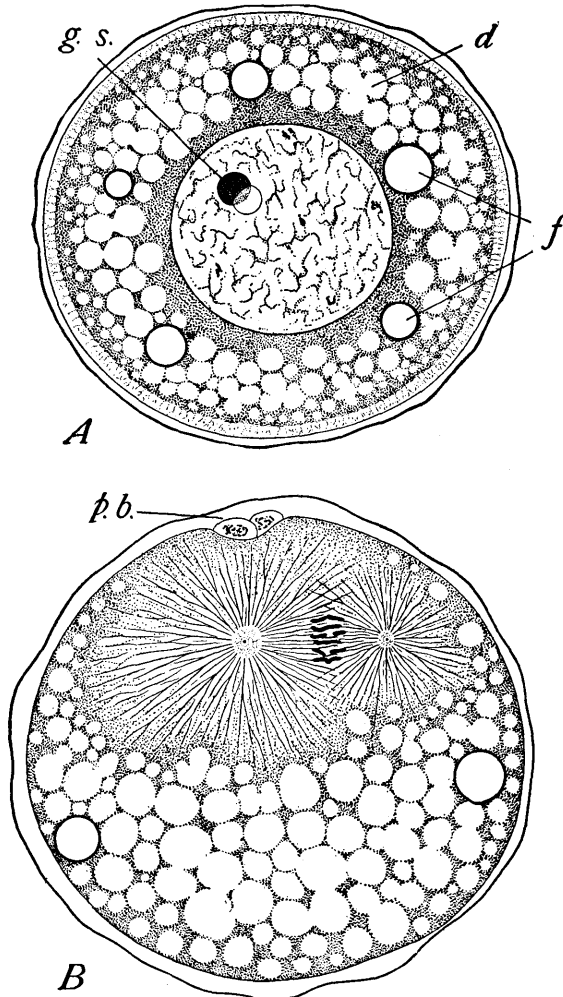


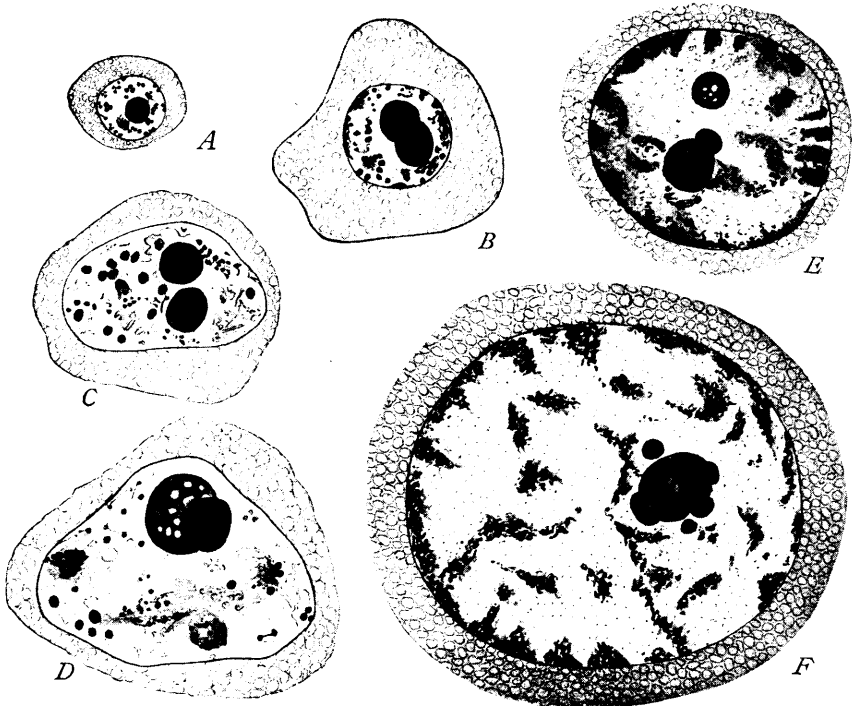
Fig. 60.—Eggs of the annelid *Nereis*, before and after fertilization,  $\times 400$  (for intermediate stages see Fig. 95).

*A.* Before fertilization. The large germinal vesicle occupies a nearly central position. It contains a network of chromatin in which are seen five small darker bodies; these are the quadruple chromosome-groups, or tetrads, in process of formation (not all of them are shown); these alone persist in later stages, the principal mass of the network being lost; *g.s.* double germinal spot, consisting of a chromatic and an achromatic sphere. This egg is heavily laden with yolk, in the form of clear deutoplasm-spheres (*d*) and fat-drops (*f*), uniformly distributed through the cytoplasm. The peripheral layer of cytoplasm (peri-vitelline layer) is free from deutoplasm. Outside this the membrane. *B.* The egg some time after fertilization and about to divide. The deutoplasm is now concentrated in the lower hemisphere, and the peri-vitelline layer has disappeared. Above are the two polar bodies (*p.b.*). Below them lies the mitotic figure, the chromosomes dividing.



serving as storehouses of material formed incidentally to the general nuclear activity, but not of further direct use.

Carnoy and Le Brun ('97, '99) reach, however, the conclusion that in the germinal vesicle of *Amphibia* the chromosomes are derived not from the chromatin-network, but solely from the nucleoli. The apparent contradiction of this result with that of other observers is,



**Fig. 61.** — Germinal vesicles of growing ovarian eggs of the lamellibranch, *Unio* (A-D), and the spider, *Epeira* (E-F). [OBSR.]

A. Youngest stage with single (principal) nucleolus. B. Older egg, showing accessory nucleolus attached to the principal. C. The two nucleoli separated. D. Much older stage, showing the two nucleoli united. E. Germinal vesicle of *Epeira*, showing one accessory nucleolus attached to the principal, and one free. F. Later stage; several accessory nucleoli attached to the principal.

perhaps, only a verbal one; for the “nucleoli” are here evidently chromatin-masses, and the disappearance of the chromatic network is comparable with what occurs at a later period in the annelid egg (Figs. 97, 128).

## 2. The Cytoplasm

The egg-cytoplasm varies greatly in appearance with the variations of the deutoplasm. In such eggs as those of the echinoderm

(Fig. 58), which have little or no deutoplasm, the cytoplasm forms a regular meshwork, which is in this case an undoubted alveolar structure, the structure of which has already been described at p. 28. In eggs containing yolk the deutoplasm-spheres or granules are laid down in the spaces of the meshwork and appear to correspond to the alveolar spheres of the echinoderm egg (p. 50). If they are of large size the cytoplasm assumes a "pseudo-alveolar" structure (Fig. 60), much as in plant-cells laden with reserve starch; but reasons have already been given (p. 50) for regarding this as only a modification of the "primary" alveolar structure of Bütschli. There is good reason to believe, however, that the egg-cytoplasm may in some cases form a true reticular structure with the yolk-granules lying in its interstices, as many observers have described. In many cases a peripheral layer of the ovum, known as the cortical or peri-vitelline layer, is free from deutoplasm-spheres, though it is continuous with the protoplasmic meshwork in which the latter lie (Fig. 60). Upon fertilization, or sometimes before, this layer may disappear by a peripheral movement of the yolk, as appears to be the case in *Nereis*. In other cases the peri-vitelline substance rapidly flows toward the point at which the spermatozoön enters, where a protoplasmic germinal disc is then formed; for example, in many fish-eggs.

The character of the yolk varies so widely that it can here be considered only in very general terms. The deutoplasm-bodies are commonly spherical, but often show a more or less distinctly rhomboidal or crystalloid form as in Amphibia and some fishes, and in such cases they may sometimes be split up into parallel lamellæ known as *yolk-plates*. Their chemical composition varies widely, judging by the staining-reactions; but we have very little definite knowledge on this subject, and have to rely mainly on the results of analysis of the total yolk, which in the hen's egg is thus shown to consist largely of proteids, nucleo-albumins, and a variety of related substances which are often associated with fatty substances and small quantities of carbohydrates (glucose, etc.). In some cases the deutoplasm-spheres stain intensely with nuclear dyes, such as hæmatoxylin; *e.g.* in many worms and mollusks; in other cases they show a greater affinity for plasma-stains, as in many fishes and Amphibia and annelids (Fig. 60). Often associated with the proper deutoplasm-spheres are drops of oil, either scattered through the yolk (Fig. 60) or united to form a single large drop, as in many pelagic fish-eggs.

The deutoplasm is as a rule heavier than the protoplasm; and in such cases, if the yolk is accumulated in one hemisphere, the egg assumes a constant position with respect to gravity, the egg-axis standing vertically with the animal pole turned upward, as in the frog, the bird, and many other cases. There are, however, many

cases in which the egg may lie in any position. When fat-drops are present they usually lie in the vegetative hemisphere, and since they are lighter than the other constituents they usually cause the egg to lie with the animal pole turned downwards, as is the case with some annelids (*Nereis*) and many pelagic fish-eggs.

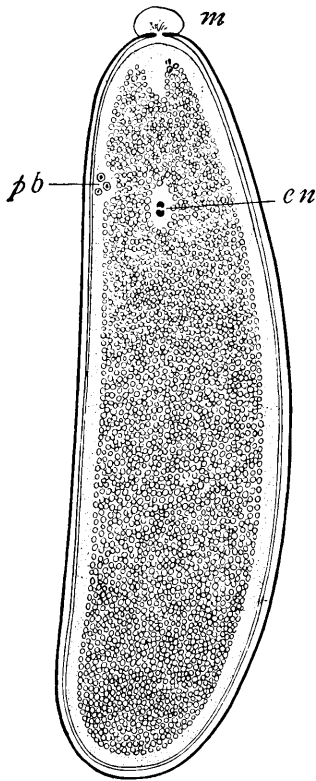


Fig. 62.—Schematic figure of a median longitudinal section of the egg of a fly (*Musca*), showing axes of the bilateral egg and the membranes. [From KORSCHULT and HEIDER, after HENKING and BLOCHMANN.]

*c.n.* The germ-nuclei uniting; *m.* micropyle; *p.b.* the polar bodies. The flat side of the egg is the dorsal, the convex side the ventral, and the micropyle is at the anterior end. The deutoplasm (small circles) lies in the centre surrounded by a peripheral or peri-vitelline layer of protoplasm. The outer heavy line is the chorion, the inner lighter line the vitelline membrane, both being perforated by the micropyle, from which exudes a mass of jelly-like substance.

### 3. The Egg-envelopes

The egg-envelopes fall under three categories. These are:—

- (a) The *vitelline membrane*, secreted by the ovum itself.
- (b) The *chorion*, formed outside the ovum by the activity of the maternal follicle-cells.
- (c) *Accessory envelopes*, secreted by the walls of the oviduct or other maternal structures after the ovum has left the ovary.

Only the first of these properly belongs to the ovum, the second and third being purely maternal products. There are some eggs, such as those of certain coelenterates (*e.g.* *Renilla*), that are naked throughout their whole development. In many others, of which the sea-urchin is a type, the fresh-laid egg is naked but forms a vitelline membrane almost instantaneously after the spermatozoön touches it.<sup>1</sup> In other forms (insects, birds) the vitelline membrane may be present before fertilization, and in such cases the egg is often surrounded by a chorion as well. The latter is usually very thick and firm and may have a shell-like consistency, its surface sometimes showing various peculiar markings, prominences, or sculptured patterns characteristic of the species (insects).<sup>2</sup>

<sup>1</sup> That the vitelline membrane does not preëxist seems to be established by the fact that egg-fragments likewise surround themselves with a membrane when fertilized. [HERTWIG.]

<sup>2</sup> In some cases, according to Wheeler, the insect-egg has only a chorion, the vitelline membrane being absent.

The accessory envelopes are too varied to be more than touched upon here. They include not only the products of the oviduct or uterus, such as the albumin, shell-membrane, and shell of birds and reptiles, the gelatinous mass investing amphibian ova, the capsules of molluscan ova and the like, but also nutritive fluids and capsules secreted by the external surface of the body, as in leeches and earth-worms.

When the egg is surrounded by a membrane before fertilization it is often perforated by one or more openings known as *micropyles*, through which the spermatozoa make their entrance (Figs. 62, 63). Where there is but one micropyle, it is usually situated very near the upper or anterior pole (fishes, many insects), but it may be at the opposite pole (some insects and mollusks), or even on the side (insects). In many insects there is a group of half a dozen or more micropyles near the upper pole of the egg, and perhaps correlated with this is the fact that several spermatozoa enter the egg, though only one is concerned with the actual process of fertilization.

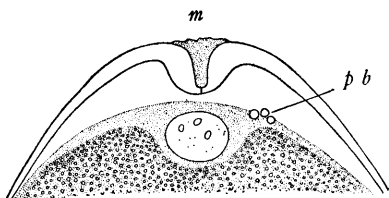


Fig. 63.—Upper pole of the egg of *Argonauta*. [Ussow.]

The egg is surrounded by a very thick membrane, perforated at *m* by the funnel-shaped micropyle; below the latter lies the egg-nucleus in the peri-vitelline layer of protoplasm; *p.b.* the polar bodies.

The plant-ovum, which is usually known as the *oösphere* (Figs. 64, 107), shows the same general features as that of animals, being a relatively large, quiescent, rounded cell containing a large nucleus. It never, however, attains the dimensions or the complexity of structure shown in many animal eggs, since it always remains attached to the maternal structures, by which it is provided with food and invested with protective envelopes. It is therefore naked, as a rule, and is not heavily laden with reserve food-matters such as the deutoplasm of animal ova. A vitelline membrane is, however, often formed soon after fertilization, as in echinoderms. The most interesting feature of the plant-ovum is the fact that it often contains plastids (leucoplasts or chromatophores) which, by their division, give rise to those of the embryonic cells. These sometimes have the form of typical chromatophores containing pyrenoids, as in *Volvox* and many other Algæ (Fig. 64). In the higher forms (archegoniate plants), according to the researches of Schmitz and Schimper, the egg contains numerous minute colourless "leucoplasts," which afterward develop into green chromatophores or into the starch-building amyloplasts. This is a point of great theoretical interest; for the researches of Schmitz, Schimper, and others have rendered it highly probable that these

plastids are persistent morphological bodies that arise only by the division of preëxisting bodies of the same kind, and hence may be traced continuously from one generation to another through the

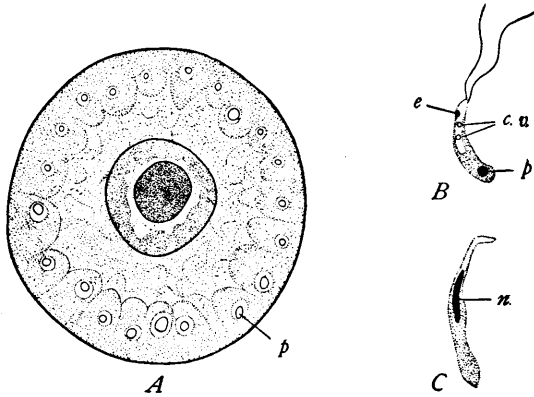


Fig. 64. — Germ-cells of *Volvox*. [OVERTON.]

A. Ovum (oösphere) containing a large central nucleus and a peripheral layer of chromatophores; *p*. pyrenoid. B. Spermatozoid; *c.v.* contractile vacuoles; *e*. "eye-spot" (chromoplastid); *p*. pyrenoid. C. Spermatozoid stained to show the nucleus (*n*).

germ-cells. In the lower plants (*Algæ*) they may occur in both germ-cells; in the higher forms they are found in the female alone, and in such cases the plastids of the embryonic body are of purely maternal origin.

## B. THE SPERMATOZOÖN

Although spermatozoa were among the first of animal cells observed by the microscope, their real nature was not determined for more than two hundred years after their discovery. Our modern knowledge of the subject may be dated from the year 1841, when Kölliker proved that they were not parasitic animalcules, as the early observers supposed, but the products of cells preëxisting in the parent body. Kölliker, however, did not identify them as cells, but believed them to be of purely nuclear origin. We owe to Schweigger-Seidel and La Valette St. George the proof, simultaneously brought forward by these authors in 1865,<sup>1</sup> that the spermatozoön is a complete cell, consisting of nucleus and cytoplasm, and hence of the same morphological nature as the ovum. It is of extraordinary minuteness, being in many cases less than  $\frac{1}{100000}$  the bulk of the ovum.<sup>2</sup>

<sup>1</sup> *Arch. Mik. Anat.*, I. '65.

<sup>2</sup> In the sea-urchin, *Toxopneustes*, I estimate its bulk as being between  $\frac{1}{400000}$  and  $\frac{1}{500000}$  the volume of the ovum. The inequality is in many cases very much greater.

Its precise study is therefore difficult, and it is not surprising that our knowledge of its structure and origin is still far from complete.

### I. *Flagellate Spermatozoa*

In its more usual form the animal spermatozoön resembles a minute, elongated tadpole, which swims very actively about by the vibrations of a long, slender tail morphologically comparable with a single cilium or flagellum. Such a spermatozoön consists typically of four parts, as shown in Fig. 65:—

1. The *nucleus*, which forms the main portion of the “head,” and consists of a very dense and usually homogeneous mass of chromatin staining with great intensity with the so-called “nuclear dyes” (*e.g.* hæmatoxylin or the basic tar-colours such as methyl-green). It is surrounded by a very thin cytoplasmic envelope.

2. An apical body, or *acrosome*, lying at the front end of the head, sometimes very minute, sometimes almost as large as the nucleus, and in some cases terminating in a sharp spur by means of which the spermatozoön bores its way into the ovum.

3. The *middle-piece*, or connecting piece, a larger cytoplasmic body lying behind the head and giving attachment to the tail, from which it is not always distinctly marked off. This body shows the same staining-reactions as the acrosome, having an especial affinity for “plasma-stains” (acid fuchsin, etc.). At its front end it is in some forms (mammals) separated from the nucleus by a short clear region, the *neck*. Like the acrosome, the middle-piece is in some cases derived from an “archoplasmic” mass, representing an attraction-sphere (*Lumbricus*) or a portion of the *Nebenkern* (insects), and it contains, or according to some authors actually arises from, the centrosome (salamander, mammals, insects, etc.).

4. The *tail*, or *flagellum*, in part, at least, a cytoplasmic product developed in connection with the centrosome and “archoplasm”

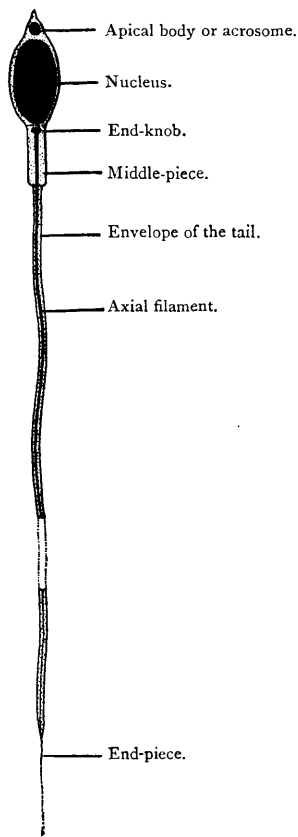


Fig. 65. — Diagram of the flagellate spermatozoön.

(attraction-sphere or "Nebenkern") of the mother-cell. It consists of a fibrillated *axial filament* surrounded by a cytoplasmic envelope, and in certain cases (Amphibia) bears on one side a fin-like undulating membrane (Fig. 66). Toward the tip of the flagellum the envelope suddenly disappears or becomes very thin, leaving a short *end-piece* which by some authors is considered to consist of the naked axial filament. The axial filament may be traced through the middle-piece up to the head, at the base of which it usually termi-

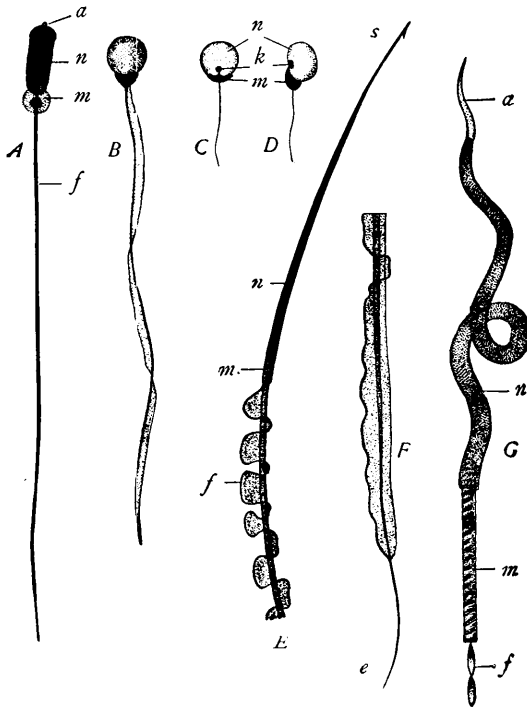


Fig. 66.—Spermatozoa of fishes and Amphibia. [BALLOWITZ]

A. Sturgeon. B. Pike. C. D. *Leuciscus*. E. *Triton* (anterior part). F. *Triton* (posterior part of flagellum). G. *Raja* (anterior part). a. apical body; e. end-piece; f. flagellum; k. end-knob; m. middle-piece; n. nucleus; s. apical spur.

nates in a minute body, single or double, known as the *end-knob*. Recent research has proved that the axial filament grows out from the spermatid-centrosome, the latter in some cases persisting as the end-knob (insects, mollusks, mammals), in other cases apparently enlarging to form the main body of the middle-piece (salamander). The tail-envelopes, on the other hand, arise either from the "archoplasm" of the Nebenkern (insects) together with a small amount of unmodified cytoplasm, or from the latter alone (salamander, rat).

From a physiological point of view we may arrange the parts of the spermatozoön under two categories as follows:—

1. The *essential structures* which play a direct part in fertilization.

These are:—

- (a) The *nucleus*, which contains the chromatin.
- (b) The *middle-piece*, which either contains a formed centrosome or pair of centrosomes (end-knob), or is itself a metamorphosed centrosome. This is probably to be regarded as the fertilizing element *par excellence*, since there is reason to believe that when introduced into the egg it gives the stimulus to division.

2. The *accessory structures*, which play no direct part in fertilization, viz.:—

- (a) The *apex* or *spur*, by which the spermatozoön attaches itself to the egg or bores its way into it, and which also serves for the attachment of the spermatozoön to the nurse-cells or supporting cells of the testis.
- (b) The *tail*, a locomotor organ which carries the nucleus and centrosome, and, as it were, deposits them in the egg at the time of fertilization. There can be little doubt that the substance of the flagellum is contractile, and that its movements are of the same nature as those of ordinary cilia. Ballowitz's discovery of its fibrillated structure is therefore of great interest, as indicating its structural as well as physiological similarity to a muscle-fibre. The outgrowth of the axial filament from the centrosome is probably comparable to the formation of spindle-fibres or astral rays, a conclusion of especial interest in its relation to Van Beneden's theory of mitosis (p. 100).

Tailed spermatozoa conforming more or less nearly to the type just described are with few exceptions found throughout the Metazoa from the cœlenterates up to man; but they show a most surprising diversity in form and structure in different groups of animals, and the homologies between the different forms have not yet been fully determined. The simpler forms, for example, those of echinoderms and some of the fishes (Figs. 66 and 100), conform very nearly to the foregoing description. Every part of the spermatozoön may, however, vary more or less widely from it (Figs. 66–68). The head (nucleus) may be spherical, lance-shaped, rod-shaped, spirally twisted, hook-shaped, hood-shaped, or drawn out into a long filament; and it is often divided into an anterior and a posterior piece of different staining-capacity, as is the case with many birds and mammals, but it is probable that the anterior of these may represent the acrosome. An interesting form of head is described by Wheeler ('97) in



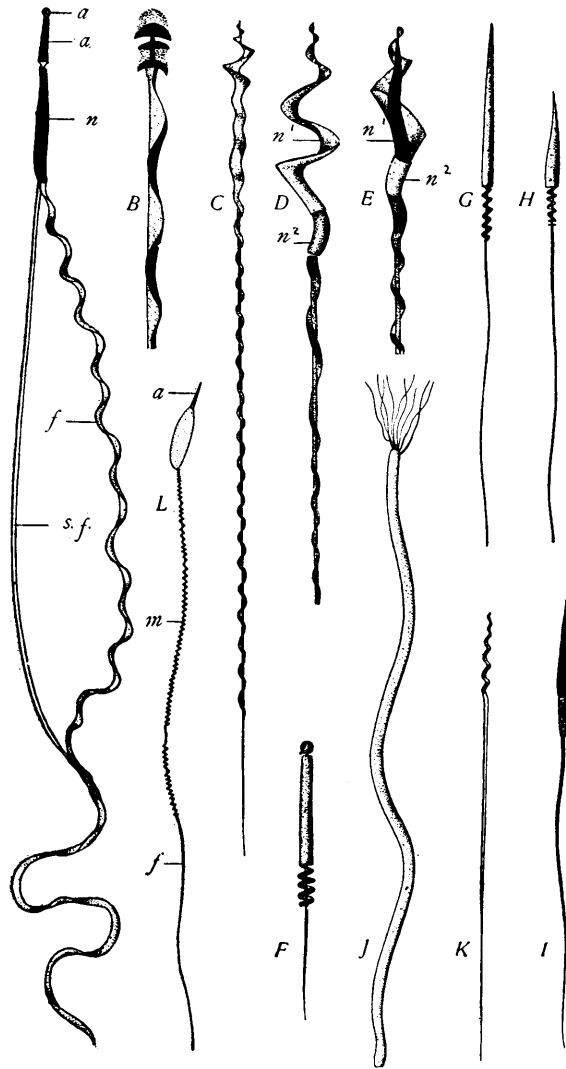


Fig. 67.—Spermatozoa of various animals. [A-I, L, from BALLOWITZ; J, K, from VON BRUNN.]

A (At the left). Beetle (*Copris*), partly macerated to show structure of flagellum; it consists of a supporting fibre (*s.f.*) and a fin-like envelope (*f.*); *n.* nucleus; *a. a.* apical body divided into two parts (the posterior of these is perhaps a part of the nucleus). B. Insect (*Calathus*), with barbed head and fin-membrane. C. Bird (*Phyllopneste*). D. Bird (*Muscicapa*), showing spiral structure; nucleus divided into two parts (*n*<sup>1</sup>, *n*<sup>2</sup>); no distinct middle-piece. E. Bulfinch; spiral membrane of head. F. Gull (*Larus*) with spiral middle-piece and apical knob. G. H. Giant spermatozoon and ordinary form of *Tadorna*. I. Ordinary form of the same stained, showing apex, nucleus, middle-piece and flagellum. J. "Vermiform spermatozoon" and, K. ordinary spermatozoon of the snail *Paludina*. L. Snake (*Coluber*), showing apical body (*a*), nucleus, greatly elongated middle-piece (*m*), and flagellum (*f*).

the spermatozoön of *Myzostoma*, where it is a greatly elongated fusiform body, passing insensibly into the tail without distinct middle-piece and containing a single series of chromatin-discs. The number of these in *M. glabrum* is 24, which is the somatic number of chromosomes in this species. In *M. cirriferum* the number of chromatin-discs is more than 60. Somewhat similar spermatozoa occur in the acœlous Turbellaria.<sup>1</sup> The acrosome sometimes appears to be wanting, *e.g.* in some fishes (Fig. 66). When present, it is sometimes a minute rounded knob, sometimes a sharp stylet, and in some cases terminates in a sharp barbed spur by which the spermatozoön appears to penetrate the ovum (*Triton*). In the mammals it is sometimes very small (rat), sometimes very large (guinea-pig), and in some forms is surrounded by a cytoplasmic layer forming the "head-cap" (Figs. 68, 86). It is sometimes divided into two distinct parts, a longer posterior piece and a knob-like anterior piece (insects, according to Ballowitz).

The middle-piece or connecting-piece shows a like diversity (Figs. 66-68). In many cases it is sharply differentiated from the flagellum, being sometimes nearly spherical, sometimes flattened like a cap against the nucleus, and sometimes forming a short cylinder of the same diameter as the nucleus, and hardly distinguishable from the latter until after staining (newt, earthworm). In other cases it is very long (reptiles, some mammals), and is scarcely distinguishable from the flagellum. In still others (birds, some mammals) it passes insensibly into the flagellum, and no sharply marked limit between them can be seen. In many of the mammals the long connecting-piece is separated from the head by a narrow "neck" in which the end-knobs lie, as described below.

Internally, the middle-piece consists of an axial filament and an envelope, both of which are continuous with those of the flagellum. In some cases the envelope shows a distinctly spiral structure, like that of the tail-envelope; but this is not always visible. The most interesting part of the middle-piece is the "end-knob" in which the axial filament terminates, at the base of the nucleus. In some cases this appears to be single. More commonly it consists of two or more minute bodies lying side by side (Fig. 68, *B, D*).

The flagellum or tail is merely a locomotor organ which plays no part in fertilization. It is, however, the most complex part of the spermatozoön, and shows a very great diversity in structure. Its most characteristic feature is the *axial filament*, which, as Ballowitz has shown, is composed of a large number of parallel fibrillæ, like a muscle-fibre. This is surrounded by a cytoplasmic envelope, which sometimes shows a striated or spiral structure, and in which, or in

<sup>1</sup> *Cf.* Wheeler, p. 7.

connection with which, may be developed secondary or accessory filaments and other structures. At the tip the axial filament may lose its envelope and thus give rise to the so-called "end-piece" (Retzius). In *Triton*, for example (Fig. 66, *F*), the envelope of the axial filament ("principal filament") gives attachment to a remarkable fin-like

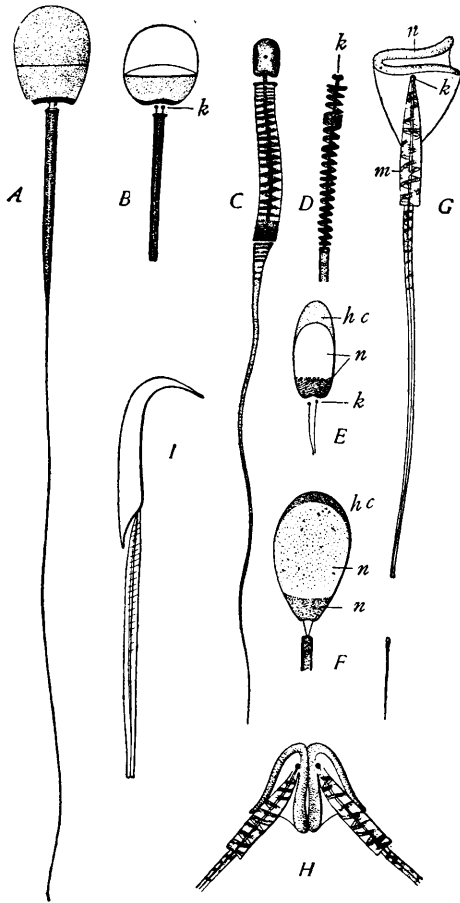


Fig. 68. — Spermatozoa of mammals. [*A-F* from BALLOWITZ.]

*A.* Badger (living). *B.* The same after staining. *C.* Bat (*Vesperugo*). *D.* The same, flagellum and middle-piece or connecting-piece, showing end-knobs. *E.* Head of the spermatozoon of the bat (*Rhinolophus*) showing details. *F.* Head of spermatozoon of the pig. *G.* Opossum (after staining). *H.* Double spermatozoa from the *vas deferens* of the opossum. *I.* Rat.

*h.c.* head-cap (acrosome); *k.* end-knob; *m.* middle-piece; *n.* nucleus (in *B, E, F*, consisting of two different parts).

membrane, having a frilled or undulating free margin along which is developed a "marginal filament." Toward the tip of the tail the fin, and finally the entire envelope, disappears, leaving only the axial filament to form the end-piece. After maceration the envelope shows a conspicuous cross-striation, which perhaps indicates a spiral structure such as occurs in the mammals. The marginal filament, on the other hand, breaks up into numerous parallel fibrillæ, while the axial filament remains unaltered (Ballowitz).

A fin-membrane has also been observed in some insects and fishes, and has been asserted to occur in mammals (man included). Later observers have, however, failed to find the fin in mammals, and their observations indicate that the axial filament is merely surrounded by an envelope which sometimes shows traces of the same spiral arrangement as that which is so conspicuous in the connecting-piece. In the skate the tail has two filaments, both composed of parallel fibrillæ, connected by a membrane and spirally twisted about each other; a

somewhat similar structure occurs in the toad. In some beetles there is a fin-membrane attached to a stiff axial "supporting fibre" (Fig. 67, *A*). The membrane itself is here composed of four parallel fibres, which differ entirely from the supporting fibre in staining-capacity and in the fact that each of them may be further resolved into a large number of more elementary fibrillæ.

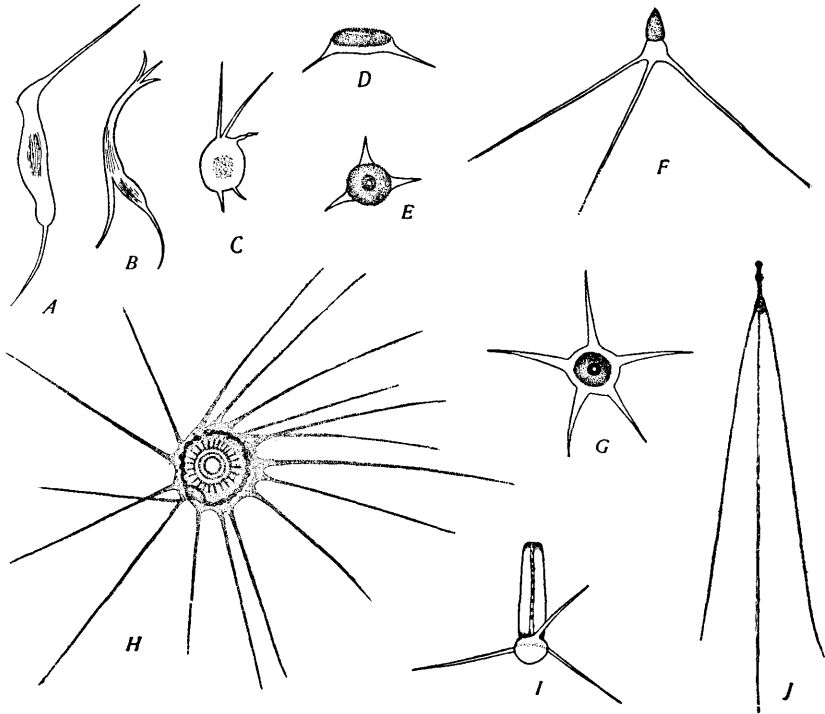


Fig. 69. — Unusual forms of spermatozoa.

- A. B. C.* Living amoeboid spermatozoa of the crustacean *Polyphemus*. [ZACHARIAS.]  
*D. E.* Spermatozoa of crab, *Dromia*. *F.* Of *Ethusa*, *G.* of *Maja*, *H.* of *Inachus*. [GROBEN.]  
*I.* Spermatozoön of lobster, *Homarus*. [HERRICK.]  
*J.* Spermatozoön of crab, *Porcellana*. [GROBEN.]

Many interesting details have necessarily been passed over in the foregoing account. One of these is the occurrence, in some mammals, birds, Amphibia (frog), and mollusks, of two kinds of spermatozoa in the same animal. In the birds and Amphibia the spermatozoa are of two sizes, but of the same form, the larger being known as "giant spermatozoa" (Fig. 67, *G, H*). In the gasteropod *Paludina* the two kinds differ entirely in structure, the smaller form being of the usual type and not unlike those of birds, while the larger, or "vermiform," spermatozoa have a worm-like shape and bear a tuft of cilia at one end, somewhat like the spermatozooids of plants (Fig. 67, *J, K*). In this case only the smaller spermatozoa are functional (von Brunn).

No less remarkable is the conjugation of spermatozoa in pairs (Fig. 68, *H*), which takes place in the *vas deferens* in the opossum (Selenka) and in some insects (Ballowitz, Auerbach). Ballowitz's researches ('95) on the double spermatozoa of beetles (*Dytiscidæ*) prove that the union is not primary, but is the result of an actual conjugation of previously separate spermatozoa. Not merely two, but three or more spermatozoa may thus unite to form a "spermatozeugma," which swims like a single spermatozoon. Whether the spermatozoa of such a group separate before fertilization is unknown; but Ballowitz has found the groups, after copulation, in the female receptaculum, and he believes that they may enter the egg in this form. The physiological meaning of the process is unknown.

## 2. Other Forms of Spermatozoa

The principal deviations from the flagellate type of spermatozoon occur among the arthropods and nematodes (Fig. 69). In many of these forms the spermatozoa have no flagellum, and in some cases they are actively amœboid; for example, in the daphnid *Polyphemus* (Fig. 69, *A, B, C*) as described by Leydig and Zacharias. More commonly they are motionless like the ovum. In the chilognathous myriapods the spermatozoon has sometimes the form of a bi-convex lens (*Polydesmus*), sometimes the form of a hat or helmet having a double brim (*Julus*). In the latter case the nucleus is a solid disc at the base of the hat. In many decapod Crustacea the spermatozoon consists of a

cylindrical or conical body from one end of which radiate a number of stiff spine-like processes. The nucleus lies near the base. In none of these cases has the centrosome been identified.

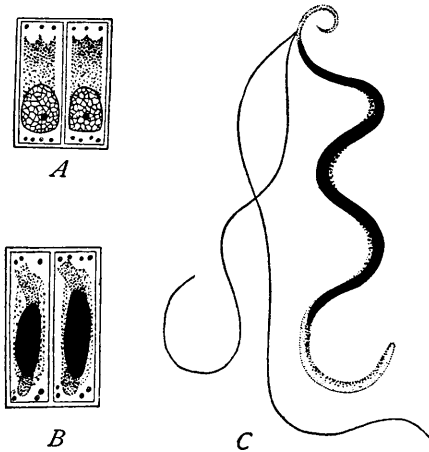


Fig. 70. — Spermatozooids of *Chara*. [BELA-JEFF.]

*A.* Mother-cells with reticular nuclei. *B.* Later stage, with spermatozooids forming. *C.* Mature spermatozoid (the elongate nucleus black).

## 3. Paternal Germ-cells of Plants

In most of the flowering plants the male germ-cells are represented by two "generative nuclei," lying at the tip of the pollen tube (Fig. 106). On the other hand, in the cycads (Figs. 87, 108) and in a large number of the lower plants (pteridophytes, Muscinæ, and many others), the male germ-cell is a minute actively swimming cell,

known as the *spermatozoid*, which is closely analogous to the spermatozoon. The spermatozoids are in general less highly differentiated than spermatozoa, and often show a distinct resemblance to the

asexual swimmers or zoöspores so common in the lower plants (Figs. 70, 71). They differ in two respects from animal spermatozoa: first in possessing not one but two or several flagella; second, in the fact that these are attached as a rule not to the end of the cell, but on the side. In the lower forms plastids are present in the form of chromatophores, one of which may be differentiated into a red "eye-spot," as in *Volvox* and *Fucus* (Figs. 57, 71, *A*), and they may even contain contractile vacuoles (*Volvox*); but both these structures are wanting in the higher forms. These consist only of a nucleus with a very small amount of cytoplasm, and have typically a spiral form. In *Chara*, where their structure and development have recently been carefully studied by Belajeff, the spermatozoids have an elongated spiral form with two long flagella attached near the pointed end, which is directed forward in swimming (Fig. 70). The main body of the spermatozoid is occupied by a dense, apparently homogeneous nucleus surrounded by a very delicate layer of cytoplasm. Behind the nucleus lies a granular mass of cytoplasm, forming one end of the cell, while in front is a slender cytoplasmic tip to which the flagella are attached. Nearly similar spermatozoids occur in the liverworts and mosses. In the ferns and other pteridophytes a somewhat different type occurs

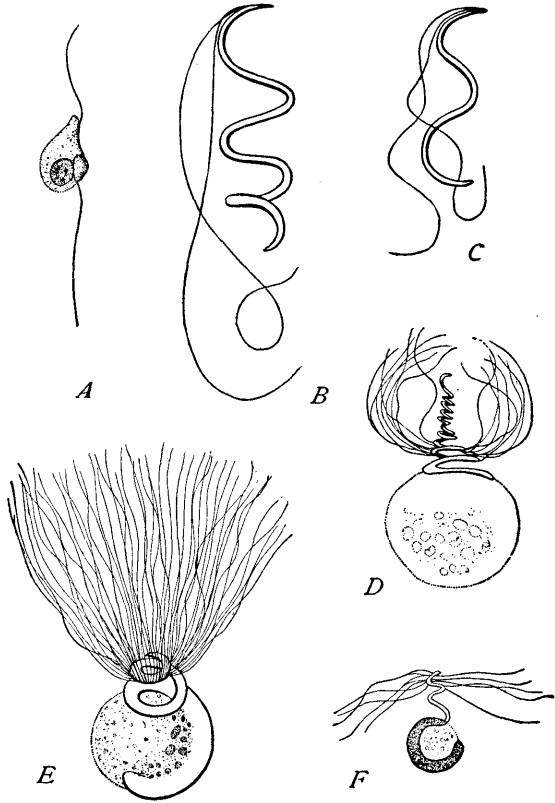


Fig. 71.—Spermatozoids of plants. [*A, B, C, E*, after GUIGNARD; *D, F*, after STRASBURGER.]

*A*. Of an alga (*Fucus*); a red chromatophore at the right of the nucleus. *B*. Liverwort (*Pellia*). *C*. Moss (*Sphagnum*). *D*. *Marsilia*. *E*. Fern, (*Angiopteris*). *F*. Fern, *Phegopteris* (the nucleus dark). (Cf. Figs. 87, 88.)

in the ferns and other pteridophytes a somewhat different type occurs

(Figs. 71, 88). Here the spermatozoid is twisted into a conical spiral and bears numerous cilia attached along the upper turns of the spire. The nucleus occupies the lower turns, and attached to them is a large spheroidal cytoplasmic mass, which is cast off when the spermatozoid is set free or at the time it enters the archeogonium. This, according to Strasburger, probably corresponds to the basal cytoplasmic mass of *Chara*. The upper portion of the spire to which the cilia are attached is composed of cytoplasm alone, as in *Chara*. Ciliated spermatozooids, nearly similar in type to those of the higher cryptogams, have recently been discovered in the cycads by Hirase (*Gingko*), Ikeno (*Cycas*), and Webber (*Zamia*). They are here hemispherical or pear-shaped bodies of relatively huge size (in *Zamia* upward of 250  $\mu$  in length), with a large nucleus filling most of the cell and a spiral band of cilia making from two to six turns about the smaller end (Figs. 87, 108).

As will be shown farther on (p. 173), the "anterior" cytoplasmic region of the spermatozoid, to which the cilia are attached, is probably the analogue of the middle-piece of the animal spermatozoön; and the work of Belajeff, Strasburger, Ikeno, Hirase, Webber, and Shaw gives good ground for the conclusion that it has an essentially similar mode of origin, though we are still unable to say exactly how far the comparison can be carried. The "posterior" region of the spermatozoid appears to correspond, broadly speaking, to the acrosome.

### C. ORIGIN OF THE GERM-CELLS

Both ova and spermatozoa take their origin from cells known as primordial germ-cells, which become clearly distinguishable from the somatic cells at an early period of development, and are at first exactly alike in the two sexes. What determines their subsequent sexual differentiation is unknown save in a few special cases. From such data as we possess, there is very strong reason to believe that, with a few exceptions, the primordial germ-cells are sexually indifferent, *i.e.* neither male nor female, and that their transformation into ova or spermatozoa is not due to an inherent predisposition, but is a reaction to external stimulus. Most of the observations thus far made indicate that this stimulus is given by the character of the food, and that the determination of sex is therefore in the last analysis a problem of nutrition. Thus Mrs. Treat ('73) found that if caterpillars were starved before entering the chrysalis state they gave rise to a preponderance of male imagoes, while conversely those of the same brood that were highly fed produced an excess of females. Yung ('81) reached the same result in the case of Amphibia, highly fed tadpoles producing a great excess of females (in some cases as high as 92%) and underfed ones an excess of males. The same result, again, is

given by the interesting experiments of Nussbaum ('97) on the rotifer *Hydatina*, which is an especially favourable case since sex is here determined at a very early period, *before the egg is laid*, the eggs being of two sizes, of which the smaller give rise only to males, and the larger only to females. The earlier experiments of Maupas ('91) on this form seemed to show conclusively that the decisive factor was temperature acting on the parent organism, since in a high temperature an excess of females produced male eggs, and in a low temperature the reverse result ensued. Nussbaum shows, however, that this is not a direct effect of temperature, but an indirect one due to the greater birth-rate and the greater activity of the animals under a higher temperature, which result in a speedier exhaustion of food. Direct experiment shows that, under equal temperature-conditions, well-fed females produce a preponderance of female offspring, and *vice versa*, precisely as in the Lepidoptera and Amphibia. These cases show that sex may be determined by conditions of nutrition either affecting the embryo itself (Lepidoptera, Amphibia) long after the egg is laid, or by similar conditions affecting the parent-organism and through it the ovarian egg.

Nutrition is, however, not the only determining cause of sex, as is shown by the long-known case of the honey-bee. Here sex is determined by fertilization, the males arising only from unfertilized eggs by parthenogenesis, while the fertilized eggs give rise exclusively to females, which develop into fertile forms (queens) or sterile forms (workers), according to the nature of the food. This is a very exceptional case, yet here too it is the more highly fed larvæ that produce fertile females. It is interesting to compare with this case that of the plant-lice or aphides. In these forms the summer broods, living under favourable conditions of nutrition, produce only females the eggs of which develop parthenogenetically. In the autumn, under less favourable conditions, males as well as females are produced; and that this is due to the external conditions and not to a fixed cyclical change of the organism is proved by the fact that in the favourable environment of a greenhouse the production of females alone may continue for years.<sup>1</sup>

We are not yet able to state whether there is any one causal element common to all known cases of sex-determination. The observations cited above, as well as a multitude of others that cannot here be reviewed, render it certain, however, that sex as such is not inherited. What is inherited is the capacity to develop into either male or female, the actual result being determined by the combined effect of conditions external to the primordial germ-cell.

<sup>1</sup> See Geddes, *Sex*, in *Encyclopædia Britannica*; Geddes and Thompson, *The Evolution of Sex*, 1889; Brooks, *The Law of Heredity*, 1883; Watasé ('92), *The Phenomena of Sex-differentiation*.



In the greater number of cases the primordial germ-cells arise in a germinal epithelium which, in the coelenterates (Fig. 72), may be a part of either the ectoderm or entoderm, and, in the higher types, is a modified region of the peritoneal epithelium lining the body-cavity. In such cases the primordial germ-cells may be scarcely distinguishable at first from the somatic cells of the epithelium. But in other cases the germ-cells may be traced much farther back in the development, and they or their progenitors may sometimes be identified in the gastrula or blastula stage, or even in the early cleavage-stages. Thus in the worm *Sagitta*, Hertwig has traced the germ-cells back to

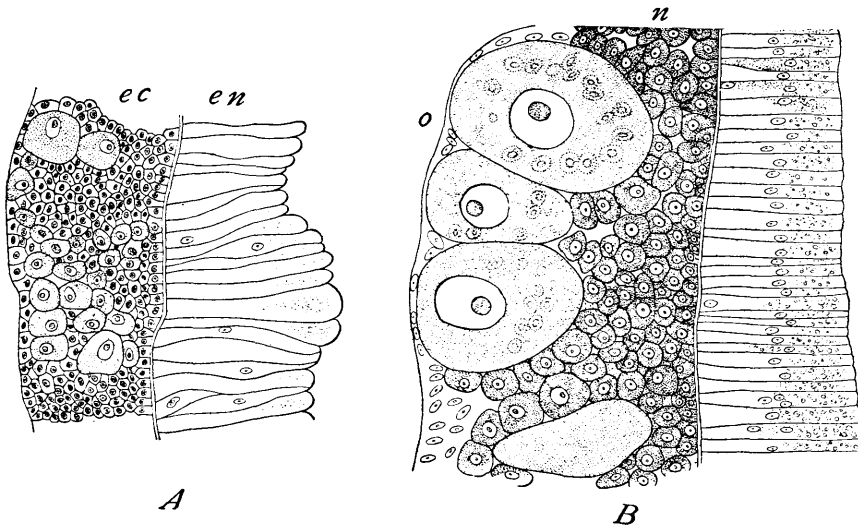


Fig. 72.— Origin of the germ-cells in a hydro-medusa, *Cladonema*. [WEISMANN.]

A. Young stage; section through wall of manubrium of the medusa; ova developing in the ectoderm (*ec*). B. Later stage, showing older ova (*o*) and "nutritive cells" (*n*). The ova contain small nuclei probably derived from engulfed nutritive cells.

two primordial germ-cells lying at the apex of the archenteron. In some of the insects they appear still earlier as the products of a large "pole-cell" lying at one end of the segmenting ovum, which divides into two and finally gives rise to two symmetrical groups of germ-cells. Häcker has recently traced very carefully the origin of the primordial germ-cells in *Cyclops* from a "stem-cell" (Fig. 74) clearly distinguishable from surrounding cells in the early blastula stage, not only by its size, but also by its large nuclei rich in chromatin, and by its peculiar mode of mitosis, as described beyond.

The most beautiful and remarkable known case of early differentiation of the germ-cells is that of *Ascaris*, where Boveri was able to trace them back continuously through all the cleavage-stages to the

two-cell stage! Moreover, from the outset the progenitor of the germ-cells *differs from the somatic cells not only in the greater size and richness of chromatin of its nuclei, but also in its mode of mitosis*; for in all those blastomeres destined to produce somatic cells a portion of

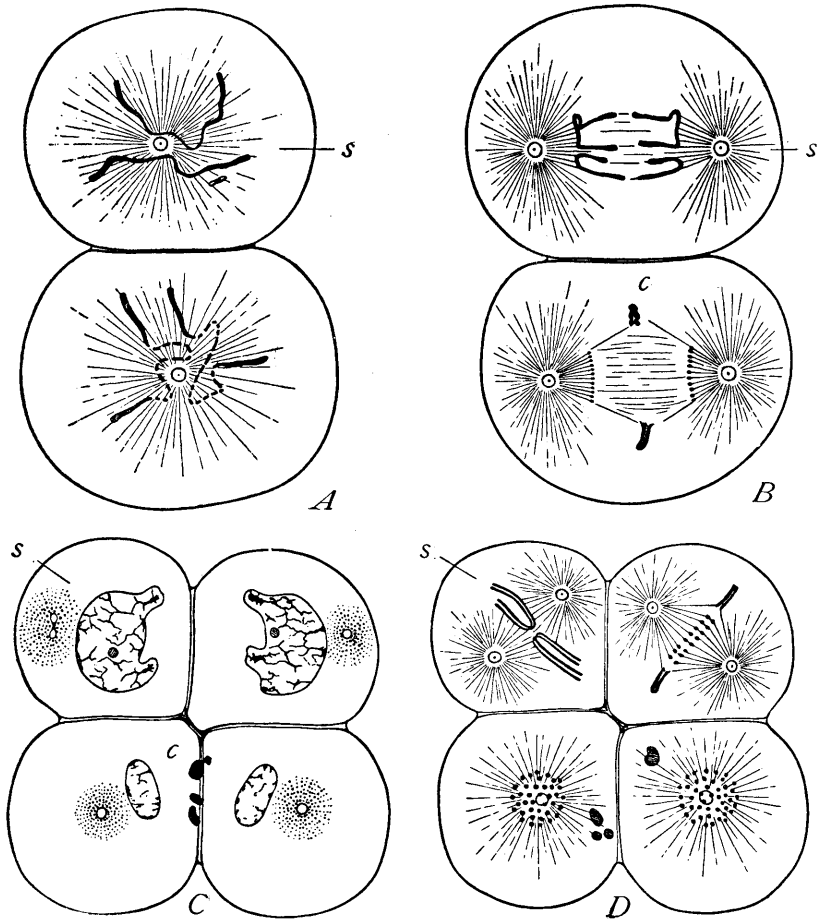


Fig. 73.—Origin of the primordial germ-cells and casting out of chromatin in the somatic cells of *Ascaris*. [BOVERI.]

*A.* Two-cell stage dividing; *s.* stem-cell, from which arise the germ-cells. *B.* The same from the side, later in the second cleavage, showing the two types of mitosis and the casting out of chromatin (*c*) in the somatic cell. *C.* Resulting 4-cell stage; the eliminated chromatin at *c*. *D.* The third cleavage, repeating the foregoing process in the two upper cells.

the chromatin is cast out into the cytoplasm, where it degenerates, and *only in the germ-cells is the sum-total of the chromatin retained*. In *Ascaris megalcephala univalens* the process is as follows (Fig. 73): Each of the first two cells receives two elongated chromosomes. As

the ovum prepares for the second cleavage, the two chromosomes reappear in each, but differ in their behaviour (Fig. 73, *A, B*). In one of them, which is destined to produce only somatic cells, the thickened ends of each chromosome are cast off into the cytoplasm and degenerate. Only the thinner central part is retained and distributed to the daughter-cells, breaking up meanwhile into a large number of segments which split lengthwise in the usual manner. In the other cell, which may be called the *stem-cell* (Fig. 73, *s*), all the chromatin is preserved and the chromosomes do not segment into smaller pieces. The results are plainly apparent in the four-cell stage, the two somatic nuclei, which contain the reduced amount of chromatin, being small and pale, while those of the two stem-cells are far larger and richer in chromatin (Fig. 73, *C*). At the ensuing division (Fig. 73, *D*) the numerous minute segments reappear in the two somatic cells, divide, and are distributed like ordinary chromosomes; and the same is true of all their descendants thenceforward. The other two cells (containing the large nuclei) exactly repeat the history of the two-cell stage, the two long chromosomes reappearing in each of them, becoming segmented and casting off their ends in one, but remaining intact in the other, which gives rise to two cells with large nuclei as before. This process is repeated five times (Boveri) or six (Zur Strassen), after which the chromatin-elimination ceases, and the two stem-cells or primordial germ-cells thenceforward give rise only to other germ-cells and the entire chromatin is preserved. Through this remarkable process it comes to pass that in this animal *only the germ-cells receive the sum-total of the egg-chromatin handed down from the parent. All of the somatic cells contain only a portion of the original germ-substance.* "The original nuclear constitution of the fertilized egg is transmitted, as if by a law of primogeniture, only to one daughter-cell, and by this again to one, and so on; while in the other daughter-cells the chromatin in part degenerates, in part is transformed, so that all of the descendants of these side-branches receive small reduced nuclei."<sup>1</sup>

It would be difficult to overestimate the importance of this discovery; for although it stands at present an almost isolated case, yet it gives us, as I believe, the key to a true theory of differentiation development,<sup>2</sup> and may in the end prove the means of explaining many phenomena that are now among the unsolved riddles of the cell.

Häcker ('95) has shown that the nuclear changes in the stem-cells and primordial eggs of *Cyclops* show some analogy to those of *Ascaris*, though no casting out of chromatin occurs. The nuclei are very large and rich in chromatin as compared with the somatic cells, and the number of chromosomes, though not precisely determined,

<sup>1</sup> Boveri, '91, p. 437.

<sup>2</sup> Cf. p. 426.

is less than in the somatic cells (Fig. 74). Vom Rath, working in the same direction, believes that in the salamander also the number of chromosomes in the early progenitors of the germ-cells is one-half that characteristic of the somatic cells.<sup>1</sup> In both these cases, the chromosomes are doubtless bivalent, representing two

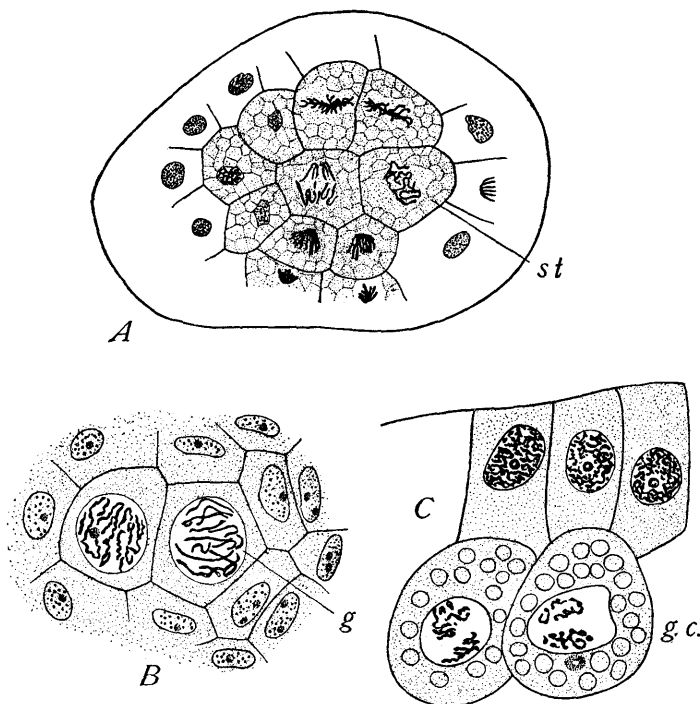


Fig. 74. — Primordial germ-cells in *Cyclops*. [HÄCKER.]

*A.* Young embryo, showing stem-cell (*st*). *B.* The stem-cell has divided into two, giving rise to the primordial germ-cell (*g*). *C.* Later stage, in section; the primordial germ-cell has migrated into the interior and divided into two; two groups of chromosomes in each.

chromosomes joined together. In *Ascaris*, in like manner, each of the two chromosomes of the stem-cell or primordial germ-cells is probably plurivalent, and represents a combination of several units of a lower order which separate during the segmentation of the thread when the somatic mitosis occurs.

<sup>1</sup> Cf. p. 256, Chapter V.