CHAPTER IV

THE GAMETES

"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. [1]

"The fertilized egg, accordingly, divides into cells that constitute the individual and cells for maintenance of the species."   M. NUSSBAUM. [2]

The structure and mode of origin of the gametes offer to the student of development and heredity a series of problems of such fundamental interest as to have made them the object of innumerable researches on the part of both botanists and zoölogists. The difficulties of observation which they offer have only in part been overcome; nevertheless we now possess a fairly adequate acquaintance with the main features of the subject.

It is probable that in their most primitive condition the gametes of both sexes were motile and structurally alike (isogamous), as is still the case in many of the lower existing forms. Deferring to a later point (Chap. VII) an account of these more primitive types, we here consider only the higher heterogamous forms in which the gametes differ widely in form and function, the macrogamete or ovum being a very large, quiescent cell, while the microgamete or sperm is a very minute and usually motile cell, typically provided with one or more flagella or cilia. This difference is clearly the result of a physiological division of labor between the gametes of the two sexes. The ovum has to supply most of the material for the body of the embryo, and often also to provide for its protection and maintenance during development. For this service it prepares by extensive growth, accumulating a large amount of protoplasm, commonly laden with reserve food-matter (*yolk* or *deutoplasm*), and in many cases becoming surrounded by membranes or other protective envelopes. During its

[1] Parthenogenesis, p. 3, 1849.   [2] *Arch. mik. Anat.*, XVIII, p. 112, 1880.

early history, therefore, the ovum is characterized by predominance of the constructive or anabolic processes of metabolism.

The microgamete or sperm, on the other hand, makes but an insignificant contribution to the mass of the embryo, and is relieved from the task of providing food and protection for the embryo. Physiologically the microgamete shows a most striking contrast to the ovum in its active movements and in its type of metabolism, which is characterized by the predominance of the destructive or katabolic processes by which the energy necessary for these movements is set free.[1] When finally matured, accordingly, the gametes of the two sexes have diverged almost to opposite extremes of cell-differentiation; and it is not surprising that while Schwann recognized, somewhat doubtfully, the fact that the egg is a cell, it was not until many years afterward that his successors proved the sperm to be of the same nature.

I. THE GAMETES OF ANIMALS

A. THE ANIMAL OVUM [2]

1. General Structure

The animal egg (Figs. 106, 107) is a cell of giant size, almost always laden with reserve food-materials in the form of suspended drops, semi-solid spheroids, granules, and other metaplasmic bodies which collectively constitute the yolk or *deutoplasm*. To this fact the egg owes, in part, its enormous size as compared with the sperm; and the question has even been raised whether the egg really contains a greater quantity of "living" (*i. e., active*) protoplasm than the sperm.[3] In some cases, however, no yolk can be distinguished other than the alveolar spheres of the protoplasm; such, for instance, are the eggs of certain sea-urchins and starfish, which offer classical examples of the alveolar structure as described by Bütschli. It seems evident, therefore, that the egg does in fact contain a much greater quantity of active protoplasm than the sperm. Like other cells the ovum tends towards a spheroidal form, and this form is commonly realized more or less nearly; in its earlier stages, however, the oöcyte is often irregular in shape, and sometimes actually amoeboid. The full-grown egg is often

[1] The metabolic contrast between the germ-cells has been discussed in a suggestive manner by Geddes and Thomson in their work on the *Evolution of Sex*. These authors regard this contrast as but a particular manifestation of a metabolic contrast characteristic of the sexes in general.

[2] The term *ovum*, or egg, is commonly applied to the female germ-cell, whether it has undergone the changes of "maturation" (*i. e.*, has formed its polar bodies) or not; but strictly speaking the unmatured egg, so long as the germinal vesicle remains intact, is still an oöcyte (p. 314). This distinction may here be disregarded, and the following account will apply primarily to the full grown egg before maturation has been completed.

[3] *Cf.* Waldeyer, '06.

more or less flattened at the poles, and sometimes elongated to a ellipsoid or almost cylindrical form (Fig. 112). In some groups, notably in the insects, the eggs of different species are of definite and characteristic shapes, which display a remarkable diversity. The most interesting of these are forms in which the bilateral symmetry and antero-posterior differentiation
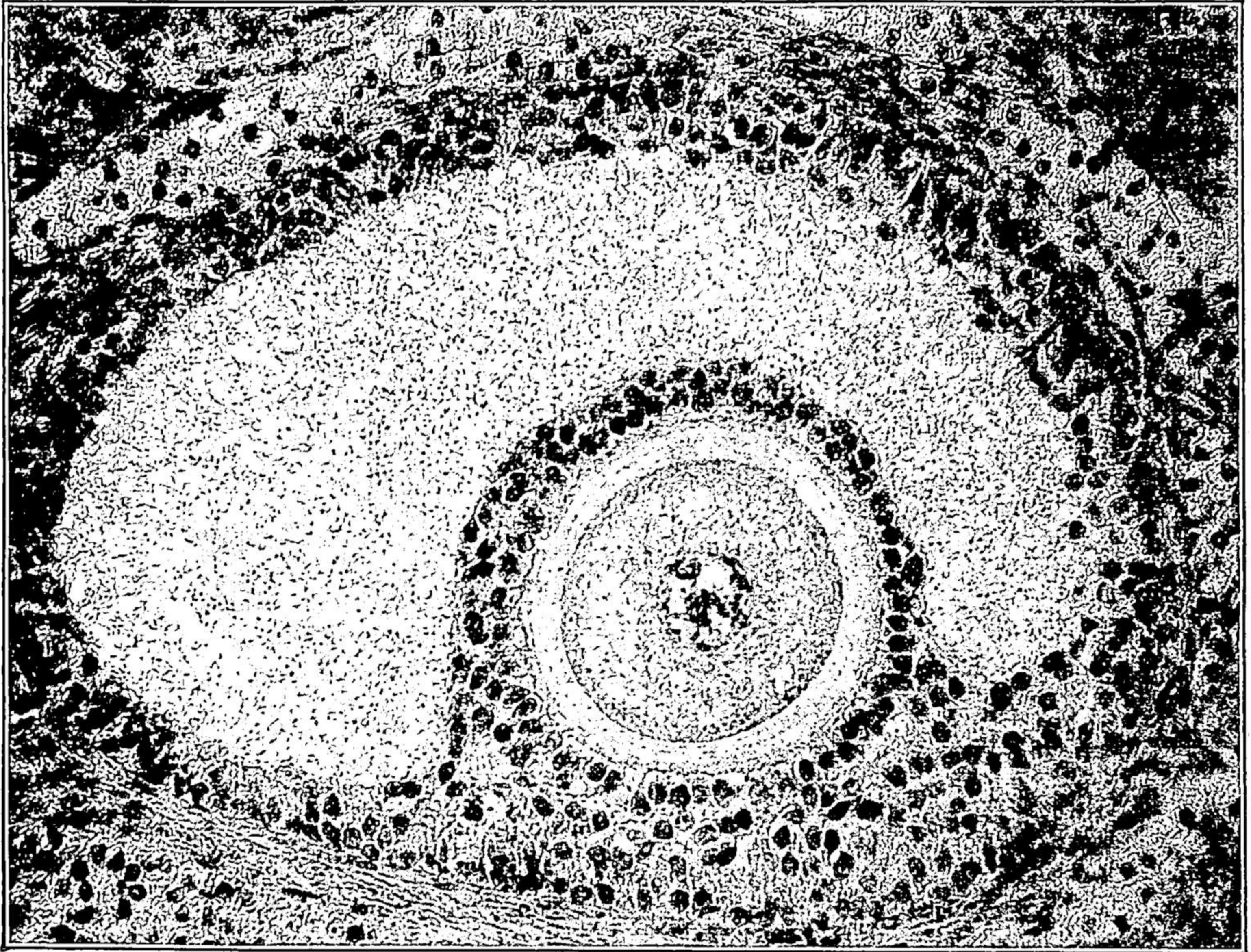

Fig. 106.—Ovum of the cat, within the ovary, from a photograph of a preparation by DAHLGREN. (Enlarged 235 diameters.) The ovum lies in the Graafian follicle within the *discus proligerus*, the latter forming the immediate follicular investment (*corona radiata*) of the egg. Within the *corona* is the clear *zona-pellucida* or egg-membrane.

of the future embryo are clearly discernible in the shape of the egg before it has been fertilized, or even before it has left the ovary (p. 275).

The eggs of some animals have been described as naked; but it is certain that in all cases the egg is bounded by a plasma-membrane (p. 55), and in many if not all cases also surrounded by a delicate *vitelline membrane* or *fertilization-membrane* closely applied to the periphery (p. 272). This membrane is often succeeded by other envelopes, and these show a great variety of structure. In many species the egg-envelope is perforated by a minute opening or *micropyle* (or a group of such openings), through which the sperm may enter the egg during fertilization (Figs. 113, 114); but in many cases no micropyle can be distinguished; and others such

as the nemertine or the sea-urchin, in which the sperm makes little use of the micropyle, being able to perforate the envelope at any point (p. 408).

Before maturation has taken place the nucleus of the egg is ordinarily of great size and is commonly called by its old name of *germinal vesicle* (Purkinje, 1825). During maturation the germinal vesicle breaks down in preparation for the formation of the polocytes (p. 398), and after completion of the process the nucleus is reformed as a much smaller body, a large part of its substance having been cast out into the cytosome. In this form the nucleus is commonly called the *female pronucleus* (Van Beneden), or more simply, the *egg-nucleus*. The germinal vesicle commonly occupies an eccentric position, lying nearer the upper or animal pole; but its position is sometimes nearly central, especially in the earlier stages of the oöcyte. As the growth of the egg proceeds, the eccentricity usually increases, and in the extreme types of telolecithal ova (such as those of elasmobranchs, birds, or reptiles) it ultimately lies close to the periphery, sometimes actually in contact with the membrane.[1] Its form is typically that of a spherical sac, surrounded by a very distinct membrane; but during the growth of the egg it may become irregular or even amoeboid (Fig. 153), sometimes sending forth conspicuous pseudopodia towards the source of food (Bambeke, Korschelt).

The relative size of the germinal vesicle varies widely in different species or groups; and this is to a certain considerable extent correlated with the mode of nutrition of the ovum, as Jörgenssen ('13) in particular has pointed out. In eggs that are accompanied by nutritive nurse-cells, follicle-cells or the like, which play an important part in elaborating food for the egg, the germinal vesicle is often relatively small— a condition conspicuously shown in many insects. When such accessory nutritive structures are wanting the germinal vesicle is commonly very large, as might be expected in view of the importance of the nucleus in nutrition. Many departures from this rule are, however, known.

In its earliest stages the oöcyte contains a pair of central bodies lying beside the nucleus in the oöplasm, and surrounded by a rounded body commonly called the *sphere* or *idiozome*, about which in turn are grouped Golgi-bodies and chondriosomes, which later, in some cases at least, scatter through the oöplasm (p. 342). The central bodies are most commonly lost to view in later stages, though there are a few cases in which they are said to be present at every period (*e. g.*, in the leech *Pisciola* (Jörgenssen, '13) and at least one case (*Thysanozoön*), in which the central body lies within the nucleus from an early stage of the oöcyte (p. 97). It is possible, therefore,

[1] *Cf.* Harper, '04, Loyez '06.

that the central bodies are always present, though often hidden among the cytoplasmic granules or in the nucleus.

2. The Oöplasm

The oöplasm (cytoplasm) of the full-grown egg always shows, more or less clearly, an alveolar or pseudoalveolar structure owing to the presence of closely crowded alveolar spheres or yolk-spheres suspended in the continuous hyaloplasm in which lie also numerous smaller granules of various kinds. As has earlier been indicated (p. 73) we can draw no precise line of demarcation between the larger disperse components (alveolar spheres) of an alveolar protoplasmic structure and the passive metaplasmic or paraplastic formed elements ("inclusions"), collectively designated as yolk or deutoplasm. In practice we are accustomed to restrict the latter terms to bodies distinguished from alveolar spheres by their larger size and which also differ in physical character and often in staining-reactions.[1] When such differences do not appear, as in many echinoderms (*Asterias, Toxopneustes, Parechinus*), the egg is commonly spoken of as *alecithal* or
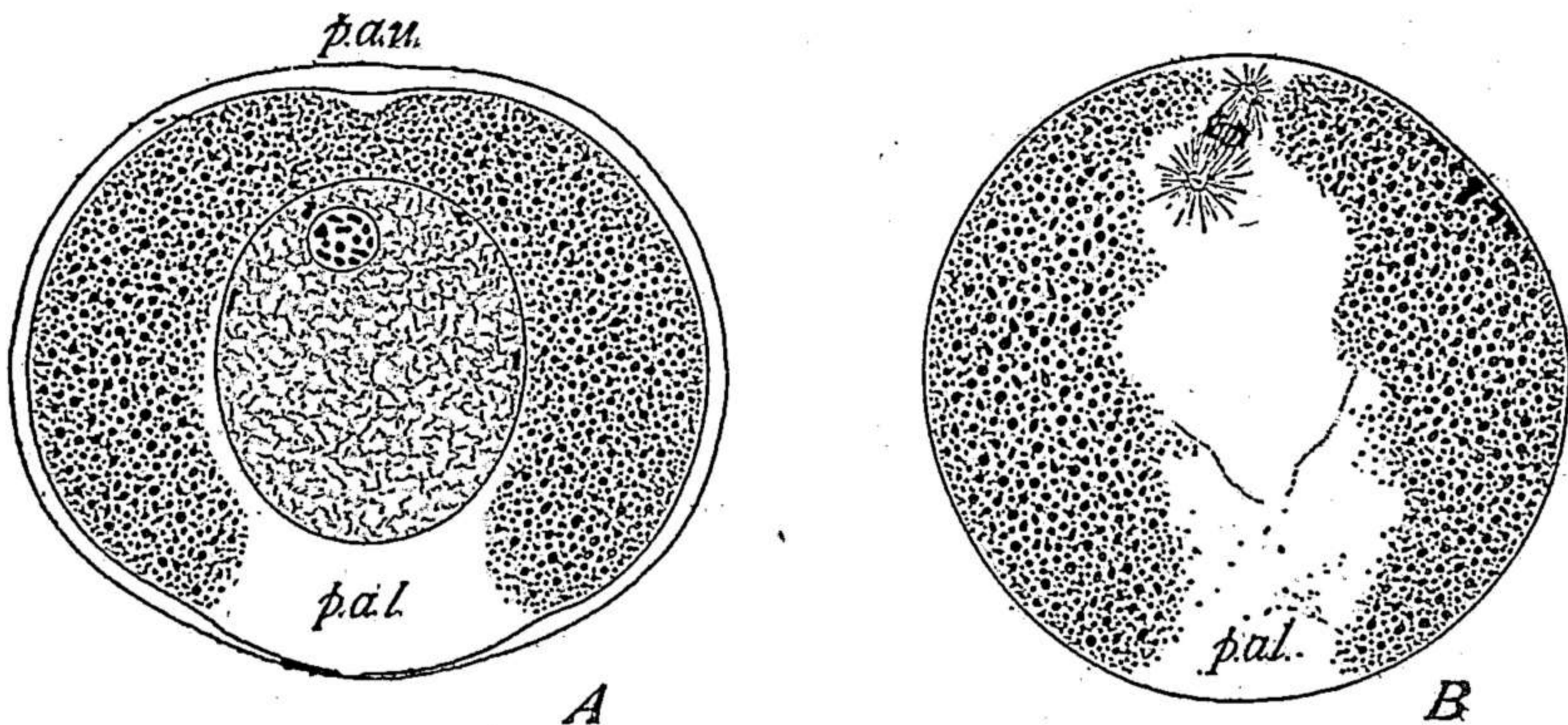

Fig. 107.—Eggs of *Dentalium* prior to Fertilization.

A, in vertical section shortly after discharge, showing intact germinal vesicle, nucleolus, and scattered chromosomes, polarization, with upper (*p. a. u.*) and lower (*p. a. l.*) clear areas, yolk black; *B*, egg after disappearance of germinal vesicle and formation of first polar spindle. (See also Fig. 509.)

homolecithal. Such eggs offer classical examples of a true alveolar structure as described by Bütschli.

The yolk is commonly more or less definitely localized, sometimes being more concentrated in the central region (*centrolecithal* type) more frequently in the vegetative hemisphere (*telolecithal* type), sometimes in other regions (*Dentalium*, Fig. 107). In such cases both types of structure appear in the same egg, the "pseudalveolar" in the yolk-bearing regions,

[1] *Cf.* p. 74. See Wilson, '99.

the "true" alveolar in the remaining; and in the latter the egg-nucleus most commonly lies.

As a rule the egg develops a more or less definite peripheral *cortical layer* ("ectoplasm," "peri-vitelline" layer) bounded externally by the plasma-membrane, often also by the vitelline membrane.[1] Cytological observation and physiological experiment alike demonstrate the extreme importance of this layer for many of the processes of development. It is for the most part free from yolk in the ordinary sense, but often contains specific granules of various kinds,[2] and sometimes differs in staining reaction from the entoplasmic material. It is this layer which first reacts to the contact of the sperm (p. 409); and during the processes of maturation, fertilization and early development it is often the seat of streaming movements towards particular regions of the egg by means of which some of the most important localizing activities of the egg are manifested (p. 415). It is from the cortical layer that the blastoderm is in large measure formed in eggs of the extreme centrolecithal (insects) or telolecithal (birds, reptiles) types; and from local thickenings of the same layer arise such structures as the polar rings (Fig. 192) of leeches (Whitman, '78, etc.) and oligochætes (Vejdovský, '87), or the "polar lobe" of certain annelids and mollusks which plays so important a part in the development (p. 1063). In some cases, the peripheral region of the cortical layer is radially striated and forms a "zona radiata" which in some cases seems undoubtedly to constitute a vitelline membrane (*e. g.*. in the eggs of fishes, Mark, '90). In the case of *Nereis* (Lillie, '11) proved that the *zona radiata* represents a radially disposed alveolar layer of protoplasm, the alveolar contents of which are discharged, after insemination, to form a thick jelly-envelope investing the egg.

a. The Deutoplasm or Yolk. Owing to the presence of yolk-spheres, chondriosomes, Golgi-bodies, fat-drops, pigment granules, and various other formed components, the oöplasm forms a complex system which varies widely in different species, and offers a difficult problem both chemically and cytologically. It is not easy to define precisely what is meant by the terms "yolk" or "deutoplasm"; and since the various components of the oöplasm can only be imperfectly separated for chemical analysis, statements concerning the composition of the "yolk" apply for the most part to a heterogeneous mixture of substances. The chemical nature of some of the formed elements may, however, in a measure be indicated by their cytological characters, *e. g.*, in the case of fat-drops, glycogen, or chrondriosomes.

With the grouping of the yolk in the egg we are here only indirectly con-

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[1] This layer is not to be confused with the so-called hyaline or ectoplasmic layer which first appears after fertilization. See p. 413.

[2] For review of this subject see Lillie, '06.

cerned. It is a very important fact that this grouping, as seen at the time cleavage begins, must be regarded as a secondary character of the egg resulting from processes of segregation that take place earlier or later during the growth-period, though often completed only at the time of maturation and fertilization (p. 1096). Apart from the general distribution of the yolk more specialized groupings are often seen, some of them of much interest to the student of development. An example of these is offered by the stratification or layered condition found in birds, elasmobranchs and reptiles, where two kinds of yolk (in the hen's egg known as the white and the yellow) occur in alternating and approximately concentric layers. Riddle ('11) has produced evidence that in the hen's egg this is an expression of the daily growth of the egg, one pair of layers being produced each day, including a white one laid down during the poorer nutritive conditions prevailing during the later hours of the night, and a yellow one during the remaining part of the day.

When analyzed chemically *en masse* the yolk of the hen's egg is found to consist of water and solid matter in nearly equal parts [1] and contains various inorganic salts of sodium, potassium, calcium, magnesium, iron, phosphorus and silica. Of the solids about 23% are fat, 11% lecithin and other phospholipins, 16% protein and 1.5% cholesterol, while the inorganic salts form about 3% (less according to some authorities). The protein consists largely of ovo-vitellin, a compound phospho-protein resembling the nucleo-proteins, but differing from them in that the acid component is stated to be not true nucleic acid,[2] though like the latter it is an organic acid rich in phosphorus. Carbohydrates seem to be nearly absent from the hen's yolk, but in some eggs are present in considerable quantity in the form of glycogen (insects). The yolk of the hen's egg contains, in addition to the foregoing, a small quantity of "hæmatogen," an iron-containing compound resembling "nuclein," and supposed to be the mother-substance of hæmoglobin.

The yolk is thus seen to contain the principal foodstuffs required by the developing embryo.[3] To a certain limited extent these are sometimes morphologically recognizable. Many eggs, for example, contain fat-drops easily recognizable as such (Fig. 470), and in such cases, owing to their lightness, they may determine the position of the egg with respect to gravity (p. 1016). Glycogen occurs in many eggs (*Ascaris*, insects) in the form of granules or irregular bodies recognizable by their staining reactions (Kemnitz, '12, Brammertz, '13). The ordinary yolk-spheres are probably largely

[1] For a general account of the chemistry of the yolk see Mathews ('15).

[2] Since it yields no purine bases; *cf.* p. 643.

[3] Riddle ('14–'17) has made an interesting attempt to show that in mammals and birds the male-producing and female-producing eggs show recognizable chemical differences. *Cf.* p. 807.

proteid in nature but undoubtedly contain in many cases lipoids and other substances that may not be recognizable as such by the eye; they are typically spheroidal but in some cases they are oval, ellipsoidal bodies (Amphibia) or even flattened and plate-like (elasmobranchs). The meaning of these variations is little understood, as are also their variations in physical characters and staining-reactions. In physical consistency they vary from viscous liquid drops to almost solid bodies; and they likewise vary widely in permeability to light, in specific gravity (p. 262) and in staining reactions. They are often intensely basophilic but may be oxyphilic in various degrees. In general, however, it may be stated that by the ensemble of their staining reactions they may as a rule be readily distinguished from the mitochondria and Golgi-bodies (with which they are often intermingled) and also from the fat-drops.[1] It is an interesting fact that in *Patella*, according to Gatenby, many of the Golgi-bodies (in the form of crescentic rodlets) are attached to yolk-spheres.

b. *Pigment.* Many ova are more or less colored, sometimes in definite patterns—a fact of much practical importance for studies on the early stages of development (pp. 1016, 1094). In some cases the pigment appears to be diffuse, and perhaps has its seat in the hyaloplasm (e. g., in *Myzostoma*, p. 1096). More commonly it is borne by formed elements, sometimes by the yolk-spheres or alveolar spheres but most often by smaller granules, as in the eggs of frogs, ascidians, ophiuroids or sea-urchins. A striking case is offered in the eggs of *Ophiura*, in which the yolk-spheres vary from reddish brown to olivaceous, while the "microsomes" scattered between them are clear lemon-yellow, offering a striking picture (Wilson, '99). In the ascidian *Styela* (*Cynthia*) Duesberg ('15) has proved that the yellow pigment-granules show the characteristic staining-reactions of mitochondria and probably arise by transformation of the latter.

The distribution of pigment in the egg often follows a definite pattern correlated with the promorphological characters of the egg, and thus offers a valuable means of embryological observation (Figs. 512, 524). It is usually most abundant in the cortical layer of the egg, and sometimes confined to it (*Styela, Paracentrotus*), but may also be scattered through the oöplasm (*Arbacia*). The pigment pattern sometimes appears early in the ovarian life of the egg. In other cases the pigment takes on a definite pattern by a sudden localizing activity at the time of maturation or fertilization. Striking examples of this are offered by the eggs of the sea-urchin *Paracentrotus lividus* or the ascidian *Styela partita* (p. 1094). It is an interesting fact, of unknown meaning, that in some cases the pigment-granules show a marked tendency to collect about the nuclei of the segmenting egg.

[1] A comparative review of these reactions is given by Gatenby ('20).

c. Chondriosomes and other Formed Elements. Besides the larger formed components the oöplasm always contains numerous small granules described as "microsomes," which graduate in size down to the limits of microscopical vision; [1] often also fibrillæ or rod-shaped elements lying between the yolk-spheres. Most of these bodies are basophilic in various degrees and by some authors have actually been described as "cytoplasmic chromatin" (p. 724) but much confusion still exists concerning their real nature. By a considerable number of observers (Goldschmidt, Popoff, etc.) these granules, or many of them, were believed to be chromidia emitted from the nucleus, as such or in the form of larger bodies that subsequently fragment. Meves, Duesberg, Fauré-Fremiet and a large group of other observers have however shown clearly that both the rod-like or fibrillar formations [2] and many of the granules (especially those of larger size) are chondriosomes. On the other hand, Schaxel has endeavored, in a series of careful studies, to show that both views are correct, both chromidia and chondriosomes being present in the oöplasm (p. 703). How dubious is the evidence based on the staining-reactions is strikingly shown by studies on *Chætopterus* by F. R. Lillie ('06),[3] who himself seems to favor the view that microsomes are in large measure "chromatin particles." Lillie found that although the cytomicrosomes are strongly basophilic those of nuclear origin are purely oxyphilic until their liberation from the germinal vesicle (at the time of maturation) when they generally become basophilic. In some cases certain of the oöplasmic granules have recently been identified as scattered Golgi-bodies which at an earlier period of the oöcyte are aggregated about the central bodies of the idiozome (p. 345).[4]

In addition to the foregoing the ovum often contains other components of doubtful character, whose relation to those already enumerated is not very clearly determined. Among these may be mentioned the so-called "archiplasm," in the form of irregular clumps of finely granular material, which may be differentiated from the remainder of the cytoplasm by certain staining-reactions (p. 723). Of similarly vague meaning is the term "ergastoplasm," originally applied by Garnier and Bouin to the basophilic fibrillar formations in certain types of cells, especially in the gland-cells, and subsequently much extended in meaning by Prenant and other writers so as to designate collectively many differentiated cytoplasmic substances of basophilic staining capacity, including the chondriosomes (p. 724). This

[1] See Wilson, '99.

[2] This does not apply to the general reticulum described in the eggs of echinoderms and other forms by Retzius who considers this structure to be typical of protoplasm generally. Reasons for doubting this are given at p. 70.

[3] This work contains a valuable study of the various types of granules in the egg.

[4] See especially Hirschler, '18, Gatenby, '20, etc.

term has recently been resuscitated by Jörgenssen ('13), Buchner ('15), Gajewska ('20), and some others, as a non-committal term applied to strongly basophilic cytoplasmic material, in the form of irregular flocculent masses, resistant to peptic digestion, and not clearly to be identified, or of a perinuclear ring.[1] It is now clear, as will later appear, that the latter is equivalent to the "pallial" or "vitellogeneous" substance, known to consist largely of chondriosomes, but also containing Golgi-bodies, and in some cases perhaps extruded nucleolar fragments (p. 340). The term ergastoplasm thus seems to be of very questionable utility.

Two other formed elements of doubtful character, known only in the insects, may here be mentioned. One of these includes the so-called accessory or *secondary* nuclei, found in the oöcytes of several orders of insects, especially the Hymenoptera (p. 347). A second and even more remarkable component of the oöplasm, likewise known only in certain insects, are rod-like or rounded bodies, sometimes present in great numbers, and variously known as "bacterioids," or "intracellular symbionts." In the ova of certain Hymenoptera (ants), Orthoptera (cockroaches) and Lepidoptera, and in some aphids, they are rod-like in form and divide by fission. In those of aphids, coccids, and some other insects they are more or less rounded and yeast-like, and like yeasts multiply by a process of budding. Blochmann ('84, '87), who first observed the bacterioid form (in *Camponotus, Formica, Blatta* and *Periplaneta*)[2] found that in their earlier stages the oöcytes are free from these bodies but are later infected with them from the surrounding cells. He therefore concluded that they are bacteria-like organisms that live symbiotically in the oöcyte and in many of the somatic cells derived from it, and this has been confirmed by many later observers who have also found the same to be true of the yeast-like symbionts of other insects. Both the bacteroid and the yeast-like forms are said to have been successfully cultivated in artificial cultures outside the body of the host,[3] and many different genera and species of them have been described.

It seems probable that in some species the presence of these intracellular fungi is due to accidental infection; but in many cases, they are invariably present as a characteristic feature of the species, the association between host and symbiont having apparently become permanent if not obligatory. A remarkable feature of such cases is that in some of them the egg is provided with special structural features which seem expressly designed to provide for its infection by symbionts from the surrounding tissue-cells.

[1] See Jörgenssen, '13.
[2] A full historical treatment of the subject is given in Buchner's interesting paper on the intracellular symbionts of Hemiptera ('12).
[3] Krassilstschik ('89), Mercier ('06, '07), Pierantoni ('10), Sulc ('10).

In the aphids this structure, which has long been known, is developed from a group of infected follicle-cells, always at the posterior pole of the oöcyte. These cells (mycetocytes) constitute the "mycetoma," long ago described by Huxley (1858) as the *pseudo-vitellus*, and they appear to be the sole means by which the egg is infected. Concerning the physiological relations between symbionts and host, nothing definite is yet known.

3. The Egg-nucleus or Germinal Vesicle

Owing to the great size of the germinal vesicle the nuclear phenomena here appear on a large scale and in spectacular fashion, but they are com-
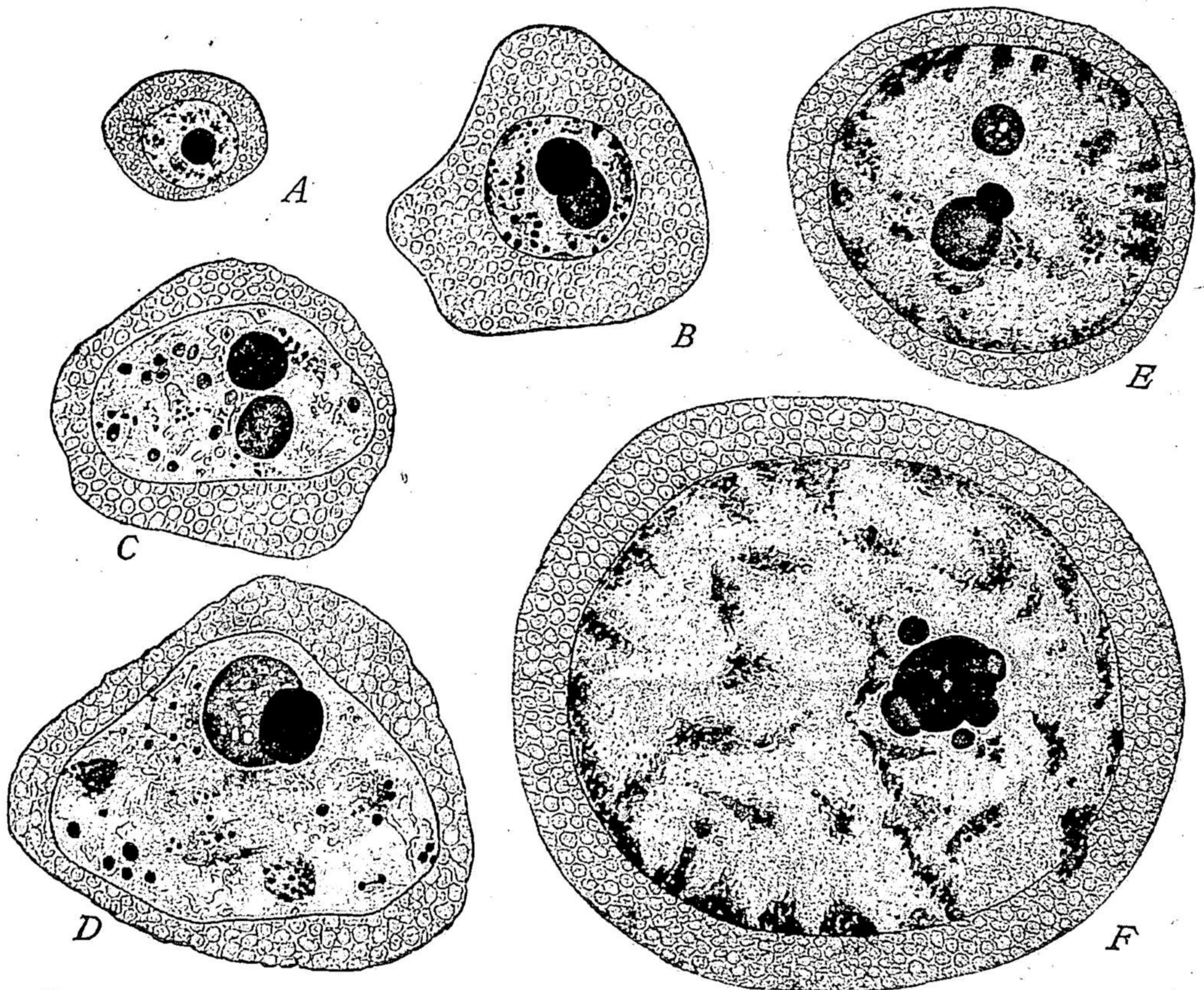
Fig. 108.—Germinal vesicles of growing ovarian eggs of the pelecypod, *Unio* (*A–D*), and the spider, *Epeira* (*E–F*) (Obst).

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.

plicated by the fact that we are dealing with a nucleus during a period not alone of intense constructive activity and growth but also of meiosis or the reduction of the chromosomes. In this respect the nucleus of the animal

ovum offers a much more intricate problem than that of plants, where in general the meiotic phenomena take place at another period of the life-history (p. 489). The structure of the germinal vesicle in the full-grown egg can therefore only be understood in the light of its earlier history. At this point we limit our consideration, so far as practicable, to the germinal vesicle at or near the time of its full maturity.

The germinal vesicle offers many of the same features seen on a smaller scale in the nuclei of the tissue-cells in their "resting" or vegetative condition; but in most cases shows also certain characters of a prophase-nucleus. Its structural details in the full-grown egg vary widely; we may usually distinguish, as in the somatic nuclei, a *nuclear framework* in the form of a fine network or alveolar structure, a well-defined nuclear wall or membrane, and one or more conspicuous nucleoli (the "germinal spots" of early observers); but in many ova, as they approach maturity, the nucleoli are already in course of disappearance.

   a. *The Chromosomes and the Nuclear Framework.* The general framework of the germinal vesicle is commonly but slightly basophilic and may even be purely oxyphilic; but in this respect wide differences exist between different species. In all cases, the full-grown germinal vesicle when ready for the final stages of maturation contains the formed chromosomes (bivalents or tetrads) now more or less strongly basophilic and preparing to pass through the final prophases of the meiotic divisions (p. 546). In many cases, particularly in the case of relatively small eggs, they are scattered irregularly through the germinal vesicle or around its periphery, sharply marked off from both the framework in which they are suspended and from the nucleolus or nucleoli. This condition, widely prevalent among invertebrates, is exemplified in the annelids (Fig. 199), mollusks (Figs. 107, 239) or teleosts (Fig. 162).

In other cases, as the germinal vesicle approaches its full term, the chromosomes show a tendency to aggregate in a definite group, suspended in the framework, and often lying near the center of the nucleus. This condition is commonly seen in the large eggs of vertebrates, such as the birds, reptiles, and in lesser degree the amphibians and fishes. In some cases they tend to aggregate in the immediate vicinity of the nucleolus, with which they may come into such intimate relation as to seem actually to arise from it. An example of this is seen in the echinoderms,[1] where a number of observers have described a nucleolar origin of the chromosomes, wholly or in part, while others have found only a close association between the two (Buchner, '11). It seems, however, to be well established

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[1] *E. g.*, R. Hertwig ('96), Wilson ('01), Hartmann ('02), Günther ('03), Jordan ('07). See also Conklin ('02), Lillie ('06).

that in some cases the central aggregation of the chromosomes may go so far as to give rise to a more or less compact and nucleolus-like body which in its more extreme forms may fairly be called a karyosphere (p. 93). This condition seems almost to be reached in some of the vertebrates (Loyez, '06), where many gradations exist in the concentration of the chromosome-groups, the process reaching a maximum in certain of the birds and reptiles (Fig. 110).[1] In such cases the chromosomes, though much reduced in size and closely crowded together, do not differ very markedly from those of the elasmobranch or reptilian egg just before the polar mitoses, when
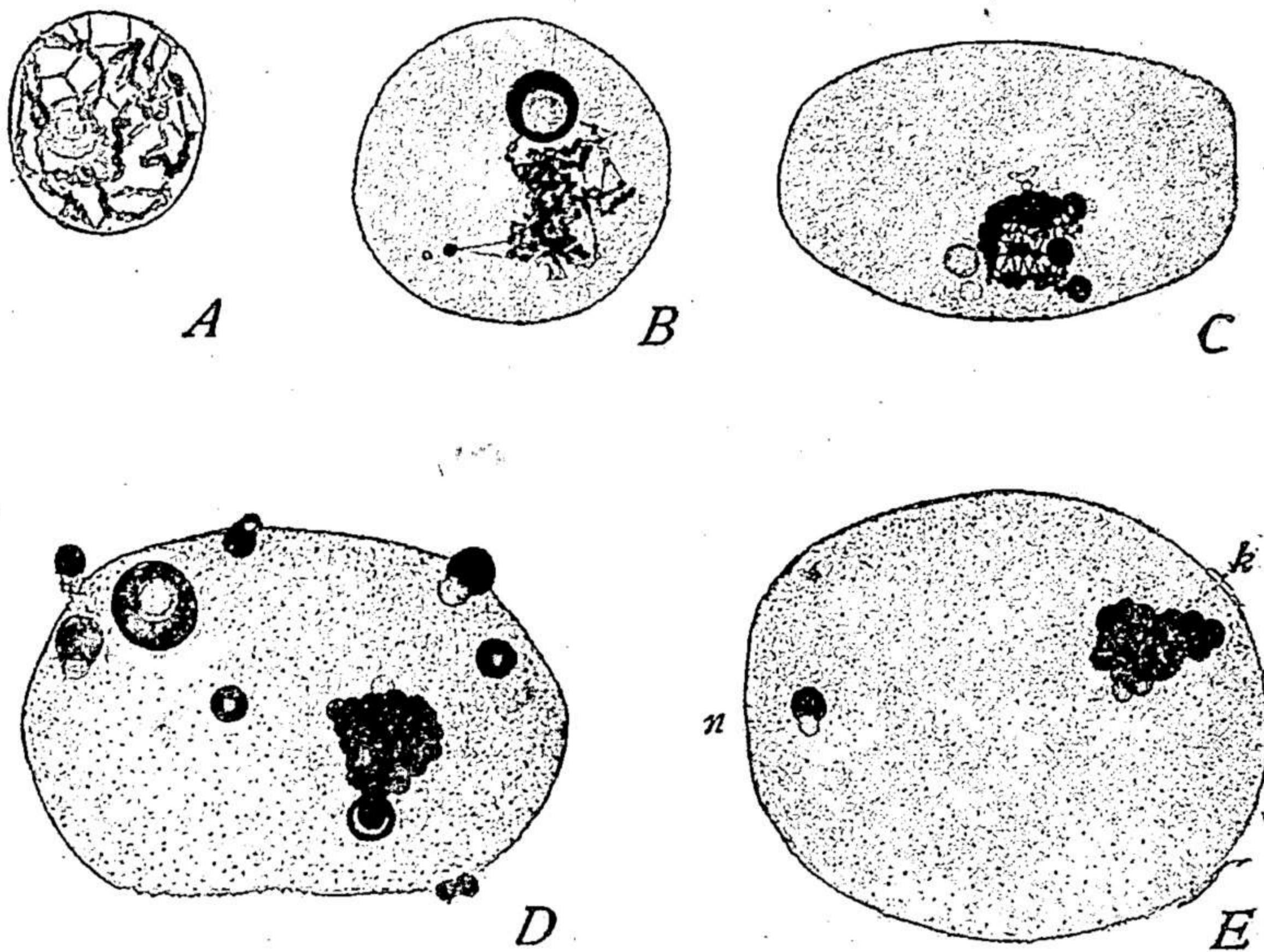
Fig. 109.—Formation of karyosphere in germinal vesicle of the leech, *Nephelis* (JÖRGENSSEN).

A, early post-synaptic spireme; B, beginning of concentration; C, D, later stages, showing amphinuclei; E, fully formed karyosphere (k) and one amphinucleolus (n).

they are likewise very small and closely crowded, though not actually forming a karyosphere (Fig. 110).[2] On the other hand, in a few of the invertebrates the chromosomes become so closely aggregated as to form a true karyosphere (Fig. 109) hardly to be distinguished from those that are sometimes found in the spermatocytes of insects and myriapods (Fig. 37).

Lastly it may be noted that the extent of the general nuclear framework as compared with that of the chromosomes also varies very widely. In some cases (e. g., in certain platodes)[3] the chromosomes constitute the main bulk of the nuclear substance with only a relatively sparse amount

[1] By some writers this has been characterized as a second contraction-figure (synizesis or "synapsis." See Vejdovský '11, '12).

[2] E. g., in the dragon-fly (McGill, '06), in the pelecypod *Cumingea* (Jordan, '10) and the leech *Nephelis* (Jörgenssen, '08).

[3] Cf. Gelei ('21 '22).

of framework. More commonly the framework constitutes the major part of the nucleus, the chromosomes being reduced to relatively small bodies suspended in it, while in extreme cases, represented by the large ova of elasmobranchs, amphibians, birds or reptiles, the chromosomes at the end of the growth-period constitute but a minute fraction of the nuclear substance. These different conditions are a consequence of the varying degrees in which the germinal vesicle returns towards the condition of a resting or vegetative nucleus. In the course of this process the chromosomes assume a more or less net-like condition and in extreme cases may even temporarily disappear from view altogether, as in an ordinary tissue-cell. In all cases, however, the germinal vesicle always retains a spireme-like character during a considerable part of the growth-period and sometimes throughout the whole of it; and even when this character seems to be wholly lost, the ensuing changes demonstrate that the germinal vesicle has undergone a far-reaching change in the earlier stages that stamps it with a type of organization widely different from that of a tissue-cell owing to the synaptic conjugation of the chromosomes. This was long since recognized by Rückert,[1] and all subsequent studies have shown that his conclusion was fundamentally correct in substance if not precisely in form.

c. The Nucleoli. The diversity of conditions shown by the nucleoli is as striking as that of the nuclear framework and the chromosomes. In the very young oöcytes the nucleolus is almost always single; and this condition may persist during the whole growth-period of the egg. In many cases, however, additional nucleoli appear, being sometimes numbered by hundreds (Fig. 111). As was long since recognized by Haecker ('95, '99, etc.) the nucleolus commonly remains single in relatively small eggs while it is usually multiple in large eggs heavily laden with yolk. The former condition ("echinoderm type" of Haecker) is of rather wide occurrence among invertebrates (various coelenterates, echinoderms, platodes, annelids, mollusks, etc.) and appears also in many insects (Fig. 111) and in some of the chordates (tunicates, *Amphioxus*, *Bdellostoma*, mammals). Multiple nucleoli ("vertebrate type" of Haecker) occur with few exceptions in the large yolk-laden eggs of elasmobranchs and other fishes, amphibians, birds and reptiles; also in some arthropods. Conspicuous exceptions to Haecker's rule are, however, known, and nearly related forms sometimes differ markedly in this respect, but the meaning of these variations is not yet clear.[2]

Like the nucleoli of tissue-cells, those of the germinal vesicle may be

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[1] "The germinal vesicle is to be regarded as a daughter-spireme of the oögonium grown to enormous dimensions, with its chromosomes double and arranged in pairs" ('92, 2, p. 51).

[2] See Jörgenssen, '13.

either basophilic, oxyphilic or of intermediate character; and in many cases both extremes coexist in the same germinal vesicle, often being united to form amphinucleoli (p. 94). Most commonly the nucleoli are strongly basophilic, and are often markedly resistant to hydrochloric-peptic digestion (Zacharias, Jörgenssen). In these respects they show a remarkable contrast to the general oxyphilic framework and often also to the chromosomes, during the middle growth-period of the egg (p. 351), a contrast
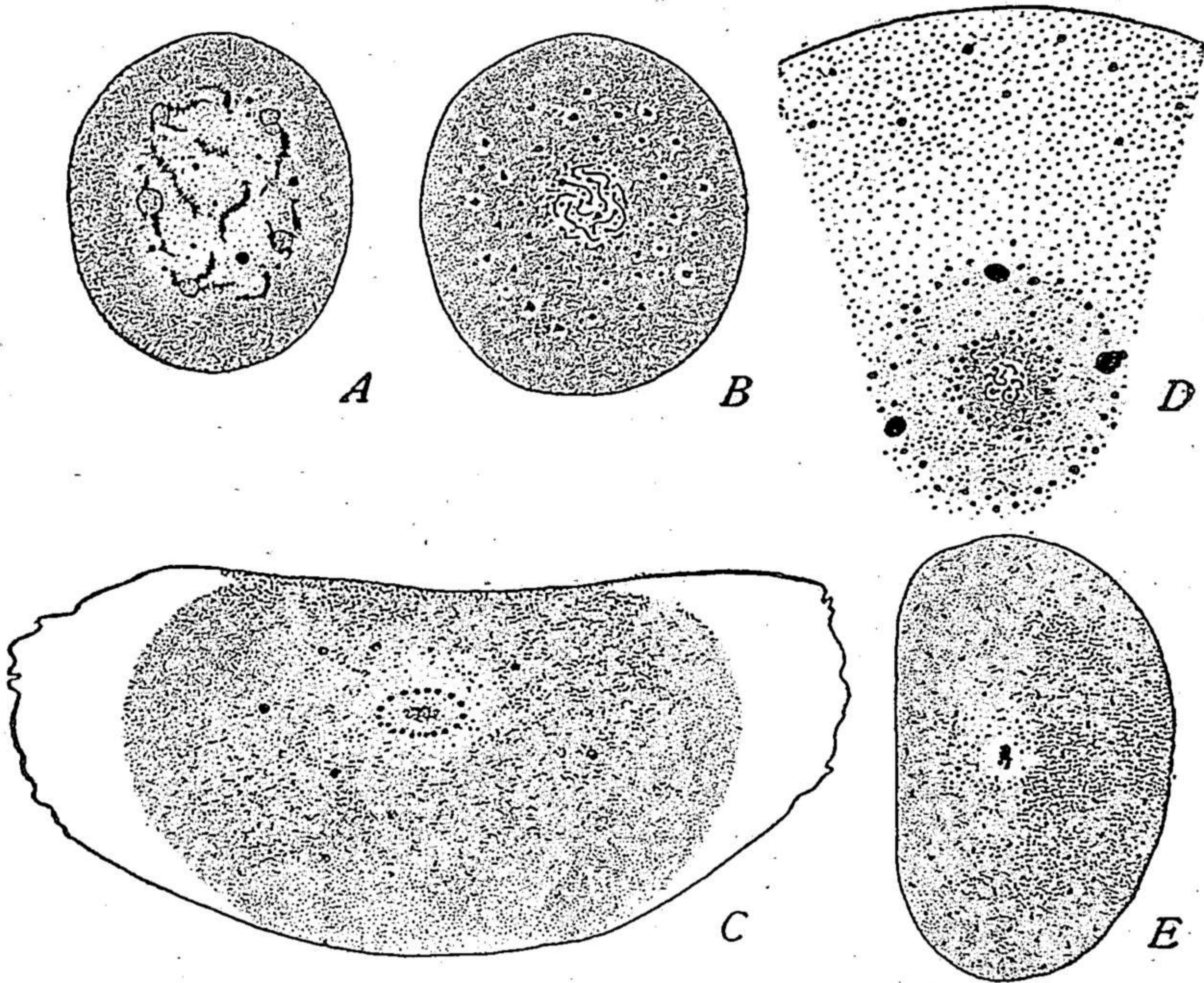

Fig. 110.—The germinal vesicle in reptiles (LOYEZ).

(A–C, *Anguis*, D, E, *Lacerta*). A and B, successive stages in the centripetal movement of the chromosomes; C, shortly before maturation, chromosomes very small, crowded at center and surrounded by nucleoli; D, portions of full grown germinal vesicle, with chromosomes massed at center, surrounded by nucleolar fragments; E, entire germinal vesicle, less magnified, showing massed chromosomes.

heightened by the fact that these nucleoli are typically spheroidal in form and sharply marked off from the framework in which they are suspended. These nucleoli often appear perfectly homogeneous; frequently, however, especially in the later stages of the uninucleolar type, they become more or less vacuolated, showing a large central vacuole or numerous smaller ones scattered through their substance. At the same time they often become less strongly basophilic and less resistant to hydrochloric-peptic digestion (Jörgenssen). In the eggs of many invertebrates, after double-staining with basic and acidic dyes, two nucleolar substances are often differentiated, one strongly basophilic and resistant to pepsin-hydrochloric digestion, the other slightly basophilic or even oxyphilic and readily di-

gestible. These substances have the same general character as those which in other species appear in the form of separate oxyphilic and basophilic nucleoli, or of two such nucleoli closely apposed to form an amphinucleolus
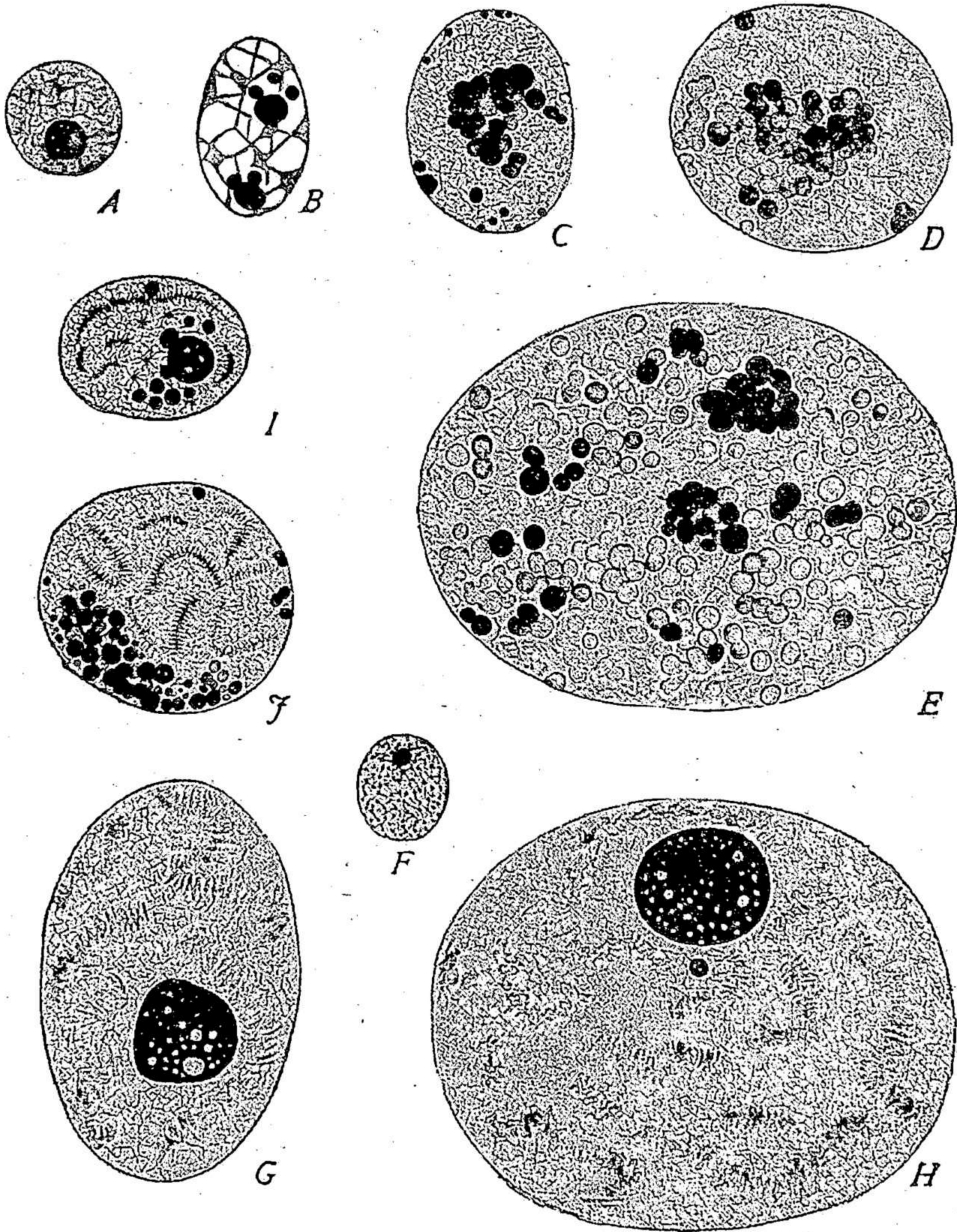

Fig. 111.—The germinal vesicle during the growth-period of tracheates (Jörgenssen).

A–E, progressive stages of the myriapod *Scolopendra*, showing multiplication of basichromatic nucleoli, chromosomes invisible as such; F–H, the cockroach *Blatta*, with single basichromatic nucleolus and oxychromatic chromosomes; I, J, the mole-cricket *Gryllotalpa*, oxychromatic chromosomes, basichromatic nucleoli.

(p. 270). The latter condition is common in annelids, mollusks, arthropods and other invertebrates (Fig. 108). Such amphinucleoli are commonly single, but in a few cases (*Patella cœrulea*), many are present in the same nucleus (Jörgenssen, '13b). In cases of this type both substances are often
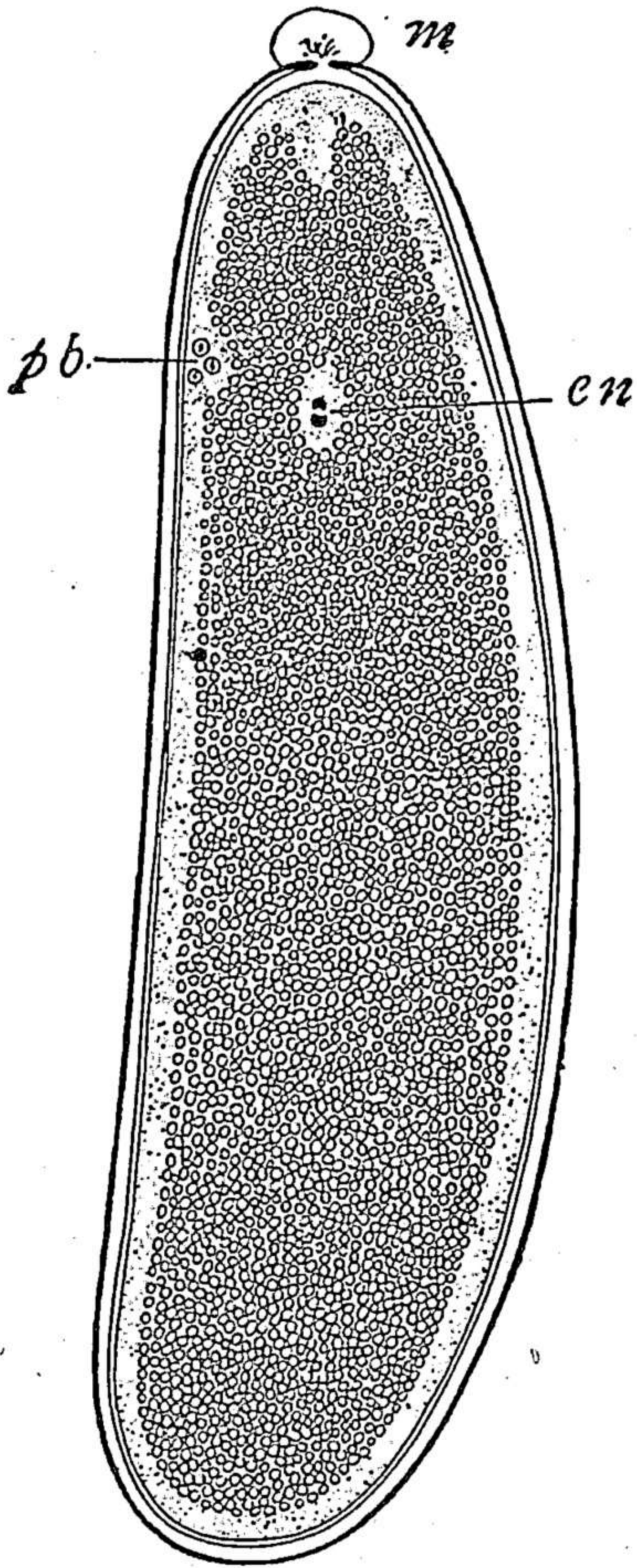
Fig. 112.—Schematic figure of a median longitudinal section of the egg of a fly (*Musca*), showing axes of the bilateral egg, and the membranes (from KORSCHELT and HEIDER, after HENKING and BLOCHMANN).

e. n., The pronuclei 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 center 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.

united in a nucleolus that is externally single but shows internally an oxyphilic basis in which are imbedded a number of sharply differentiated, rounded, elongate or cap-like basophilic bodies. The changes of staining reaction, and remarkable structural transformations of the nucleoli during the growth of the oöcyte will be later considered (p. 353).

4. The Egg-envelopes

Following Ludwig ('74) it is convenient to class the egg-envelopes as *primary*, formed by the egg itself, *secondary*, formed by the follicle-cells immediately surrounding the egg, and *tertiary*, formed by the oviduct or other maternal structures not immediately connected with the egg.

(1) The primary or "vitelline" envelopes include at least three types of structures, namely: (1), the *fertilization-membrane*, or *vitelline membrane* (p. 258), commonly structureless and very delicate; (2) a thicker and more conspicuous envelope, sometimes showing a pronounced radial striation and in such cases called the *zona radiata*; (3) a much thicker, structureless jelly surrounding the egg. Of these the fertilization-membrane is the most constant and is probably always present though often difficult to see before fertilization (p. 411). At the instant of fertilization this membrane suddenly separates from the egg, often to a considerable distance, thus affording a ready means of determining when the egg is fertilized. This membrane was formerly supposed to be formed only at the moment of fertilization; but it is now certain that in many cases it is present before the sperm touches the egg.

The *zona radiata* of the vertebrate ovum, conspicuously shown in the fishes, is a thick and often double membrane traversed by fine radial canals through which in many cases fine protoplasmic bridges are said to pass

from the follicle-cells into the cortical protoplasm of the egg (Fig. 156). By some observers this has been supposed to be a product of the surrounding *granulosa* or follicle-cells, but the evidence seems decisive that in certain cases, at least, the *zona radiata* is formed by the egg itself.[1]

In many cases this layer has been called a "chorion"; but it is doubtful whether this term can properly be applied to it. In the egg of the annelid *Nereis* the recent studies of F. R. Lillie demonstrate that the so-called *zona radiata* is formed by the closely crowded, palisade-like cortical alveoli; and that upon fertilization the clear contents of these are discharged to the exterior through the vitelline membrane and swell up in the water to form a thick layer of jelly by which the egg is surrounded.

(2) The secondary envelope is a product of the follicle-cells surrounding the ovum and hence is a purely maternal product. This membrane, typically seen in the insect-egg (Fig. 112), is the *chorion*. Owing to its mode of formation it is comparable to a cuticular membrane, and like the latter is often composed of a hard substance related to chitin, which forms a solid and almost impervious outer protection to the egg (insects). It is often marked by a more or less complicated pattern, determined by the activities of the surrounding follicle-cells, which commonly appears in the form of polygonal areas, often complicated by the formation of spines and other characteristic forms of sculpturing.[2]

Both the primary and the secondary envelopes are in some groups perforated by a *micropyle*, or a group of them, most commonly at or near one pole of the egg. In echinoderms, insects, cephalopods and fishes the micropyle is near the upper pole (Figs. 113, 512) while in other mollusks and nemertines it is near the lower pole. When single the micropyle sometimes is in a deep infolding of the membrane or *micropylar canal* (Fig. 114). When several micropyles are present they are usually grouped at the anterior end, sometimes at some distance from the original pole of the egg, sometimes
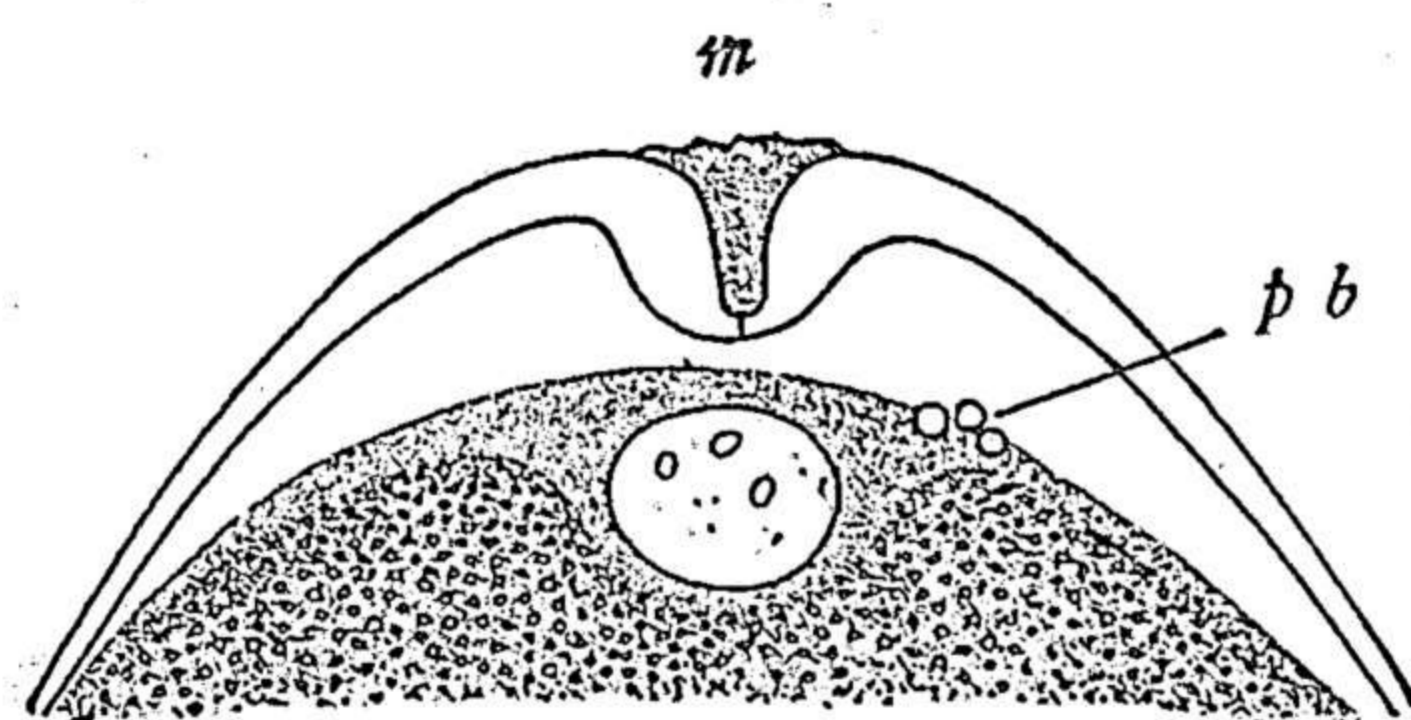

Fig. 113.—Upper pole of the egg of *Argonauta* (Ussow).

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.

in a circle surrounding a pit-like micropyle-field. In other cases, a ring of micropyles seems to surround the egg some distance below the anterior end. A good example of this is seen in *Metapodius* (Fig. 485), though the nature of the 40–50 "micropyles" is here not certain. It is possible that the pres-

[1] See especially Eigenmann ('90), Mark ('90).
[2] For a fuller account see Korschelt and Heider ('02) and literature there cited.

ence of several or many micropyles in the insect egg may be correlated with the fact that in these animals several sperms normally enter the egg, though only one of them actually·fertilizes it. In some cases, perhaps always, the position of the micropyle marks the point at which the oöcyte is attached to the ovarian wall during the period of its growth (p. 1023).

(3) The tertiary envelopes include a great variety' of protective and nutritive structures. Some are formed as secretions of the walls of the oviduct or uterus, or of special glands connected with them. Examples of these are the albumin, shell-membrane, and shell of birds and reptiles; the egg-capsules of the selachians, chimæroids, mollusks and platodes; or
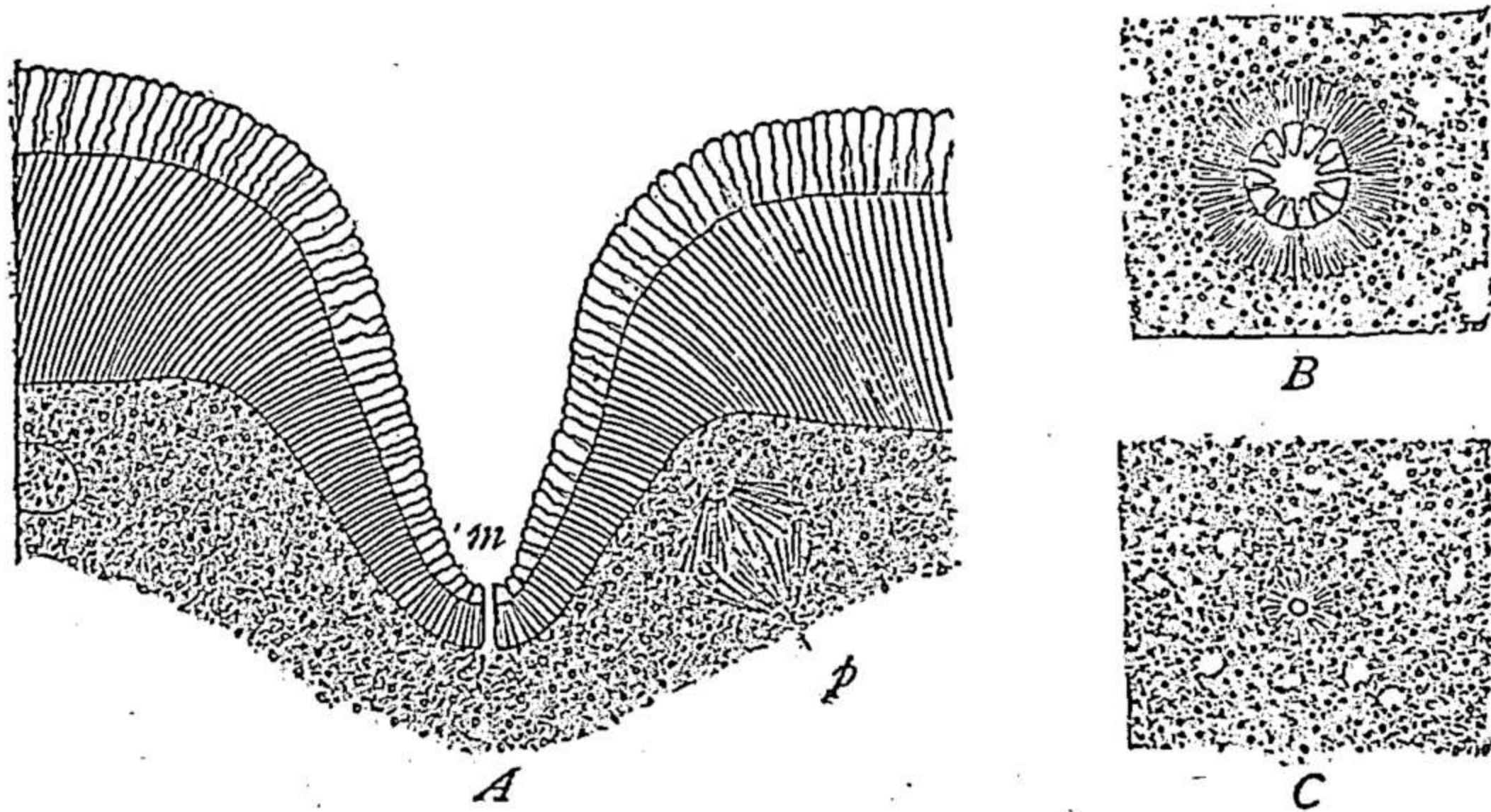

Fig. 114.—The micropyle in the egg of the ganoid *Lepidosteus* (MARK).

A, radial section through micropyle (*m*) at bottom of the micropylar funnel, traversing the outer villous layer and inner zona radiata of envelope; both these layers are believed to be products of the egg itself, hence "vitelline "membranes; at *p* is the anastral polar spindle; *B*, transverse section through the funnel, and *C* through the micropylar canal.

the gelatinous mass investing the ova of various fishes, amphibians, and mollusks. Other tertiary envelopes are secreted by the external' surface of the body, such as the protective capsules and nutritive fluids of the leeches and earthworms and a variety of other structures.

The tertiary envelopes are highly characteristic of different groups and species, and sometimes assume a definite form that may in some degree foreshadow that of the future embryo. A remarkable example of this is offered by the fish *Chimæra* [1] which produces an egg-capsule (Fig. 115) of elongate form, showing a perfect bilateral symmetry, dorso-ventral differentiation and antero-posterior differentiation that accurately correspond to those of the future embryo. This is of much interest because the general shape of the capsule does not correspond to that of the egg (which is elongate ovoid), but to that of the developed embryo, having an enlarged anterior region in which the head and body came to lie and a long posterior portion for the reception of the tail. The capsule is, there-

[1] See Dean, '03, '04, '06.

fore, moulded neither on the egg nor on the embryo to be developed from it, but is an apparently independent product of the wall of the oviduct. This capsule, like the insect egg (p. 1020) is definitely oriented in the oviduct, lying with its larger (anterior) end turned backwards; and at this end the capsule is provided with a valvular opening through which the embryo makes its escape. How this striking adjustment between embryo and capsule has come into existence forms an interesting puzzle of adaptation.

5. Promorphological Features of the Ovum [1]

The animal egg always shows in greater or less degree certain features that foreshadow general characters of the future embryo and adult and for
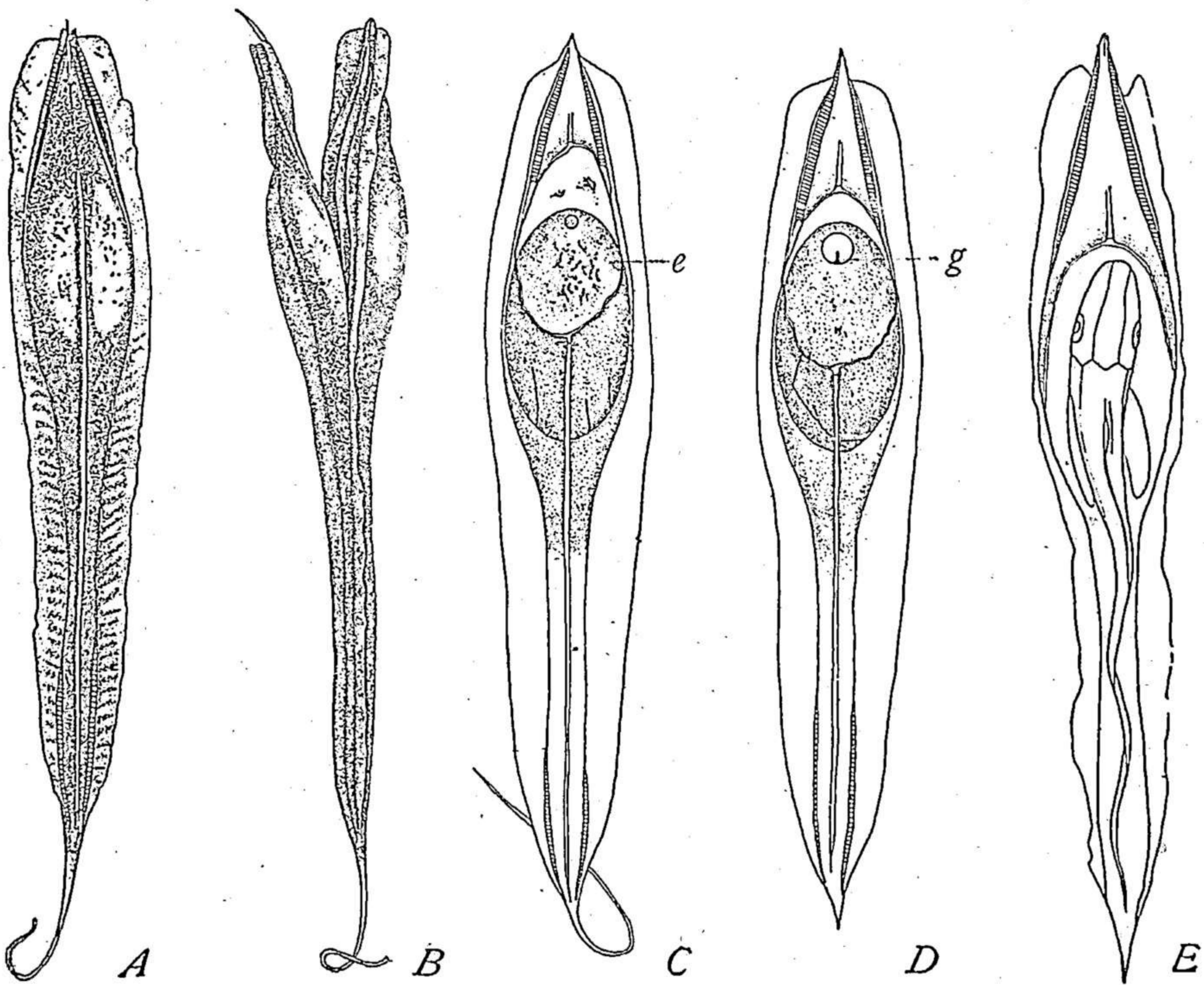

Fig. 115.—Egg-capsule, egg and embryo in the chimæroid fish *Chimæra collici* (DEAN).

A, egg-capsule in dorsal view; *B*, the same in lateral view, with open valve after escape of the young fish; *C, D, E*, successive stages in dorsal view, after removal of portion of capsule-wall to show the egg and embryo; *C, e*, the egg, "late blastula"; *E*, young *Chimæra* nearly ready to hatch.

this reason are spoken of as *promorphological*. The most important of them are as follows:

a. Polarity, probably of universal occurrence in the ova of animals, though not always clearly evident to the eye before the egg begins its development. Its fundamental nature is unknown; but it is made evident

[1] A further account of this subject is given at p. 1014.

in many ways. One of its most constant manifestations is the formation of the polar bodies or polocytes at the so-called upper pole, and the correlated fact that before these bodies have been formed the egg-nucleus or germinal vesicle often lies excentrically towards this pole. In correlation with the axis thus marked out the egg very often shows a polarized or stratified disposition of its cytoplasmic components, such as the granules, yolk, and pigment. In many cases these components show differences of specific gravity; and when they are symmetrically grouped with respect to the egg-axis, as often happens, the egg floats in a constant position with the axis vertical and one or the other pole turned upward. In the telo-
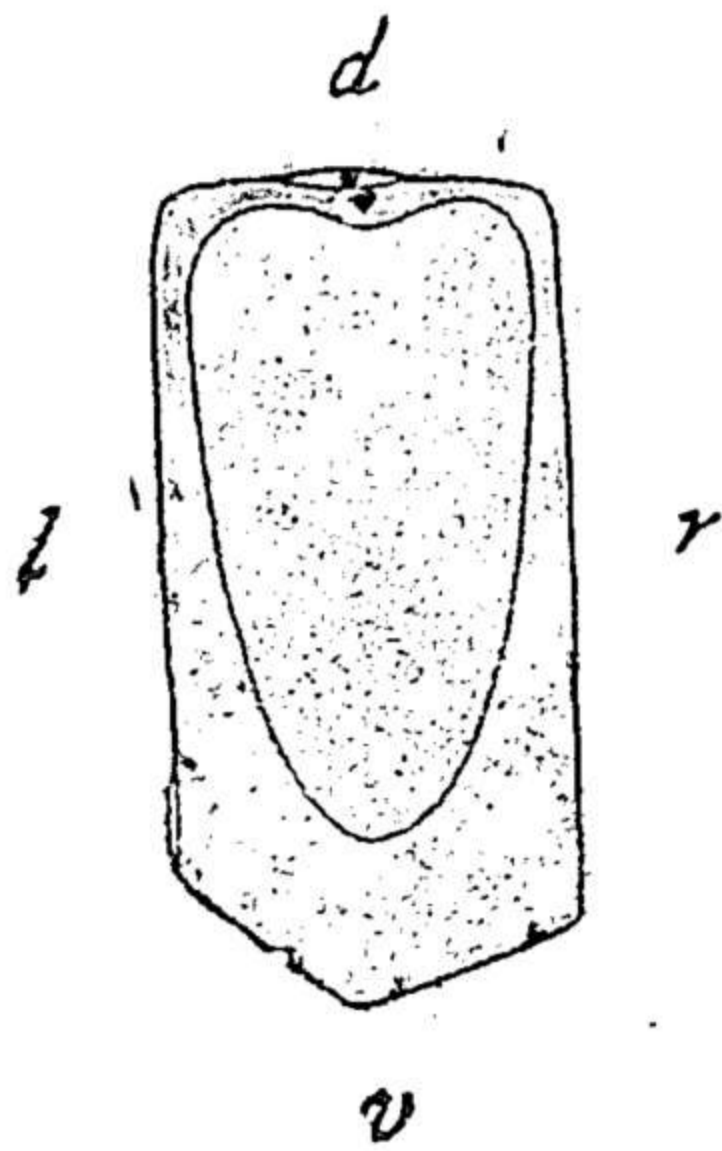

Fig. 116.—Schematic cross-section of egg of cockroach, showing bilateral shape and distribution of yolk (BLOCHMANN).

lethical eggs of many vertebrates, for example, the yolk is relatively heavy, and being more abundant in the vegetative hemisphere causes the egg to float with this hemisphere turned downwards (elasmobranchs, frogs, reptiles, birds)—hence the terms "lower" and "upper" poles, as used by the early embryologists, and often still employed. In other cases fat-drops are present, commonly in the "lower" hemisphere, and thus cause this hemisphere to be turned upwards and the "upper" hemisphere downwards (commonly in pelagic annelid-eggs, fish-eggs, etc.). In many eggs, however, no perceptible difference of specific gravity exists, the egg floating indifferently in any position. Polarity is often shown also by the form of the egg and its envelopes, and by the position of the micropyle or micropyles (when such are present) which are often situated at or near one of the poles, or sometimes symmetrically grouped around it.

The polarity of the egg shows a definite relation to the formation of the future body, the outer germ-layer or ectoblast being formed in a general way from the so-called upper hemisphere, at the pole of which the polar bodies are formed, while the inner germ-layer or entoblast is formed in the lower hemisphere (p. 1014).

b. Bilaterality. In the eggs of some bilateral animals the egg is bilaterally symmetrical in form, and sometimes also in the grouping of its cytoplasmic components, thus foreshadowing the form of the future embryo. Remarkable examples of this are offered by the eggs of insects and of cephalopods (Figs. 116, 484) in which all the future axes of the body are often clearly distinguishable in the egg before it has been fertilized and even before it has been laid (insects). It was suggested by Van Beneden that the eggs of all bilateral animals may also be bilateral; but there is little evidence to support this. Both polarity and bilaterality were assumed by Driesch

and Boveri to be referable to the properties of minute particles of which the oöplasm were assumed to consist (p. 110); but this is quite hypothetical.

c. Sexual Dimorphism. From the genetic evidence on birds and Lepidoptera we are led to infer the existence in these groups of a sexual dimorphism of the eggs in respect to their nuclear constitution analogous to that known to exist in the sperms (p. 748). Such a dimorphism has, in fact, been demonstrated in certain of the Lepidoptera by Seiler, who shows in several species that maturation causes the production of two kinds of eggs, one of which receives one chromosome more than
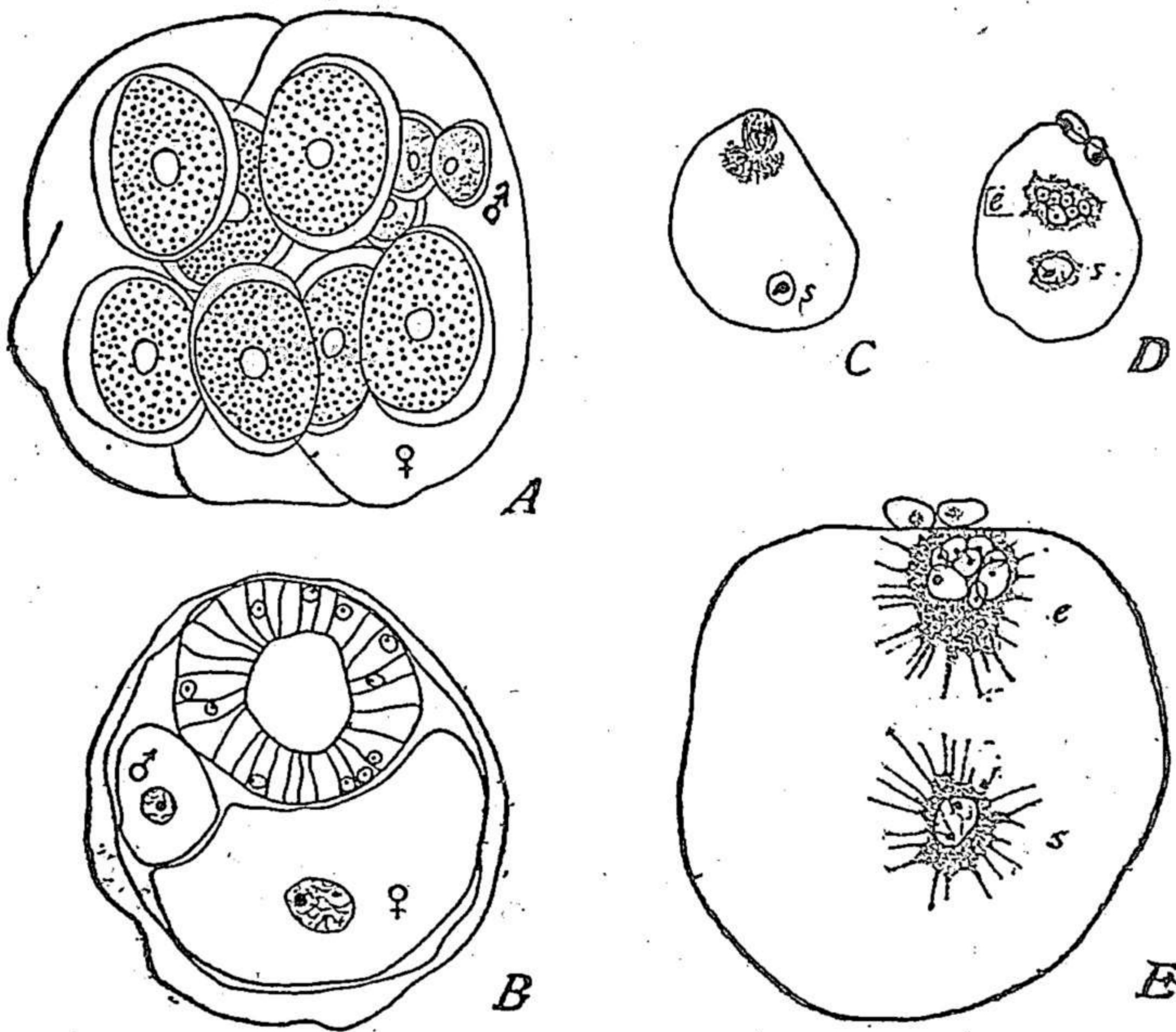

Fig. 117.—Sexual dimegaly of the eggs in *Dinophilus apatris*; (*A*, from KORSCHELT; *B–E* from NACHTSHEIM.)

A, egg-capsule, containing large (female-producing) and small (male-producing) eggs; *B*, cross-section of female individual, showing the two kinds of eggs in the ovary, *C*, *D*, small male-producing eggs, two stages of fertilization; *E*, similar stage of the female-producing egg.

e, egg nucleus; *s* (sperm-nucleus).

the other, and gives rise to males (p. 784). Externally these two types of eggs show no visible structural differences, so far as known, and hence can hardly be considered as examples of promorphology in the egg. Not to be confused with these cases is a visible sexual dimorphism or *dimegaly* in certain animals, the eggs being of two sizes, the larger ones producing females, the smaller males; and this is a case of true promorphology, since it foreshadows a corresponding size-difference between the adult sexes. This condition is known with certainty in only a few cases (rotifers, phylloxerans, *Dinophilus* (Fig. 117; see also p. 806).

B. THE ANIMAL SPERM

Introductory

The sperms of different species of animals exhibit remarkable differences of size, form and structure, nearly related species often differing characteristically in this respect. Many of these variations seem to be of little or no physiological significance; and beneath the structural diversity of the sperms exists a fundamental common plan of organization.

Most commonly the animal sperm is a motile, flagellate cell, though non-flagellate forms occur in several groups of invertebrates. In its more typical form the flagellate sperm is a greatly elongated cell which commonly shows two principal parts known as the *head* and the *flagellum* or *tail*, between which is often seen a third region called the *middle-piece* or *connecting-piece*. In most cases the sperm swims actively by the whip-like lashings of the flagellum, usually in a more or less spiral course and with the head directed forwards. In some animals the tail bears a longitudinal fin-like membrane, and in the urodele amphibia the sperm, here relatively very large, moves very slowly by the undulations of this structure. The middle-piece is extremely variable, being sometimes hardly distinguishable from the flagellum (of which it then obviously forms the anterior part), as in mammals; in other cases it is apparently wanting (insects), while in still others it appears sharply distinct from the flagellum, both in structure and in mode of origin (salamanders, echinoderms, fishes, etc.). It is now evident that the name middle-piece or connecting-piece has been applied to a number of quite different structures between which no exact homology exists; but if this be clearly understood no harm is done by employing the word as a convenient descriptive term. As will be seen, the middle-piece often forms a considerable part of the flagellum (mammals, birds, reptiles) or even its major part (urodeles, some gasteropods).

Sperms of this general type are found in all the main groups of animals from the sponges and cœlenterates up to man, showing many modifications, of which the most complicated, perhaps, occur among the amphibians, birds and mammals. Atypical forms of flagellate sperms occur in certain Turbellaria (rhabdocœles), Bryozoa, myriapods and some Crustacea, notably the barnacles, copepods, ostracodes, isopods and schizopods and in a few insects. In a few of the rhabdocœles (e. g., *Procerodes*, Fig. 127) two separate flagella are present, attached at an acute angle near one extremity of the elongate head, so as strongly to recall the sperm-cells of lower plants. Biflagellate sperms are, however, of great rarity among animals save as abnormalities. Sperms of the flagellate type are closely

paralleled in both form and structure by the vegetative forms of certain flagellates, in particular by species of *Leptomonas* (*Herpetomonas*) (Fig. 286) and related forms.

Non-flagellate sperms occur only in the nematodes, the chilognathous myriapods, the Crustacea (Cladocera, Decapoda), and a few arachnids (mites). In some of these cases the sperms appear to be non-motile; but as a rule they perform slow movements, either by amœboid changes or by the operation of spine-like processes (decapods). Some of these sperms are of strange forms and complicated structure (Figs. 128, 129), but the study of their development shows (as Koltzoff has demonstrated) that they are constructed upon the same fundamental plan as the flagellate forms. It is almost certain, therefore, that non-flagellate sperms have arisen secondarily from those of flagellate type, a conclusion borne out by the fact that the latter alone are found in the lowest Metazoa (sponges, cœlenterates), while flagellated microgametes are common in the Protista and in lower metaphytes.

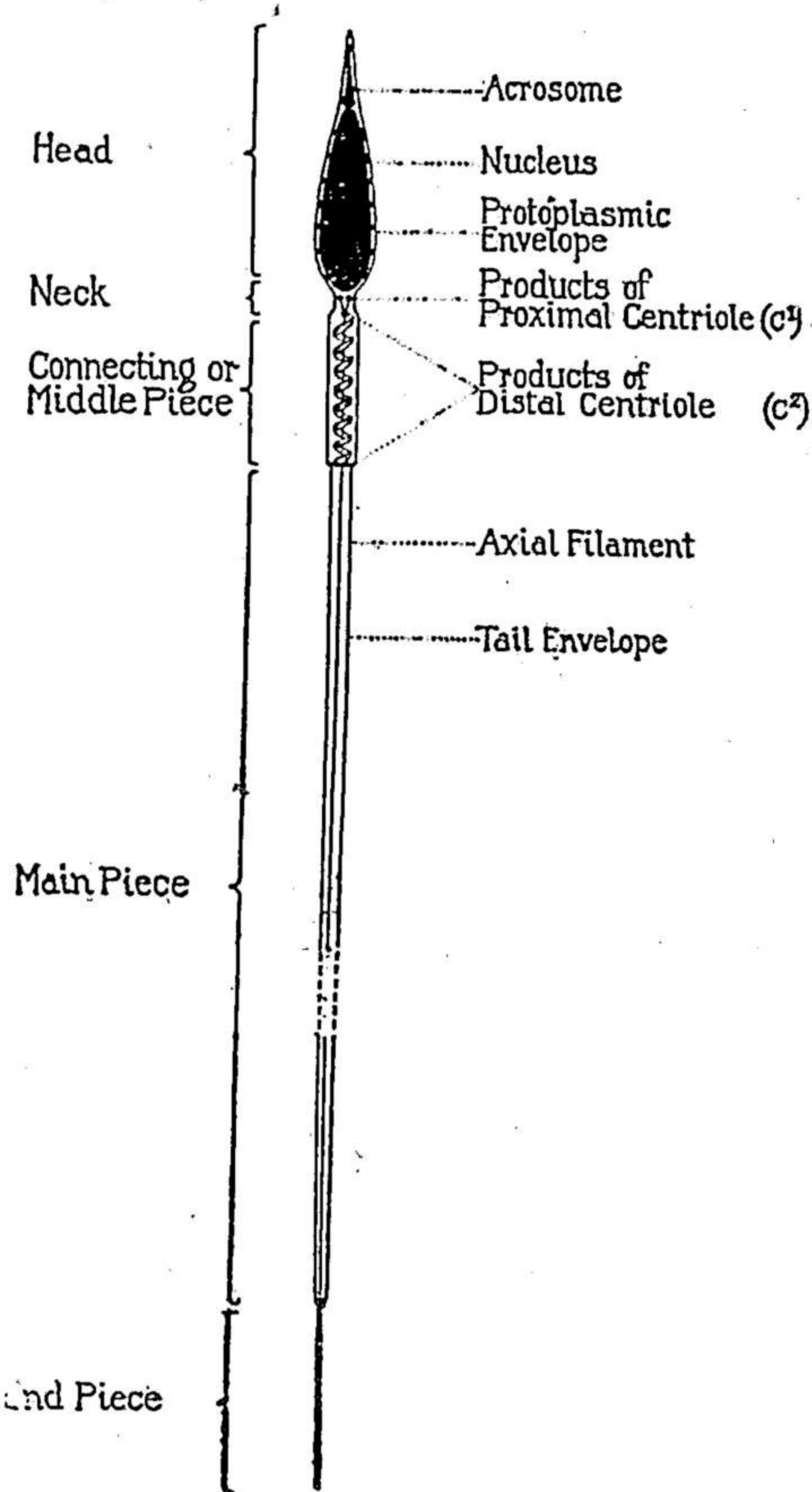### 1. Structure of the Flagellate Sperm

General Outline

In considering the structure of the mature sperm we encounter many difficulties of terminology; for it displays so great a diversity of form and structure in different species and groups that its morphology can only be understood through a study of its development. An account of the formation of the sperm in detail will be given later (p. 356); but our account of the mature sperm will be facilitated by mention of the following main facts. The sperms arise by differentiation of cells known as *spermatids* (Figs. 166–171, etc.), which have a well-developed cytoplasmic cell-body containing a nucleus, one or two centrioles, mitochondrial formations, and Golgi-bodies. The centrioles at first lie close together near the periphery of the cell, with one nearer the nucleus, the other nearer the periphery (Fig. 167); the former is then designated as the inner or *proximal*, the other as the *distal*. All these structures take part in the formation of the sperm, but a considerable amount of "residual protoplasm" is ultimately cast off. The centrioles take an important part in the formation of the flagellum, the distal one playing the part of a blepharoplast from which the axial filament of the tail grows forth.

The conventional grouping of the sperm-structures into head, middle-piece and tail, as shown at the left, below, is based on merely superficial characters. A more careful study, which takes into account the development of the sperm, shows that in many cases each of these parts typically consists of two regions, as in the middle column.

A. Head.   { 1. Acrosome or Apical Body. }   A. Head
                      { 2. Nucleus.   }
                                                             B. Neck
B. Middle-   { 3. Neck.
   piece   { 4. Middle-piece or Con-
                      {   necting-piece.   }

                      { 5. Main-piece
C. Tail or   {   (*pars principalis*).   C. Tail or
   Flagellum.   { 6. End-piece.   }   Flagellum.

Some writers (*e. g.*, Waldeyer, Retzius) prefer to group these regions somewhat differently, as in the right column. In the following account we shall adhere on the whole to the old-fashioned grouping shown at the left (Fig. 118) reckoning, however, the neck as a separate region (as at the right) whenever it is convenient to do so. All the regions posterior to the head are recognized here in a *merely topographical sense*, for no satisfactory basis for a consistent morphological classification has yet been found.

Head

Neck

Connecting or
Middle Piece

Main Piece

End Piece

----Acrosome
---- Nucleus
Protoplasmic Envelope
Products of Proximal Centriole (c¹)
Products of Distal Centriole (c²)
----Axial Filament
----Tail Envelope

Fig. 118.—Diagram of animal sperm, based on the conditions found in mammals. A long section of the flagellum, indicated by dotted lines, is omitted. In some cases the mitochondrial sheath extends far beyond the middle-piece.

a. The Head, considered as a whole, displays a great diversity of form in different species and groups. It may be spheroidal (common among invertebrates, teleosts), conical (*Cyprina, Flustra*), or lance-shaped (salamanders), rod-shaped or filiform (insects), spirally twisted (passerine birds), flattened or spoon-shaped (man, guinea-pig, and many other mammals), hood-shaped (opossum), hook-shaped (mouse, rat, etc.), as may be seen from the accompanying figures. So great is the diversity in this respect that it is hardly an exaggeration to say that most species of animals might be identified from the sperm alone. The functional significance of these various forms is practically unknown.

The main bulk of the head is constituted by:

(1) The *Nucleus,* which occupies all but the anterior tip of the head. It often seems to consist of a solid and homogeneous mass of basichromatin that stains with great intensity in all nuclear dyes, but in some cases shows a more deeply staining cortical layer and a lighter central region. In a few forms the nucleus is represented by a group of separate chromosomes, visible even in the living object, so that they may readily be counted (some nematodes, Fig. 357). In a few cases, as shown by Retzius and Koltzoff, the nucleus is traversed by a fine cytoplasmic axial rod or filament that extends from the base of the flagellum through the nucleus to its anterior extremity. Examples of this are offered by the annelid *Nereis* (Fig. 119, I, J) and the spider *Opilio* (Fig. 119A). These cases have an important bearing on certain theories of fertilization; for, although the origin of the cephalic axial filament is not known, it may possibly be a derivative of the centriole, like that of the middle-piece and flagellum. This filament is not to be confused with a longitudinal extra-nuclear filament (Fig. 119B) described in various forms (*Aurelia, Formica*) and in certain cases known to be an acrosome (p. 282).

The foremost part of the head is typically occupied by:

(2) The *Apical body* or *Acrosome,* often known also as the *perforatorium* (Waldeyer) in allusion to its formerly supposed function as a means of boring into the egg. This structure is usually much smaller than the nucleus; in a few cases, however (passerine birds), it is the larger of the two (Fig. 125). It exhibits a great diversity of form, varying from a small granule or knob to a large conical or spine-like process, which in extreme cases (urodeles) is provided with a prominent barb like that of a fish-hook (Fig. 123). By a further development of this type, the acrosome may be drawn out into a long filiform process that almost simulates an anterior flagellum (some Lepidoptera). By a different type of modification it spreads out to form a large, crescent-shaped body molded upon the anterior part of the nucleus (Fig. 126) of which it was formerly supposed to be a part (a condition commonly seen in mammals). In this case, the most peripheral layer of the acrosome (or by some writers the whole acrosome) is called the " head-cap," which often extends backwards over a considerable part of the nucleus. In such sperms the head is often flattened, the acrosome forming a thin, knife-like edge, which has been supposed to faciliate the entrance of the sperm into the egg (Waldeyer); but its function is still problematical (p. 716). [1] In some animals the acrosome lies more or less on the side of the nucleus, and is sometimes drawn out along almost the

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[1] For this type of acrosome see especially the work of Papanicolau and Stockard ('18) on the guinea-pig.

entire length of the nucleus (in certain Coleoptera, Bowen, '22, '23). In Lepidoptera, Bowen found the acrosome, the basal portion of which lies beside the nucleus, to be drawn out anteriorly far beyond the nucleus to form a very long attenuated filament.[1]

The development of the sperm shows that both nucleus and acrosome are covered by a very thin cytoplasmic covering, perhaps a cell-membrane;
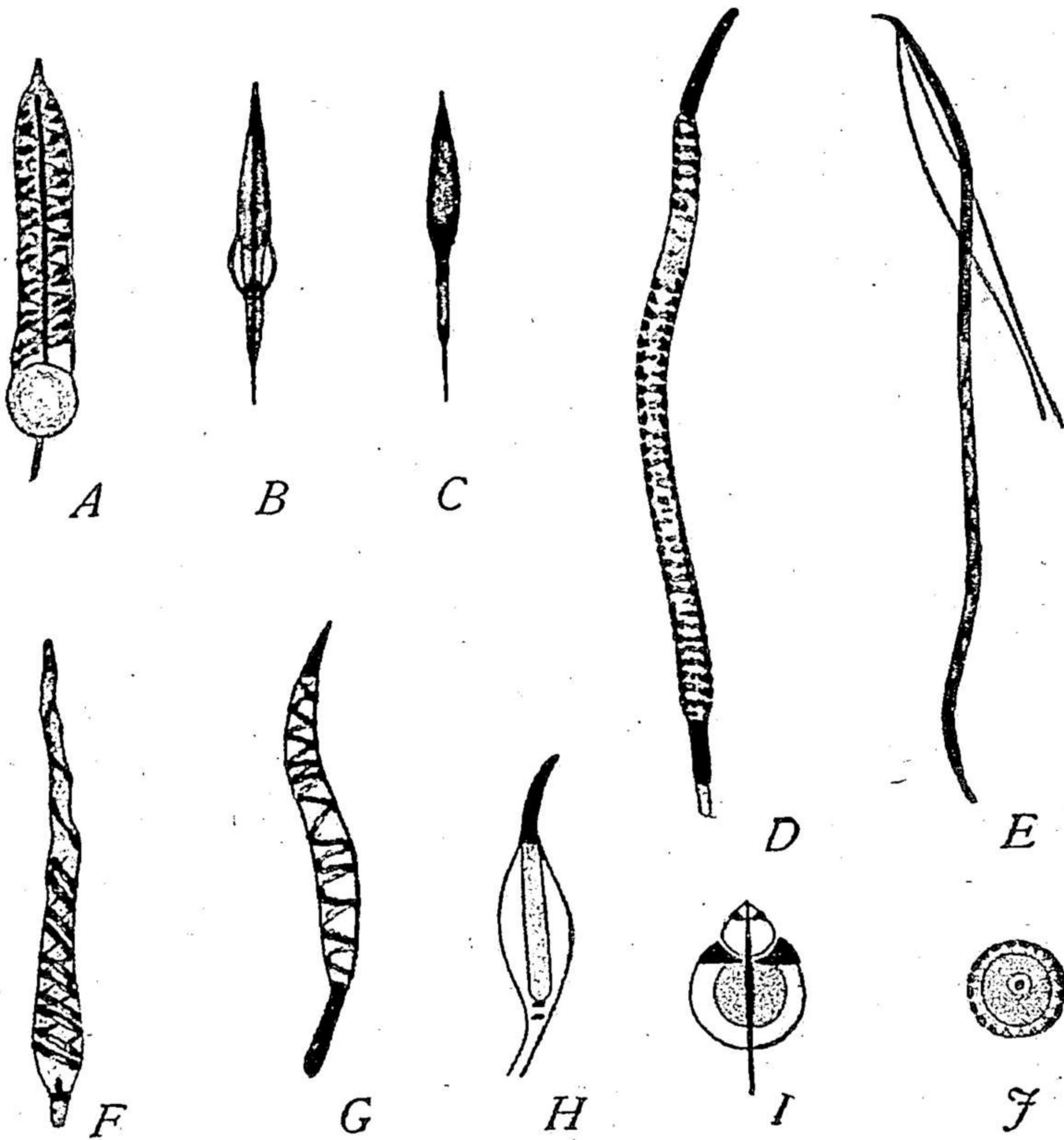

Fig. 119.—Details of sperms of various animals after staining with methyl-green-acid-fuchsin (Biondi mixture) dark portions red (oxyphilic) in the preparations, light portions mostly green (basophilic) (KOLTSOFF).

A, head and middle-piece of the spider *Opilio*, showing axial filament of head and spiral cytoplasmic fibrillæ; B, C, from the medusa *Aurelia*, to show *superficial* longitudinal filament of head; D, *Lumbricus* with spiral cytoplasmic fibrilla; E, biflagellate sperm of the turbellarian *Monotus*, spiral cytoplasmic filament; F, head of sperm in the gasteropod *Paludina*, double cytoplasmic spiral filament; G, from the domestic fowl, *Gallus*, single spiral; H, from the snake *Coluber* (plasmolyzed) showing oxyphily of acrosome and neck-knobs (as in D); I, from the annelid *Nereis* showing *axial* oxyphilic filament of head; J, the same in optical cross-section.

but in the mature sperm it is of such tenuity and so closely applied to the underlying structures as to be invisible under ordinary conditions. Its presence, as shown by Koltzoff ('09), is often readily revealed by plasmolysis, which causes it to separate from the nucleus. After such treatment

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[1] For the even more extraordinary condition of the acrosome in *Lepisma*, see p. 296.

accompanied by suitable staining, the heads of many kinds of sperms have been found to contain cytoplasmic fibrillæ which stain intensely in various plasma-dyes, and have various arrangements which are characteristic of different forms (Koltzoff, Retzius). Most often these fibrillæ lie in the cytoplasmic investment of the nucleus, winding spirally about the latter (Fig. 119); thus recalling the spiral fibrillæ of the tail-envelope. This gives some reason to suspect that these fibrillæ may likewise be of mitochondrial origin, but of this nothing is certainly known. Koltzoff regards them as skeletal or supporting structures.

b. The Neck. This region, often not externally distinguishable, owes its name to the fact that in a few cases (among mammals) it is narrower than the regions between which it lies, and thus forms, as it were, a stalk by which the flagellum is attached to the head (Fig. 126). Internally it is distinguished by the presence of one or more centrioles, or their derivatives, in the form of basal granules, basal rods, "end-knobs," or the like. In some cases these are lost to view in the mature sperm, either by passing into the base of the nucleus or being converted into larger bodies or plate-like structures (urodeles). The relations of the centriolar apparatus to the neck-region are of great interest because of the evidence that *from this region of the sperm, or in its neighborhood arises the sperm-center during the fertilization of the egg* (p. 440). This region often appears not to be surrounded by a mitochondrial sheath such as is so characteristic of the succeeding regions.

In the urodeles (Fig. 123) the neck is a clearly marked, short cylindrical region (the "middle-piece" of earlier writers), which constitutes a basal body that arises by enlargement of the anterior centriole (Meves). The short and often indistinguishable "middle-piece" of insects and of most anurans is also a neck region, in which lie two basal bodies (centrioles). In some forms (*e. g.*, in *Paludina,* Fig. 167), the basal body is pushed up into the basal region of the nucleus, in which case no neck region can be distinguished as such; but it seems probable that the basal body here represents only a part of the proximal centriole (p. 380).

The neck region marks the beginning of the *axial filament*, originally a very delicate fibrilla which in the mature sperm is often considerably thickened and by maceration may be split up into still finer parallel fibrillæ (Jenson, Ballowitz). This, among other reasons, has led to the conclusion that the axial filament is a contractile structure, analogous to a muscle-fiber, by which the whip-like movements of the tail are performed. The axial filament is surrounded by a thin envelope or sheath, the anterior portion of which is composed largely of chondriosome-substance derived from the chondrioma of the sperm-producing cells. This sheath typically

begins just behind the neck region, and extends to the end of the main piece.

c. The Middle-piece or Connecting-piece. By Waldeyer and Meves, the term "middle-piece" or "connecting-piece" is restricted to the region of
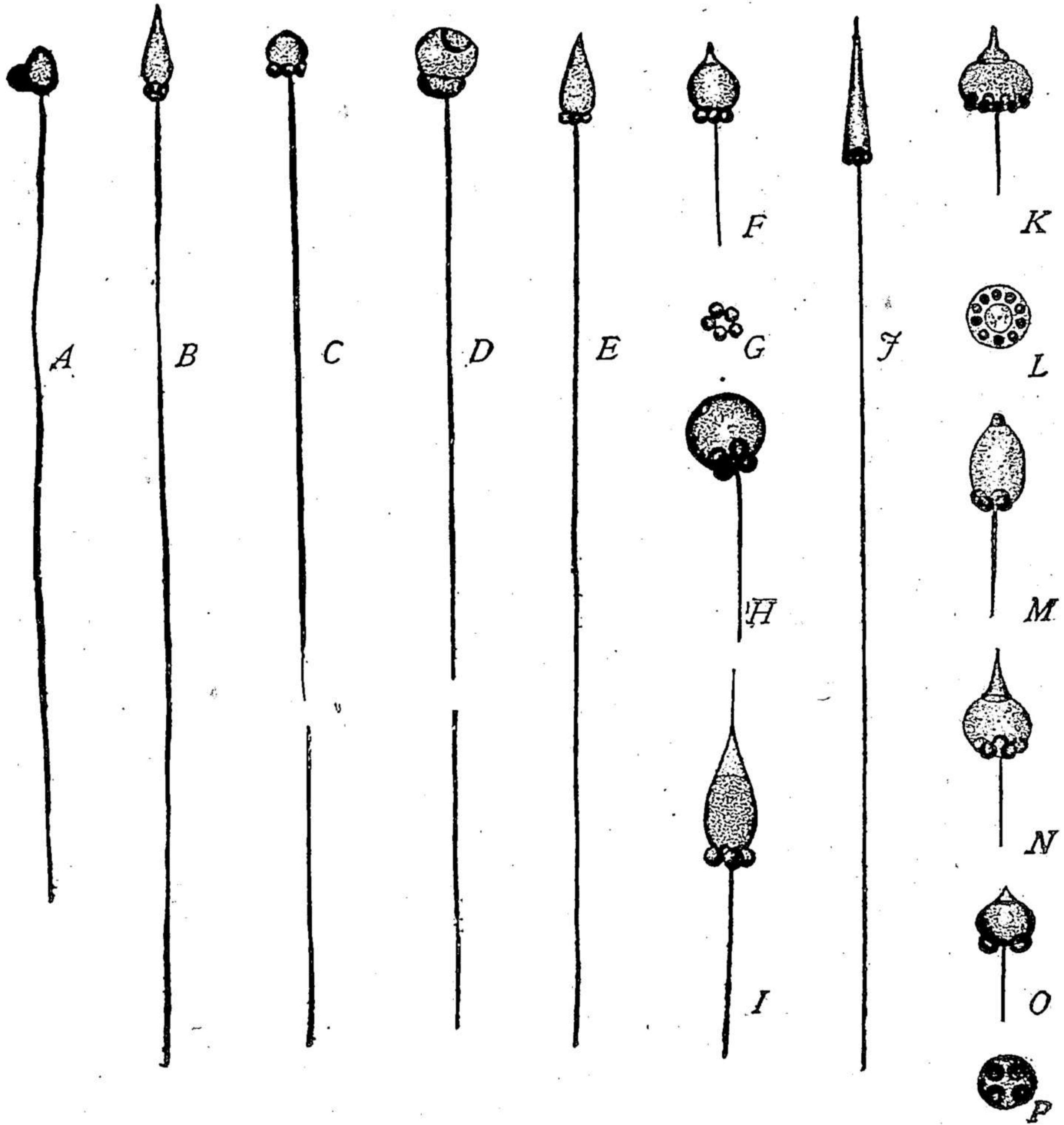

Fig. 120.—Sperms with primitive type of middle-piece (RETZIUS).

A, of the cœlenterate *Tealia*, with lateral middle-piece; *B*, the sea-urchin *Arbacia*; *D*, the starfish *Asterias*; *E*, the sea-urchin *Sphærechinus*; *F*, the nemertine *Carinella*; and *G*, axial view of same; *H*, the annelid *Glycera*; *I*, the mollusk *Chiton*; *J*, the pelecypod *Cyprina*; *K*, the pelecypod *Modiola*; *L*, the same in axial view; *M*, the limpet *Patella*; *N*, the pelecypod *Mytilus*; *O*, the protochordate *Ptychodera*; *P*, the same in axial view.

the distal centriole, since this body commonly divides into two parts which move apart, the proximal one marking the anterior limit of the middle-piece and the distal one the posterior. This definition, though perfectly valid in case of the mammals, and probably also in birds, reptiles, elasmobranchs, and some invertebrates, breaks down in other cases, *e. g.*, in

urodeles, where the posterior half of the distal centriole moves out nearly to the tip of the flagellum.

The middle-piece is traversed through its center by the axial filament; but in some forms, which have a short and rounded middle-piece, it lies eccentrically (*Nereis, Fundulus*), apparently at the side of the axial filament or even of the nucleus (Fig. 121). Its main bulk is constituted by a mitochondrial sheath surrounding the axial filament, and in its turn probably surrounded by a very delicate cytoplasmic covering. The mitochondrial sheath often shows a distinct spiral structure, being differentiated into one or more delicate fibrillæ which wind spirally about the axial filament, often in very fine and closely coiled turns. The backward extension of the mitochondrial sheath seems to vary widely in different species. In many cases it seems to cease at the posterior limit of the middle-piece, a condition characteristic of most of the mammals, in which the thin sheath of the main piece is believed by some observers to have a different origin.[1] Like all other parts of the sperm, this region displays a remarkable diversity; sometimes it is short and rounded (as in the "nebenkernorgan," later referred to), in other cases, cylindrical and more or less elongated, so as often to appear as a part of the flagellum (mammals, some birds). Its posterior limit is often marked by a disc-shaped or ring-shaped body, a derivative of the distal centriole, and its anterior limit by the basal bodies of the neck-region. These limits are often clearly marked externally (as in the sperm of man, Fig. 126), but in other cases can only be clearly seen during the early development.

d. The Flagellum. The middle-piece is followed by the flagellum proper, which consists of two regions. The first and more extensive is:

(1) The *Main-piece* or *pars principalis*, which comprises the greater part of the flagellum. Like the middle-piece, this region is traversed by the axial filament, often considerably thickened, which is surrounded by a very delicate sheath, the origin of which has been much discussed. In the case of the mammalian sperm, some of the most competent observers believe that the mitochondrial formations do not extend into the main-piece,[2] and that the sheath of the axial filament in this region may be a differentiation of the thickened axial filament itself. On the other hand, as above noted, the spiral chondriosome-formations have been described as extending far out into the flagellum in the bats (Ballowitz, Retzius, Fig. 126); and the same is true of the sperm of some birds (Fig. 125), gastropods and scorpions (Fig. 170). In the urodeles, the cytoplasmic sheath (probably in large measure mitochondrial in origin) extends throughout the whole of the main-

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[1] See Meves, '99, Korff, '02, Benda, '97, '06, Jordan, '11, Duesberg, '08, '20, etc.
[2] E. g., in the guinea-pig (Meves, '99) and the rat (Duesberg, '09).

piece to the beginning of the end-piece, at which point lies the distal half
of the centriole (p. 378). We are thus confronted with the paradox that
if the middle-piece be characterized as the region of the distal centriole
(Waldeyer) and the main-piece as that lying beyond the region of the mi-
tochondrial sheath (Meves, Duesberg), the entire flagellum consists of
middle-piece and end-piece.

The axial filament is sometimes supplemented by longitudinal acces-
sory filaments, and the flagellum may be further complicated by the pres-
ence of an undulating membrane that strongly suggests that seen in the
trypanosomes. In the urodeles this membrane is an outgrowth of the axial
filament (McGregor, '99), and is thickened along its free edge to form a
contractile marginal filament that runs along its free edge and by the move-
ments of which those of the membrane seem to be produced, while the
axial filament itself shows no sign of contraction.

The main-piece is succeeded, finally, by:

(2) The *End-piece*, which has no envelope, being formed by the naked
axial filament after it has issued from the envelopes to form the extreme
tip of the flagellum. This seems to be one of the most constant and well-
defined features of the flagellum, and it is an interesting fact that in some
of the flagellate Protozoa the flagellum likewise consists of a protoplasmic
sheath traversed by an axial filament which forms a naked end-piece near
the tip; [1] and here, too, the evidence indicates that the axial filament is the
contractile element.

The foregoing structures will be further considered in connection with
the processes of spermiogenesis, or histological differentiation of the sperm
(p. 368). In fertilization the entire sperm usually enters the egg. Only
the nucleus is yet known with certainty to play an essential part in the
process; but there is strong evidence that the centriole or its products is
likewise of importance. These two bodies accordingly have often been
spoken of as the "essential structures" of the sperm; but more recent re-
searches have shown that the acrosome and the mitochondrial elements
are also carried by the sperm into the egg and may likewise be of functional
importance (p. 434).

Comparative Details. Flagellate sperms conforming more or less nearly
to the type just described are widely distributed throughout the animal
kingdom. The brief sketch here offered is based largely on the extended
work of Ballowitz and of Retzius, whose indefatigable labors have made
known the sperms of a great number of animals from the coelenterates
up to the mammals.[2]

The sperms of sponges, coelenterates and echinoderms are for the most

[1] See Doflein, '09, p. 36.   [2] Retzius, *Biologische Untersuchungen*, 1902–1914.

part of typical flagellate type and usually have relatively short heads and a distinct, short middle-piece. In the cœlenterates first occurs an interesting simple type of sperm in which the middle-piece is formed by a ring of large spheroidal bodies at the base of the nucleus, the axial filament of the
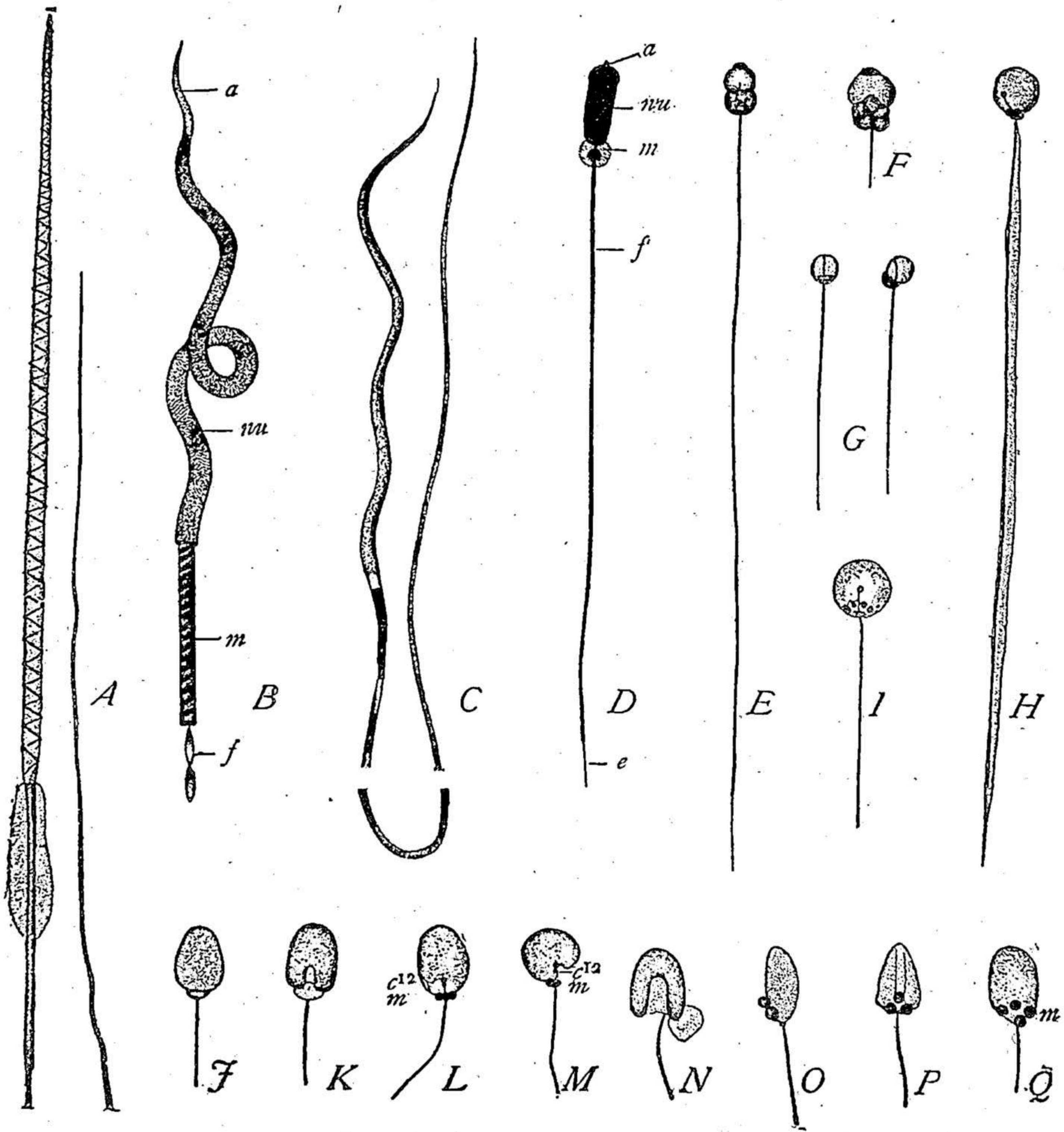

Fig. 121.—Sperms of fishes and protochordates (*A, C, F–I*, from RETZIUS; *B, C, J–N*, from BALLOWITZ; *O–Q* from DUESBERG).

A, sperm of the elasmobranch *Scyllium*, stained to show spiral cytoplasmic head-filament; *B*, *Raja*, spiral envelope of middle-piece; *C, Chimæra; D*, the sturgeon, *Acipenser; E, F, Amphioxus; G*, the tunicate *Oikopleura; H, I*, the pike *Esox; J, K*, the trout *Salmo*, living *L, M*, the same stained to show middle-piece and both centrioles; *N*, the herring *Clupea*, living; *O–Q*, the salt water minnow *Fundulus*, stained to show middle-piece (nebenkern-organ).

flagellum passing through the center of the group up to the base of the nucleus, or even into it (Fig. 120). This structure, called by Retzius the "nebenkern-organ," is found in various Hydromedusæ, Scyphomedusæ, and Anthozoa and also in several of the higher groups. This simple type of sperm resembles an embryonic type of sperm which in many higher

animals only appears as a transitory stage in the formation of a more highly elaborated type (p. 371). With slight modifications it appears also in nemertines, archiannelids (*Polygordius*), some polychætes and gephyreans, Amphineura (*Chiton*), many pelecypods (*Mytilus, Arca*), some of the lower gastropods (*Haliotis, Patella*), and also in the protochordate *Ptychodera*, though in some of these cases the ring of spheroidal bodies is less regular or obscured by close crowding or partial fusion of its spheroidal components. It seems probable, therefore, that many of the forms of sperms having a short and rounded middle-piece may arise from such a ring or group of nebenkern-spheroids; and according to Retzius traces at least of such a structure may be seen in the middle-piece of echinoderms (Fig. 120), *Amphioxus* and even in the teleost fishes (Fig. 121). It is not known in such cases to what extent (if any) the mitochondria may contribute to the tail-formation.

The sperms of platodes and of bryozoa, though flagellated, are for the most part of unusual type (p. 295). Those of annelids and mollusks are
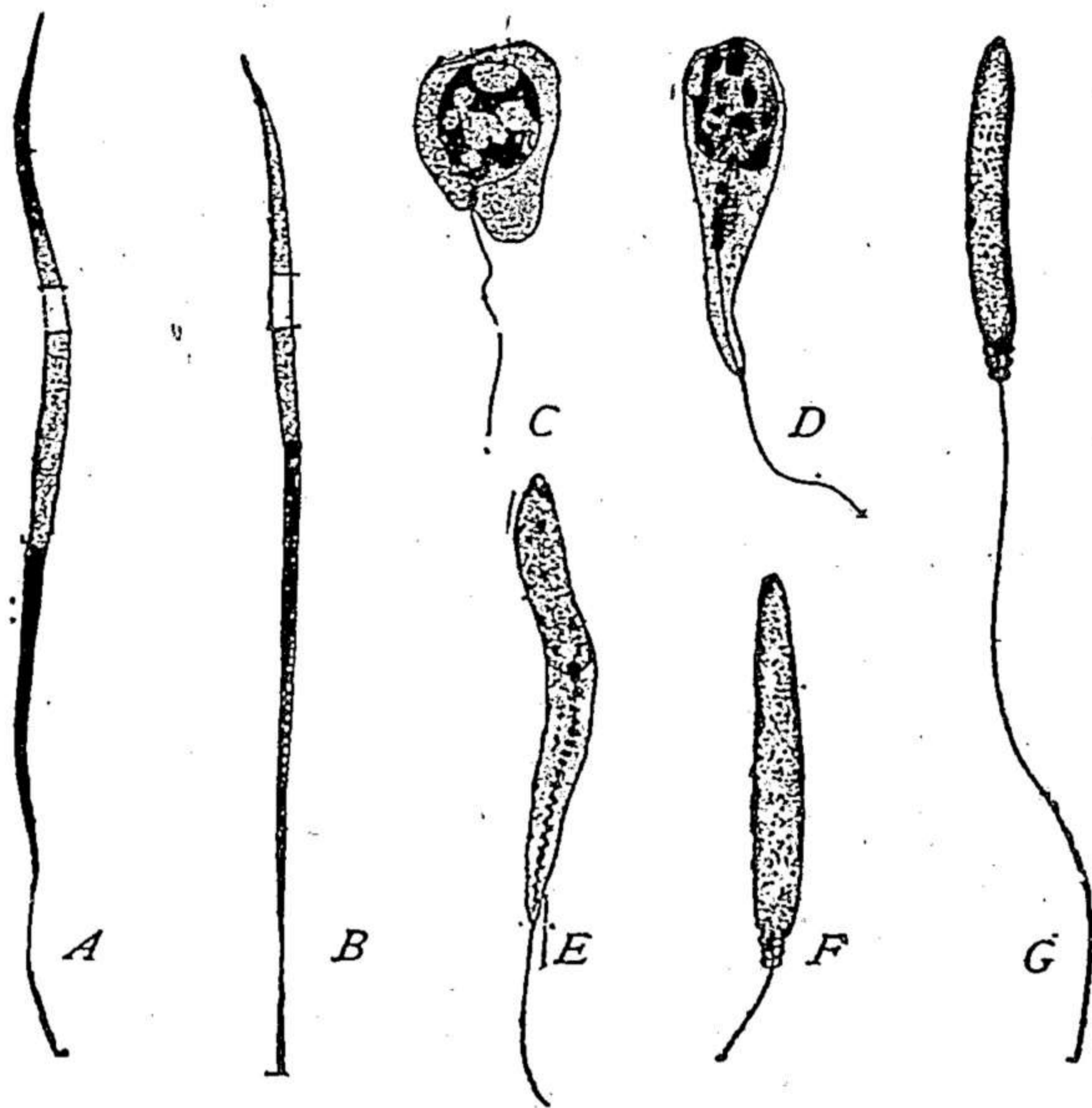

Fig. 122.—Sperms and spermiogenesis in frogs (BROMAN).

A, Mature sperm of *R. fusca* (osmic vapor); *B*, same after staining with gentian violet, centrioles; *C–E*, spermatids of same; *F*, head of sperm, *R. mugiens;* *G*, sperm of *R. esculenta.*

most commonly more typical, often with elongate head and middle-piece. In the mollusks, the sperm is often characterized by a much elongated head, often also by a very long middle-piece which in some cases seems to constitute the greater part of the flagellum (e., g., in the nudibranchs), a condition that seems to be parallel to that seen in the urodele Amphibia. In some of these forms the flagellum conspicuously shows two or more

fibrillæ twisted into a close spiral and in some cases even the head region is also spirally twisted (as in the passerine birds).

The sperms of arthropods display a great diversity; some are of simple flagellate type (insects), others non-flagellate and often of extremely complex structure (decapod Crustacea). In insects generally the sperms commonly possess rod-shaped heads, sometimes even filiform and hardly distinguishable from the flagellum until after suitable staining. The middle-piece is inconspicuous or invisible externally and of limited extent, showing no sharp external line of demarcation with either the head or the flagellum. Flagellate sperms of the ordinary type are the rule among the arachnids (spiders, scorpions), but non-flagellate sperms also occur in this group (mites). In the Crustacea the diversity of the sperm reaches its maximum. Flagelliform sperms occur in ostracodes, barnacles, schizopods, amphipods and isopods, but are always of modified type. In most of the higher Crustacea the sperms are non-flagellated and not actively motile (p. 297).

In the vertebrates the sperms, always of the flagellate type, show a multitude of special modifications. The simplest forms occur in the teleosts where (as also in *Amphioxus*) the head is usually spheroidal with a very short middle-piece, probably comparable to the nebenkern-organ of lower types. In some cases (*Esox, Perca*) the flagellum bears an undulating membrane of simple type. The axial filament terminates anteriorly (sometimes inside the nucleus) in one or two centrioles or basal bodies. The elasmobranch sperm is of more complicated aspect, the head being much elongated and more or less spirally twisted (*Raja*) and showing both an axial filament and spiral peripheral apparatus continuous in front with the acrosome. A fairly short cylindrical middle-piece is present, with a spiral envelope. The flagellum is constituted by two or three filaments connected by a membrane and spirally twisted around each other (Fig. 121).

The sperms of Amphibia are of two main types of which the simpler appears with many variations, in the Anura. In most of these forms the head is much elongated, [1] and a distinct middle-piece often does not appear, though present in some forms (*Hyla, Rana*). In the toads (*Bufo, Alytes,* etc.) the middle-piece is very short and hardly distinguishable externally. In *Alytes* (Fig. 123) two definite basal bodies are present, a proximal and a distal; and the same is true in *Bombinator*, where Bromann ('00) has traced them directly to the spermatid-centrioles (Fig. 124). In *Rana esculenta* no definite middle-piece is externally visible, but at the base

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[1] A remarkable example of this is offered by the anuran *Discoglossus* (Ballowitz, '03) in which the head is quite filiform and constitutes fully half the length of the sperm. In linear dimensions these sperms are among the largest known in animals, measuring upwards of 2 mm. in length; but this is far surpassed by those of the hemipter *Notonecta*, said by Pantel and Sinéty ('06) to measure more than 12 mm. in length.

of the nucleus (neck-region) are two deeply staining basal bodies. In
R. temporaria Bromann finds a distinct middle-piece, containing a distal
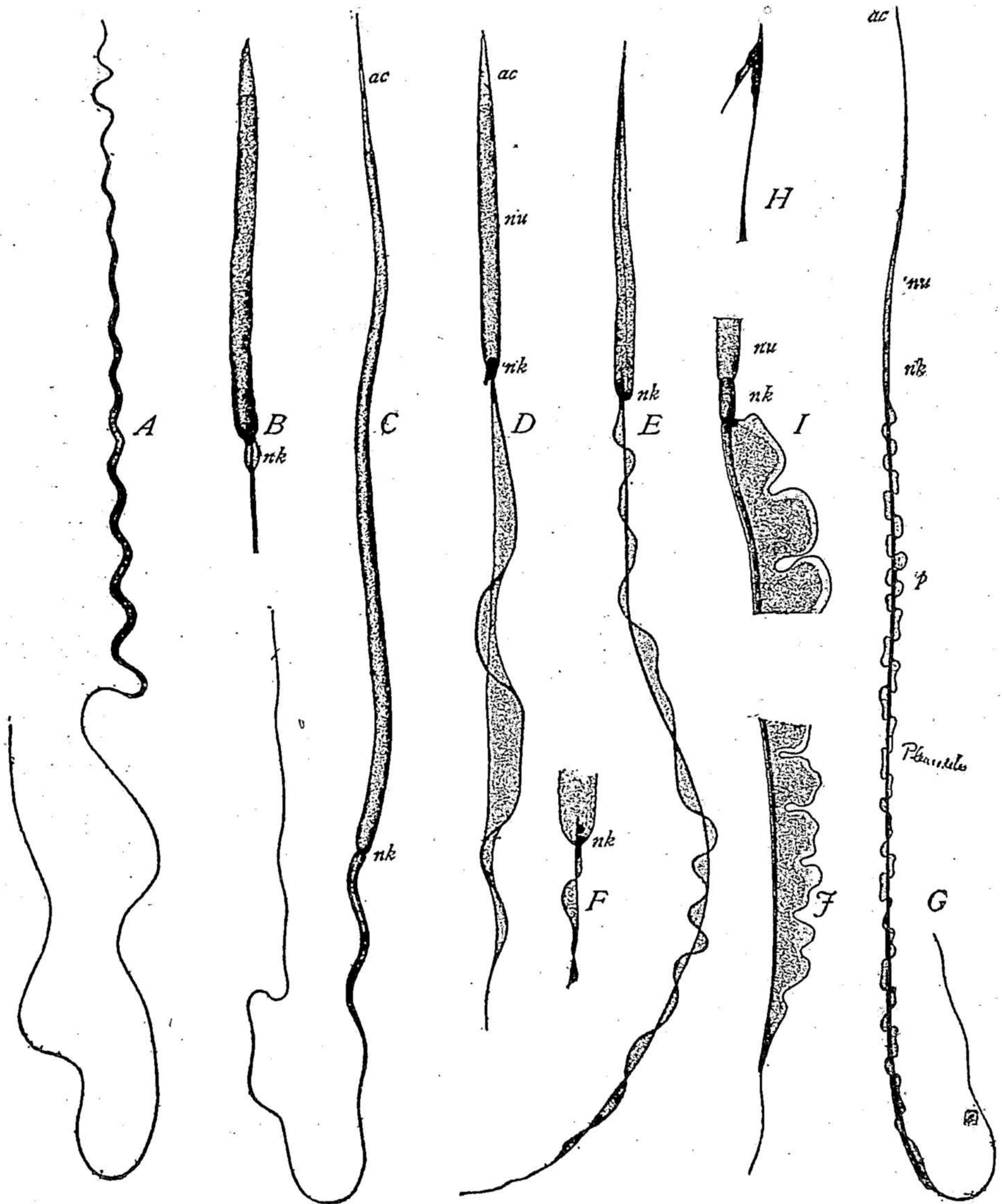and a proximal centriole, and in *R. mugiens* this has a spiral envelope

Fig. 123.—Sperms of Amphibia (RETZIUS).

A, of the toad *Pelobates; B*, head and middle-piece of the tree-toad *Hyla; C*, the frog *Rana escu-
lenta: D*, the toad *Bufo; E*, the obstetrical toad *Alytes; F*, neck-region of same; *G*, the salamander
Pleurodeles; H, acrosome of similar sperm of the salamander *Molge; I*, neck-region of same; *J*,
terminal part of flagellum.

(Fig. 122). Retzius, on the other hand ('06), finds in *R. esculenta* two
basal bodies lying side by side. In the tree-toad, *Hyla arborea*, a short
middle-piece is present, showing at its proximal end a group of about four

granules, and at its distal two distinct pairs of such granules. These no doubt represent the centriole-apparatus, but their genesis is not yet known.

In the toads generally the flagellum contains two longitudinal filaments between which stretches an undulatory fin-membrane which in some cases closely simulates that of the salamanders, as described below (*Alytes*, Fig. 123). A singular modification of this type of sperm occurs in the toad *Bombinator* which in its general aspect recalls a *Trypanosome* flagellate, and also somewhat resembles the sperms of certain Turbellaria (*Macrorhynchus*, Fig. 124).[1] The flagellum is here inserted at one side of the elongated head, near the anterior end, running thence along the head and attached to it along one side, terminating in a free end-piece. The flagellum possesses a thick axial filament (non-motile) and a conspicuous undulating membrane along the free edge of which runs a contractile marginal filament (as in salamanders), which is continued to form the end-piece. These filaments terminate in the centriole-pair, and no middle-piece is present. Since Bromann has traced these granules to the spermatid-centrioles we find here some reason to think that in some other Anura (as in the insects) both centrioles remain in the neck-region of the sperm and that no true middle-piece is present.

The urodeles offer a type of sperm superficially similar to that of some of

Fig. 124.—Sperm of the toad *Bombinator igneus* (BROMAN).

A, mature sperm, showing two persistent centrioles (*c*), the axial rod (*r*), the supporting fiber (*s*), and the undulating membrane and marginal filament (*m*); *B*, younger and *C*, older spermatid.

the Anura (*e. g., Alytes*) owing to the presence of a conspicuous undulating membrane, but apparently very different in its underlying morphology. In these sperms the head is typically of elongate lance-shape and terminates in a long, sharp perforatorium, barbed at the tip. Behind the nucleus lies a distinct, short, so-called "middle-piece," followed by the flagellum with its undulating membrane and terminal end-piece (Fig. 123). The develop-
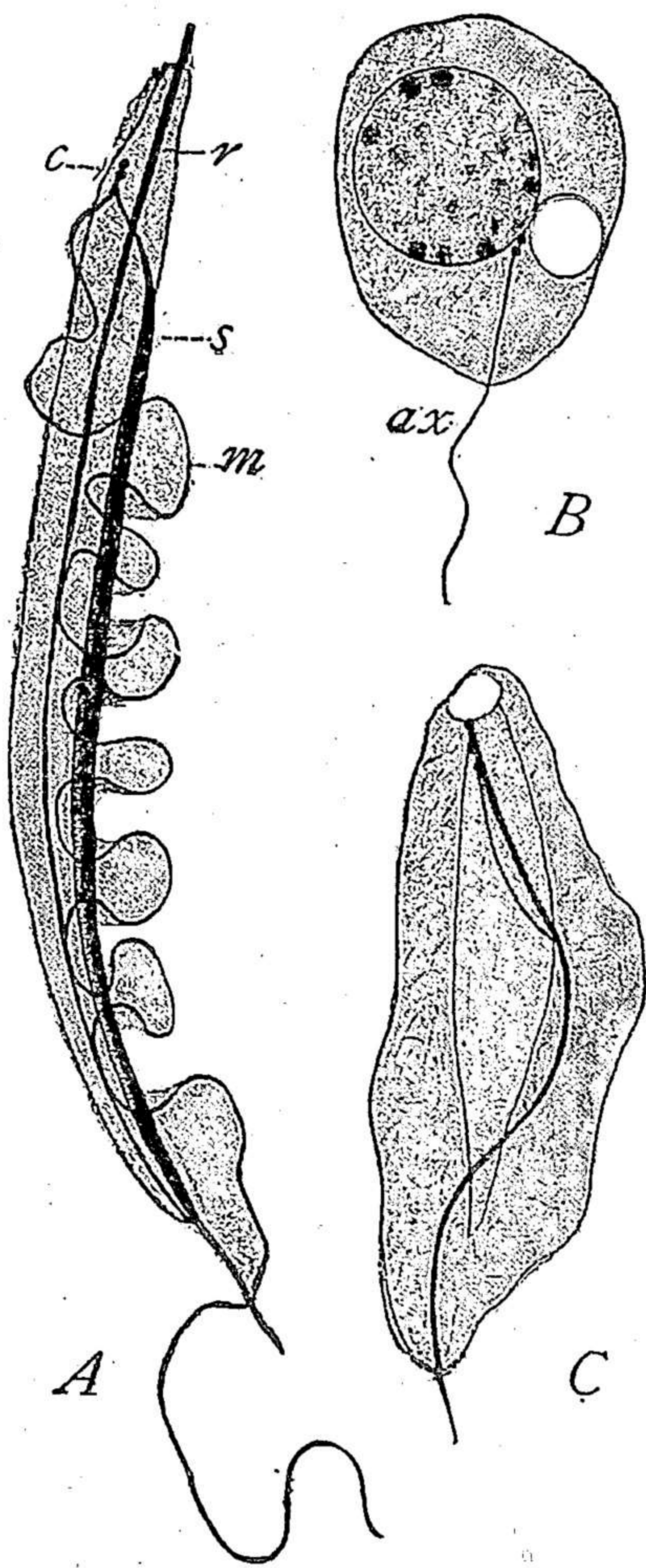
[1] Bromann, '00.

ment of the sperm, as earlier indicated (p. 283), proves that the middle-piece is a large basal body derived from the proximal centriole alone (hence the true "neck" of the sperm), while the true middle-piece or connecting
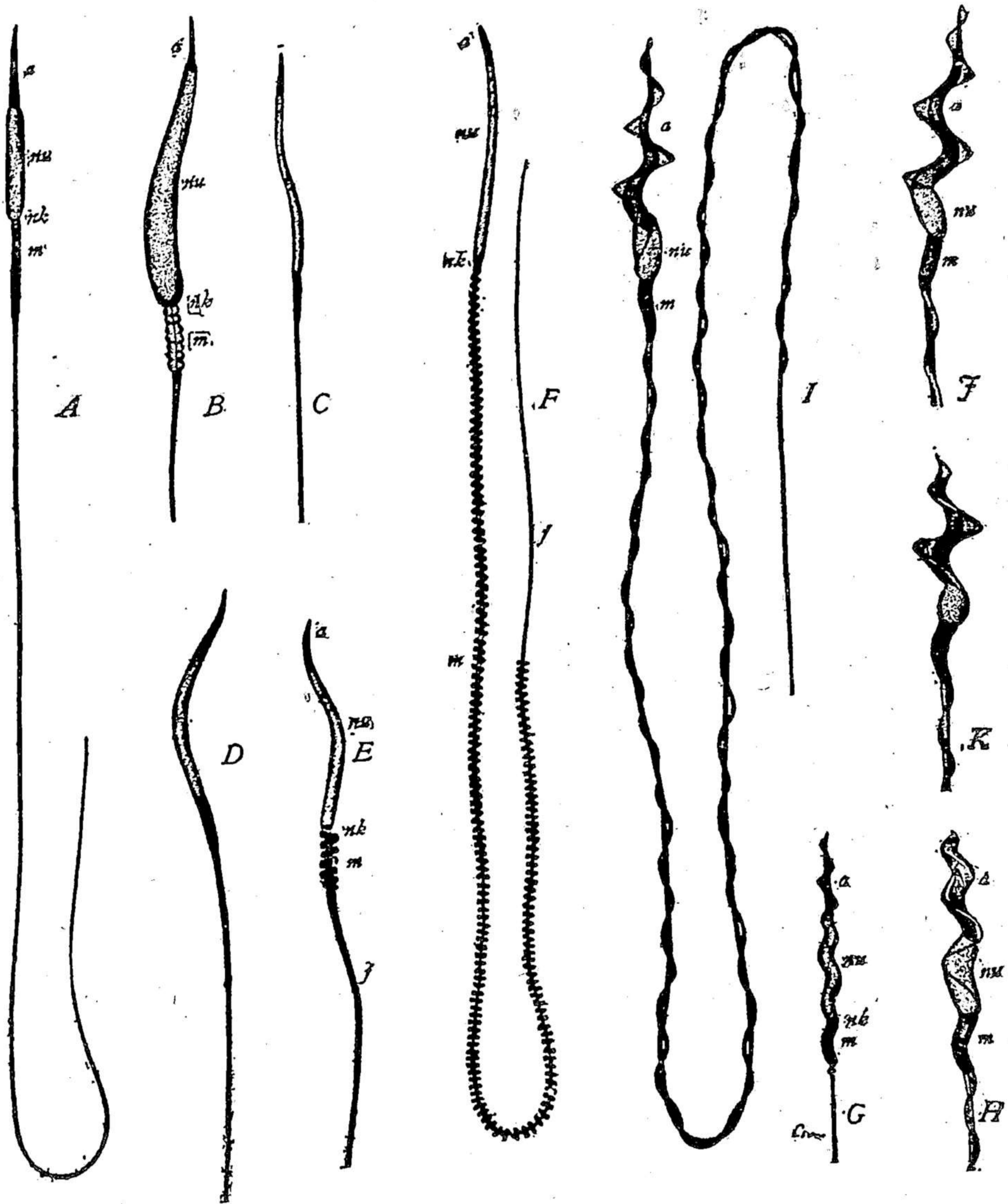

Fig. 125.—Sperms of reptiles and birds (RETZIUS).

a, acrosome; *f*, flagellum; *m*, middle-piece; *nk*, neck; *nu*, nucleus.

A, of *Chameleon*; *B*, of *Testudo*; *D*, *E*, of the fowl *Gallus*; *F*, of the pigeon *Columba* with enormously long middle-piece; *G*, anterior part, *Corvus*; *H*, *Passer*; *I*, nearly complete sperm of *Chloris*; *J*, *Chrysomitris*; *K*, *Fringilla*.

piece (region of the distal centriole) is so enormously elongated as to constitute almost the whole of the flagellum except the short "end-piece" (*cf*. p. 379).

The sperms of Sauropsida are of two general types (Ballowitz), of which one, of simpler aspect, is common to reptiles and most birds (*e. g., Gallus*), and is designated by Ballowitz and Retzius the "sauropsid" type, while the other and more complex type is characteristic of the passerine birds. In the former type generally the sperm is straight and clearly shows three typical regions of the ordinary type. The middle-piece in this type is sometimes greatly elongated so as to constitute a large part of the flagellum (*e. g.*, in the snake *Coluber*, or in the pigeon *Columba*, Fig. 125). It appears always to possess a spirally twisted envelope, no doubt developed from the mitochondria, as in mammals. The second, and more complex type appears in most of the passerine birds and is characterized by the pronounced spiral character of the head-region and the enormous development of the acrosome, which in some cases may be three or four times the length of the nucleus (*Fringilla*, Fig. 125) and by earlier writers (Ballowitz, etc.) was described as belonging to the latter. The nucleus is sometimes cylindrical and more or less spirally twisted, sometimes almost spheroidal. The acrosome shows a pronounced spiral twist, and bears a conspicuous spiral membrane traversed near its free edge by a marginal filament which in some cases may be traced into connection with a spiral filament surrounding the nucleus (*Pica, Turdus*) and is said even to extend into the tail-region. The head is followed by a short cylindrical or conical and deeply staining middle-piece the true nature of which is still uncertain. The tail or flagellum shows one or two conspicuous spiral filaments twisted about the axial filament but ceasing some distance from the tip so as to leave a long end-piece.

The mammals as a group possess fairly typical sperms, with a well-developed cylindrical middle-piece and a simple flagellum and end-piece; the envelopes of the former show a spiral structure as in so many other forms. The middle-piece follows a short neck-region which contains two or more basal bodies (Figs. 126, 173) derived in part from the proximal centriole. The middle-piece is limited proximally by the basal bodies of the neck-region, distally by a disc or ring derived from the distal centriole (*cf.* p. 377).

The diversity of the mammalian sperm is due mainly to modifications of the head-region, and they are to a certain extent characteristic of different groups. It is interesting to find that the sperms of the monotremes (*Echidna*) are quite of the sauropsid type (Fig. 126) which, so far as known, does not occur elsewhere among the mammals. In mammals generally the acrosome is commonly spread out laterally to form a cap-like structure moulded on the anterior part of the head and called by the earlier observers the "head-cap." In the mice, rats and some other Rodentia, the acrosome is drawn out to form a remarkable perforatorium curved like a nook

(Fig. 126). In the marsupials generally the head is greatly flattened and is attached to the middle-piece by a very narrow neck in which two or more distinct basal bodies are distinguishable. In the opossum, *Didelphys* (Fig. 132), it is hood-shaped, surrounding the proxial part of the flagellum;
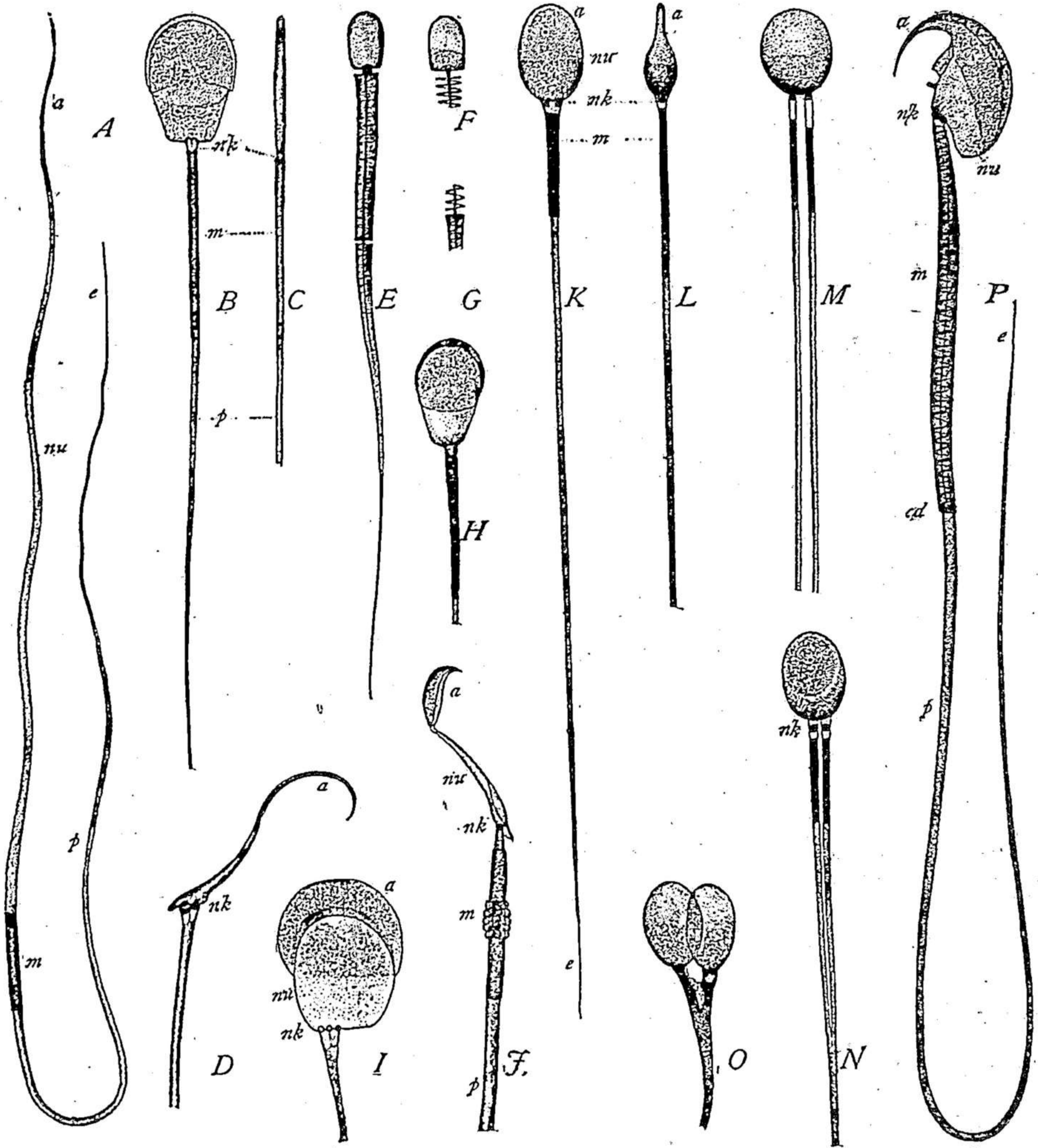

Fig. 126.—Sperms of mammals (RETZIUS).

a, acrosome; *c*, *d*, distal centriole or its products; *c. p.*, proximal centriole or its products; *e*, end-piece of flagellum; *m*, middle-piece or connecting-piece; *nu*, nucleus; *nk*, neck; *p*, main piece of flagellum.

A, sperm of *Echidna*; *B*, *C*, of the deer, *Cervus* (*C* in side-view); *D*, of the squirrel *Sciurus* in side-view; *E*, of the bat *Vesperugo*; *F*, *G*, details of same, after slight maceration; *H*, of the wolf; *I*, head and neck, sperm of guinea-pig; *J*, same in side-view; *K*, *L*, human sperm, *K*, in face view, *L* in side-view; *M*, *N*, *O*, abnormal, partially double sperms; *P*, sperm of the field-mouse, *Mus agrarius*.

and these sperms (p. 305) are typically coupled by their heads, two by two (Fig. 132). In the insectivores (*Talpa, Erinaceus, Bradypus*) appears a type of sperm that is widely distributed among mammals, including man and

other primates [1] characterized by a head of rounded, ovate, or obovate outline, and more or less flattened, in extreme cases becoming spoon-shaped and reduced to a thin plate. The extreme forms of this type occur among rodents (squirrel, guinea-pig), where the front margin is drawn out into a conspicuous hook-like perforatorium (rat, mouse, Fig. 126). In the guinea-pig the head is extremely flat and rounded in front, but sharply flexed at the margin. In many of these forms the basal bodies or centriole-products are seen with great clearness. In all these forms the flagellum is of simple type and shows no fin-membrane. The middle-piece commonly shows a conspicuous spiral mitochondrial envelope, which ordinarily cannot be traced beyond its distal limit.

We cannot here further consider the special modifications of the sperm which have been studied with so much zeal and patience by Ballowitz, Retzius and their fellow spermatologists. A not infrequent anomaly may here be mentioned, namely, the presence of two flagella attached to the head side by side (Fig. 126), and either separate or united posteriorly, branching in front like a Y, and in such cases two heads are commonly present (p. 303).

2. Atypical Flagellate Sperms

The most interesting of the atypical forms of flagellate sperms occur in the lower Turbellaria (Fig. 127) where they show a resemblance in some cases to trypanosome flagellates, in others to the spermatozoids of lower plants. The first type is represented by a number of forms among the rhabdocœles and acœles (*Plagiostoma*, *Aphanostoma*, *Darwinia*) and in certain polyclades (*Leptoplana*). In these cases the distinction between head and tail is often scarcely apparent until after careful study, the sperm being pointed at both ends and bearing two undulating membranes along nearly its whole length. In *Macrorhynchus* the sperm is similar, but possesses only one undulating membrane.

These interesting forms of sperms come into relation with those of the more ordinary type through those seen in some of the Crustacea. In the barnacles (*Lepas*, *Balanus*, Fig. 127) occur very long and apparently headless sperms that were until recently supposed to be devoid of nuclei or "apyrenous." Koltzoff demonstrated, however, that as in *Macrorhynchus* the nucleus is present in the form of a long filament of chromatin from one end of which a still longer cytoplasmic filament runs along the side of the nucleus and attached to it, finally extending beyond it to form the terminal part of the flagellum. These sperms, like those of *Bombinator* (p. 291), give the impression of being sharply flexed at the neck-region, so that the

[1] Retzius has shown that the sperms of the anthropoid apes are closely similar to those of man, and that the resemblance is closer in case of the chimpanzee than in that of the orang.

head is directed backwards; and this is still more striking in certain of the schizopods (*Paradopsis, Protosiriella*) in which the head seems to be turned straight backwards from the point where the flagellum is attached (Fig. 127). Recent studies in certain atypical insect sperms indicate, however, that the true explanation of these cases is a different one. In the tiger beetle *Cicin-*
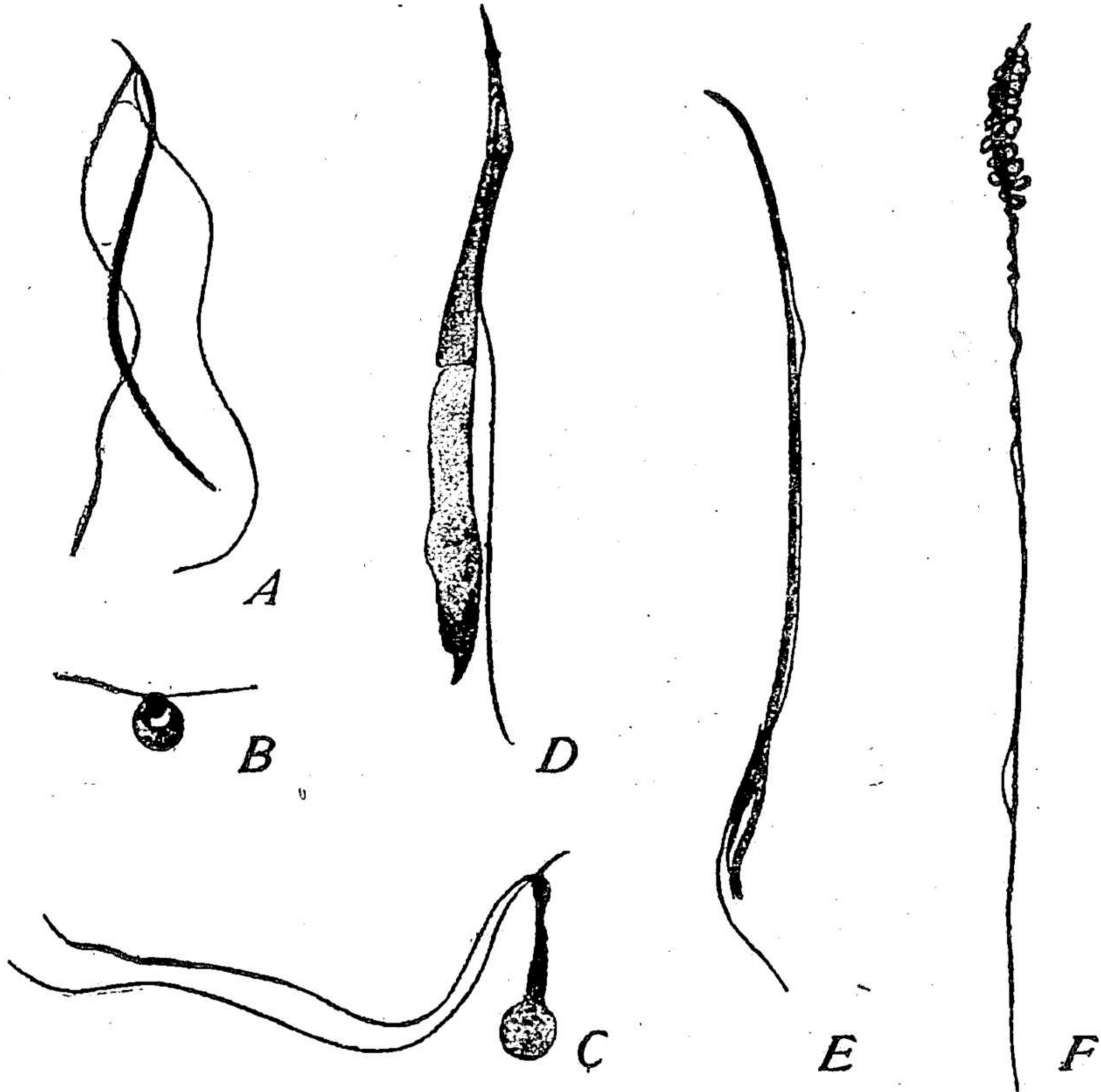

Fig. 127.—Aberrant types of flagellate sperms (KOLTZOFF).

A biflagellate sperm of the platode *Procerodes; B, C,* earlier and later spermatids of same; *D,* sperm of the schizopod *Protosiriella; E,* of the barnacle *Balanus* (slightly macerated); *F,* of the platode *Macrorhynchus* with undulating membrane and marginal filament.

dela the centriole was found by Goldsmith ('19) to pass to the *anterior* end of the nucleus; and this has been confirmed by Bowen ('23), who has traced every step in the backward growth from it of the axial filament alongside the nucleus and into the flagellum. The sperm, therefore, is not flexed on itself, but the flagellum reverses the usual rule by being attached to the *anterior* instead of the posterior end of the nucleus! A similar explanation probably applies to the barnacles and other exceptional cases referred to above. Even more remarkable are the conditions described in *Lepisma.* Here too,[1] as in *Cicindela,* the centriole passes to the anterior tip

[1] Bowen, *op. cit.,* also Charlton, '21

of the nucleus and the axial filament grows backward from it; but the acrosome remains in the neck-region, sending backwards a long filamentary outgrowth alongside the axial filament into the flagellum. Here, accordingly, the usual positions of acrosome and neck-region are reversed (!)

3. Non-flagellate Sperms

Non-flagellate sperms occur in the nematodes and arthropods (certain myriapods, arachnids, and crustaceans). In all cases, probably, these have
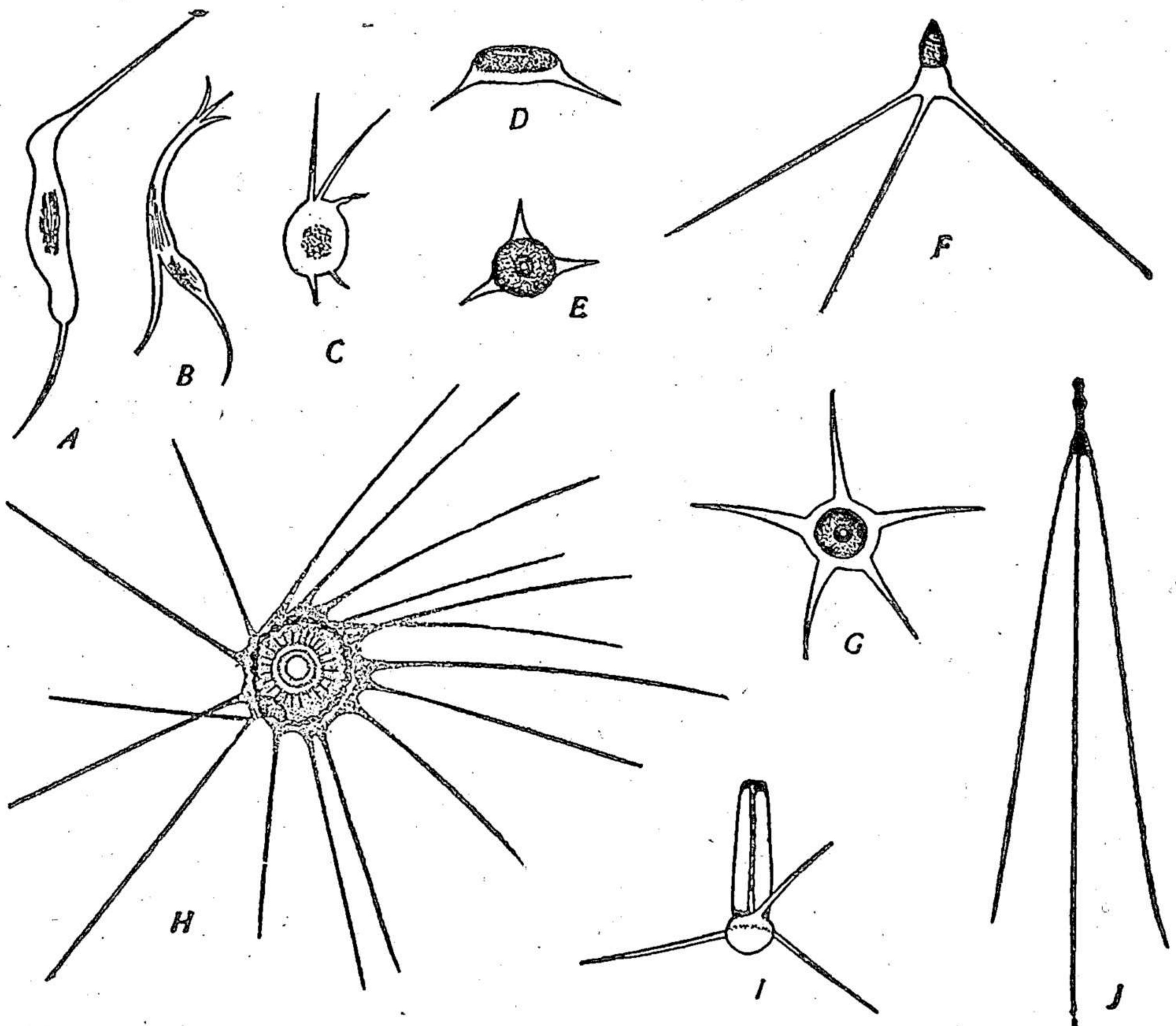

Fig. 128.—Non-flagellate sperms of Crustacea, A, B, C, living amoeboid sperms of *Polyphemus* (ZACHARIAS); D, E, sperms of crab, *Dromia*, F of *Ethusa*; G, of *Maja*; H, of *Inachus* (GROBBEN); I, sperm of lobster, *Homarus* (HERRICK); J, sperm of crab, *porcellana* (GROBBEN).

been derived from flagellate forms, for the lowest Metozoa have flagellate sperms (p. 286). In the Crustacea all the higher types have non-flagellate sperms (decapods) while in many of the lower forms they are of the flagellate type (schizopods, amphipods, isopods, cirripeds, ostracodes). The tracheates generally (including *Peripatus*) have flagellate sperms, but in the myriapods only the chilopods have flagellate sperms, the chilognaths non-flagellate. Again, among the arachnids the typical forms, such as the scor-

pions and spiders, have flagellate sperms, the aberrant mites non-flagellate. An interesting transitional form between the two is seen in some chilognaths of the *Julus* group (Œttinger, '09).

So far as can be judged from the rather scanty data non-flagellate sperms agree with the typical forms in the presence of nucleus, mitochondrial formations, and centrioles or their products. In their simplest form, seen in some of the nematodes, they are spheroidal in shape with the power of slow amœboid movement. In some of the daphnids the sperms are more actively
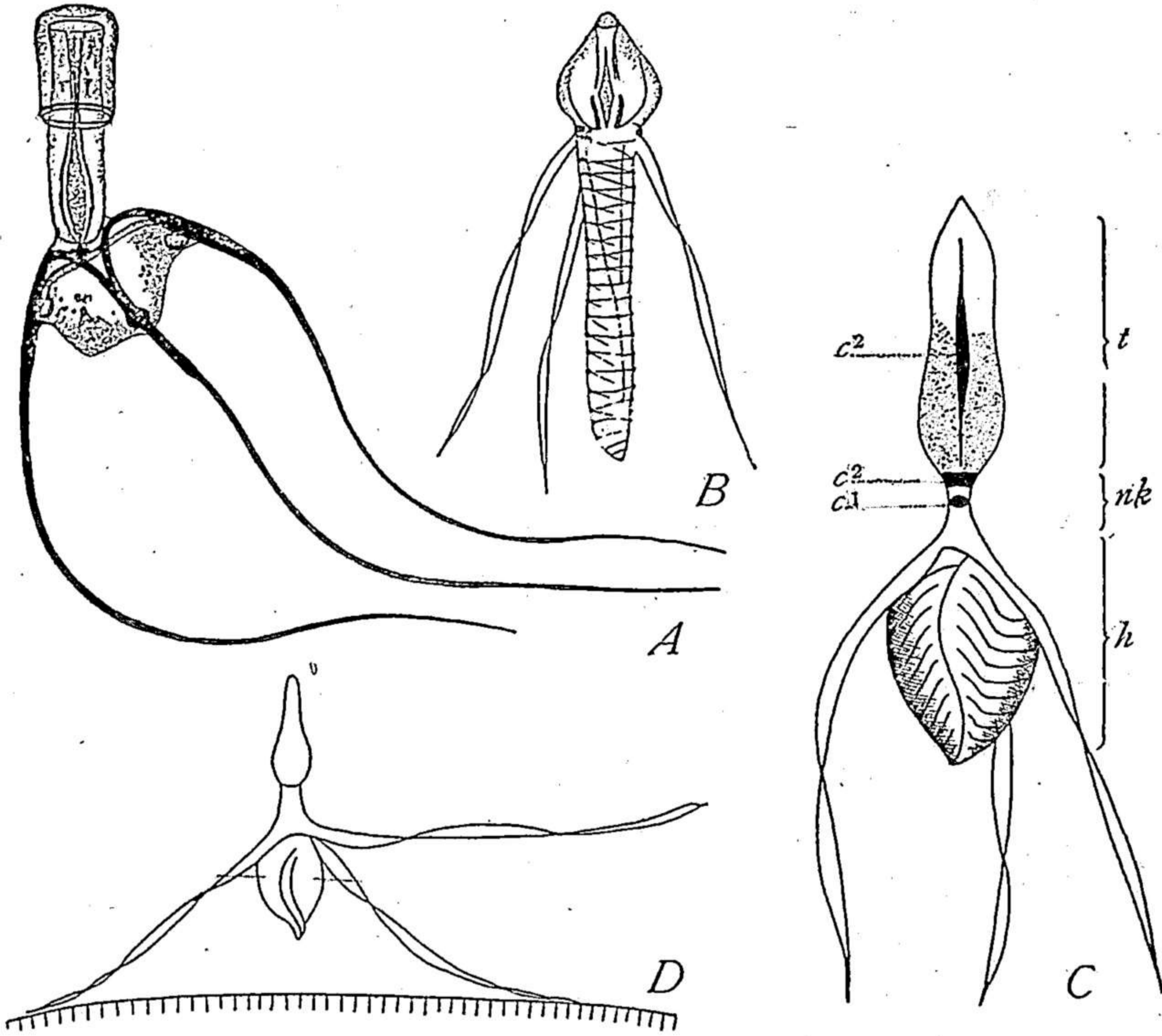

Fig. 129.—Sperms of decapod Crustacea (*A* from RETZIUS, the others from KOLTZOFF).
A, *Nephrops* (*Macrura*); *B*, *Eupagurus* (*Anomura*), showing spiral formation (presumably mitochondrial) in tail-region; *C*, *D*, *Galathea* (*Anomura*), in *D* attached to the egg-periphery; c^1, c^2, products of the proximal and distal centrioles; *h*, head-region; *nk*, neck; *t*, tail-region.

amœboid and may undergo extensive changes of shape (Fig. 128). In these cases there is no approach to the flagelliform type of sperm. In others, such as those of *Ascaris*, the sperm may be regarded as a much shortened and thickened flagelliform cell with a relatively large amount of cytoplasm and a very short and non-vibratile tail. In this case, the sperm contains numerous spheroidal chondriosomes of peculiar type which, as Meves ('11) has proved, are carried into the egg in the process of fertilization (p. 436).

The most remarkable types of non-flagellate sperms occur in the decapod Crustacea, where they have been studied by many cytologists. These

sperms are in general characterized by a rounded, conical or cylindrical body from which radiate a number of rather stiff but movable processes by means of which the sperm may slowly move and by means of which it attaches itself to the egg. The morphology of these sperms, long an unsolved puzzle, has been cleared up by the valuable researches of Koltzoff ('06) who has demonstrated that they are in every detail reducible to the ordinary type and like the latter often show spiral envelopes of mitochondrial origin. These studies have proved that the radiating processes (which contain derivatives of the mitochondria) are developed from the neck region of the sperm; that the rounded portion in which the nucleus lies corresponds to the head; while the conical or cylindrical part, formerly regarded as the head-region, is the homologue of the tail of the flagelliform types. The proximal centriole passes into the neck region, the distal divides into two, of which one remains in the neck while the other elongates to form a kind of axial filament that traverses the posterior extension of the sperm. (Fig. 129) A complete homology thus seems to exist between the several parts of these sperms and those of the flagellate type.

A singular peculiarity of these sperms is the presence in the central-posterior region of a chitinous capsule, containing a rod-like or tube-like "central-body" which was shown by Koltzoff ('06) to be a derivative of the distal centriole. After attachment of the sperm to the egg by its anterior tip the capsule suddenly "explodes," evaginating to the exterior and carrying with it the central body; and both structures may be thrown off entirely. Koltzoff considers that the force of the explosion drives the sperm upon, or even into, the egg.[1]

4. Dimorphism and Polymorphism of the Sperms

In many animals the sperms are of different classes, in some cases visibly distinguishable in size, structure or both, so that we may speak of the sperm as dimorphic, or in some cases even as polymorphic. Dimorphism is of two main types, which may be characterized respectively as *sexual* and *pathological;* the latter again comprising several different forms. The latter result from pathological processes in the testis, through which are produced in addition to the normal or *eupyrene* sperms, certain definite structural aberrations (*oligopyrene* and *apyrene* sperms) and also giant sperms, normally formed, but of twice or four times the normal size.

Besides the preceding types of dimorphism we have to recognize a polymorphism or *polymegaly* characteristic of certain insects in which two or several sizes of sperms are produced by different lobes of the same testis.

a. *Sexual Dimorphism of the Sperm.* This subject, treated more fully

[1] See Koltzoff, '06, Binford, '13, Fasten, '21.

in Chapter X, is here only touched on in passing. In many animals two kinds of sperms are produced, equal in number, which are respectively male-producing and female-producing, and differ in respect to the composition of their nuclei. These classes can rarely be distinguished by the eye in the mature sperm. Two such cases are offered by the nematodes *Ancyracanthus* (Mülsow) and *Filaria* (Meves), in which the nuclei of the sperms consist of separate chromosomes, readily visible in preparations, and in *Ancyracanthus* even in life. In both these cases the two classes are at once recognizable by the number of chromosomes, which is respectively 5 and 6 (Figs. 357, 358). In most cases the two classes do not seem to differ visibly; but exact measurements have shown that in certain cases (*e. g.*, among nematodes, insects, and mammals) the sperms fall into two groups with respect to their heads (or nuclei), which are measurably larger in one group than in the other. Conclusive demonstration of the existence of the two classes is afforded by the history of the sperms during the spermatogenesis (p. 751).

b. *Degenerative Dimorphism. Oligopyrene and Apyrene Sperms.* Dimorphism of this type, much more marked than the foregoing, is displayed in the presence of so-called *oligopyrene* or *apyrene* sperms which differ markedly in structure from the normal or *eupyrene* forms. During the development of these sperms in the testis the oligopyrenes retain only a part of the original chromosomes of the spermatocytes, while in the apyrenes all of the chromosomes degenerate and the mature forms are non-nucleated. It is now nearly certain that neither of these forms of sperms is functional, the eupyrene sperms alone being capable of fertilizing the egg.[1]

The oligopyrene type (Fig. 130) was first described by von Siebold (1837) in *Paludina*, under the name of the "worm-shaped" sperm, in contradistinction to the "hair-shaped" normal (eupyrene) form, and have since been described in various other protobranch gastropods by many observers. In *Paludina* they are of elongate cylindrical form, and consist of three main regions, namely, (1) a short head, containing a small cap-shaped nucleus, (2), a very long cylindrical middle-piece which constitutes the main body of the sperm, (3) at the distal end a tuft of long cilia, each attached at its base to a basal body, or blepharoplast, which is morphologically a centriole. The middle-piece is traversed by a thick axial rod, through which run 12 axial filaments, each terminating distally in one of the blepharoplasts, while in front they end in a cap-like plate surrounded by the cap-like nucleus, and composed of centriolar substance. The genesis of this strange sperm was first determined by Meves ('00, '02), who found

[1] Literature of the subject in Meves ('03), Kuschakewitsch ('13) and Gatenby ('17).

that during one or both spermatocyte-divisions a varying number of the chromosomes are lost, first lagging on the spindle and then becoming separately converted into karyomeres which finally degenerate in the cytoplasm (Fig. 130). Only a few of the chromosomes undergo regular division and distribution to the poles, their number in the first division varying from one to four. In the second division only a single chromosome
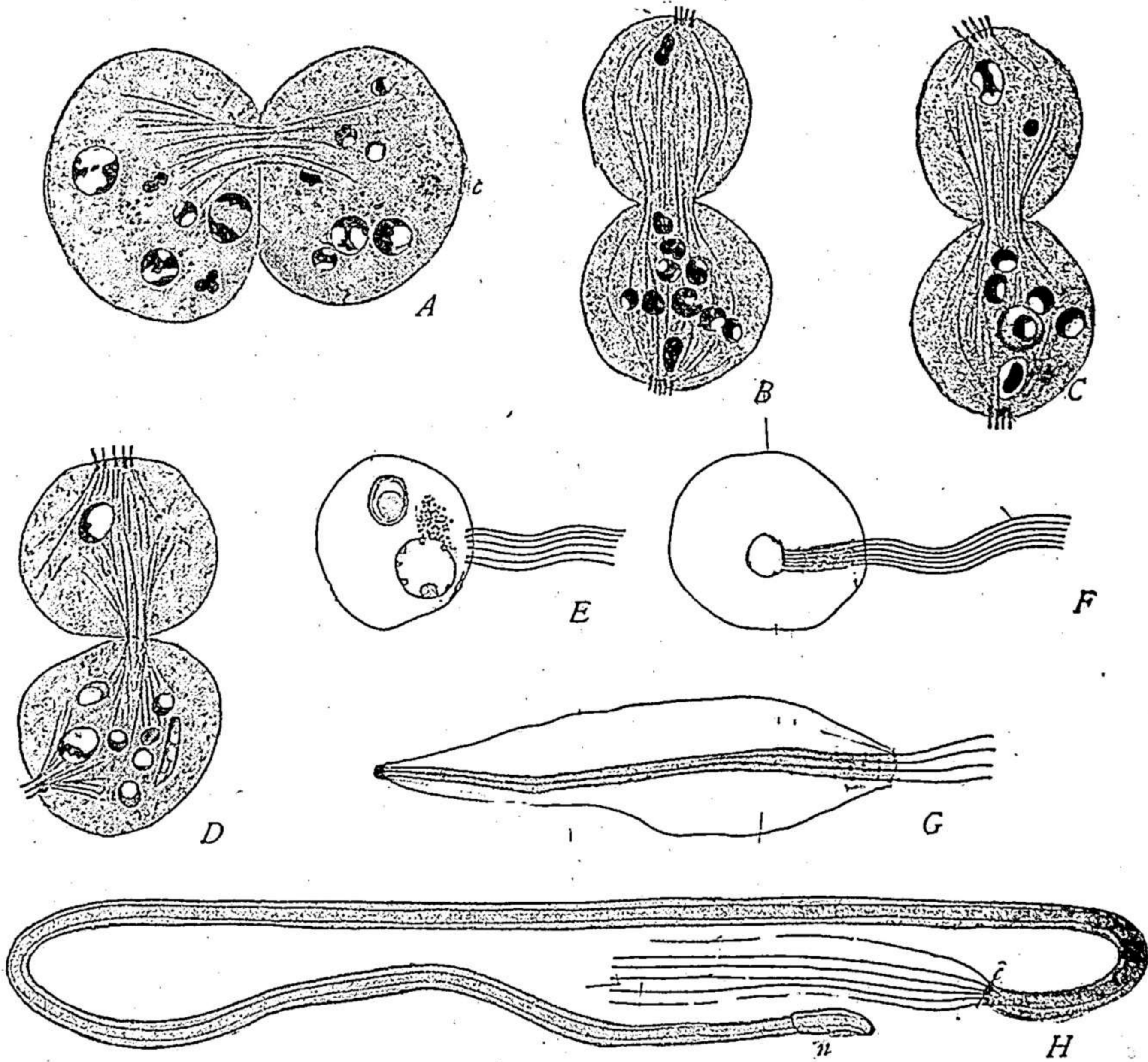

Fig. 130.—Formation of the oligopyrene sperms in *Paludina* (MEVES).

A, telophase of first spermatocyte-division, with scattered chromosomes (karyomerites) and multiple centrioles (c); B, telophase of second division, one chromosome to each pole; C, D, similar stages, slightly later; E, F, early spermatids; G, middle-spermatid; H, fully formed sperm, showing multiple centrioles (c) and flagella; nucleus at n.

undergoes regular division, all the others (now in the form of karyomeres) entering one of the daughter-cells where they degenerate. The nucleus of the sperm is formed from the single normal chromosome in each cell (hence the term *oligopyrene*).

In the meantime each of the original centrioles has undergone a remarkable process of multiplication so that two groups of centrioles are produced, ultimately lying at the poles of the first mitosis. In the interkinesis these centrioles scatter through the cell and lie near its periphery; and here they

often form the foci of fibrillæ which radiate through the cytoplasm—a fact of much interest for its bearing on the mechanism of anastral mitosis. In the second mitosis they are again gathered together in two groups which lie at the spindle-poles (Fig. 130). Each spermatid thus receives one such group, lying close to the periphery; and each of them repeats the history of the centriole (blepharoplast) in the normal spermatogenesis. Each becomes double, an axial filament grows forth from the outer one (which remains at the periphery). The inner one moves inwards until it lies upon the nuclear membrane, while a delicate axial filament stretches between each inner and the corresponding outer centriole. The mature sperm is formed by simple elongation. It is clear, therefore, that so far as the nucleus is concerned the oligopyrene sperm is defective, while as regards the cytoplasmic structures the reverse statement might be made. Cytoplasmically this sperm is somewhat like a bundle of normal sperms fused together.

Apyrene sperms were discovered in *Pygæra,* by Meves ('oo) who found them to arise from abnormally small spermatocytes; and they have since
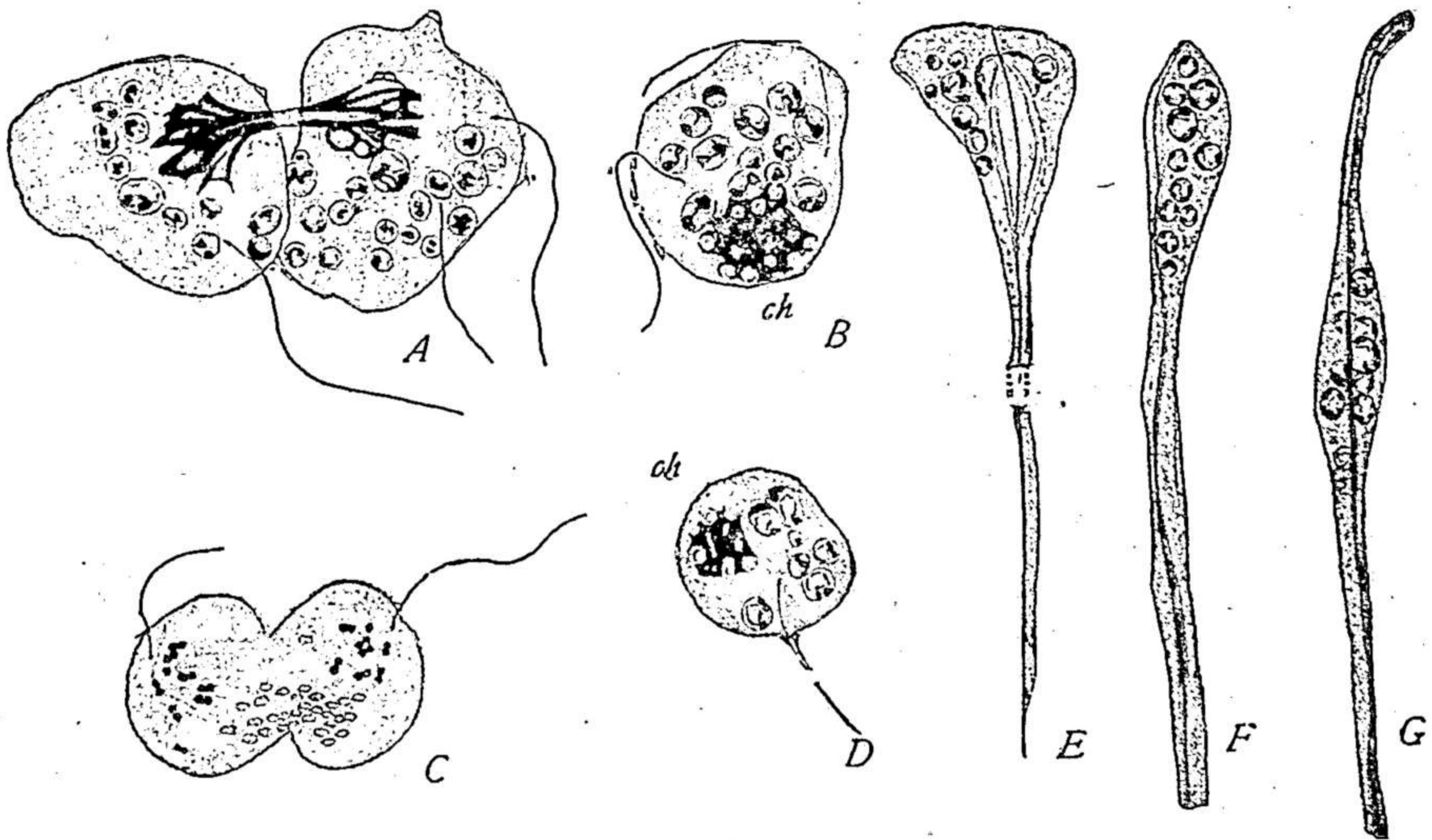

Fig. 131.—Formation of the apyreme sperms in *Lepidoptera* (MEVES).

A, telophase of first spermatocyte-division; scattering of the chromosomes, division of chondriosome-mass, axial filaments present; *B*, second spermatocyte, with karyomeres and chondriosome-mass; *C*, second spermatocyte-anaphase; mitochondria below; *D*, young spermatid, with nebenkern at *ch; E–G*, elongation of the spermatids.

been described in various other Lepidoptera and in certain gasteropods by Kuschakewitsch, Reinke, Gatenby and others. In *Pygæra* these sperms are similar in appearance to the normal, but a study of the spermatogenesis shows that they are *entirely devoid of a nucleus.* The chromosomes divide normally in the first division (Fig. 131) but the karyomeres to which they

give rise fail to unite into a single nucleus. In the second division they give rise separately to chromosomes which are irregularly distributed to the poles and after being again converted into karyomeres wander out along the outgrowing tails, undergo chromatolysis and degenerate, probably being sloughed off finally with the residual protoplasm of the primitive tail-sheath. In *Pieris* Gatenby ('17) found a somewhat different process, the spermatid-nucleus being re-formed in the normal manner but subsequently moving backward into the tail region and finally degenerating; and the same was found also by Bowen ('23) in *Callosamia* and other saturnid moths. The final result is the same as in *Pygœra*. The anterior tip of these sperms is occupied by the blepharoplast or centriole, from which the axial filament extends backwards. The outgrowth of the axial filament, formation of the nebenkern, and general history of the tail are similar to those of the eupyrene sperm. The acrosome, as is more recently shown by Gatenby ('17) follows the chromatin down along the outgrowing tail. This author finds that in the Lepidoptera (species of *Smerinthus*, *Pygœra*, *Spilosoma*) various degrees of nuclear degeneration occur, some of the sperms being completely devoid of a nucleus, others oligopyrene in various degrees; he therefore concludes that apyrene, oligopyrene and eupyrene sperms are all variants of a single type. In *Strombus* (Reinke, '12, '14) the apyrene sperms, of enormous size and peculiar type, are said to arise directly form the primary spermatocytes without dividing or elimination of protoplasm, hence their great size.

The functional significance of these peculiar sperms is a long-standing subject of controversy, now apparently terminated by the conclusion that they are abnormalities or degeneration products, which degenerate without ever reaching the sperm-receptacle.[1]

c. Dimegaly and Polymegaly of the Sperms. The occasional presence of sperms that are nearly or quite normally formed but of unusually large size has been observed in many groups of animals, notably in insects, nemertines, annelids, amphibians, and birds. Such sperms are formed in two wholly different ways, one of which is a pathological process, the other apparently normal. Both these types occur in the insects where their history is now fully known.

(1) *Pathological Dimegaly.* This form of dimegaly, first made known in Hemiptera by Henking ('91) and more fully worked out by Paulmier ('99) results from incomplete division of the spermatocytes, both nucleus and cytosome remaining undivided (or reuniting after division) while division of the centrioles and the outgrowth of the axial filaments proceed (p. 363).

[1] See R. Hertwig ('03), Popoff ('02), Lams ('10), Kuschakewitsch ('12), Reinke ('14), Goldschmidt ('15), Gatenby ('19).

Paulmier showed in *Anasa* that the giant sperms arise from giant spermatids which are either twice or four times the size of the normal. The internal structure of these spermatids shows that they are likewise either double or quadruple in respect to the blepharoplast (centriole) and axial filament, those of double size having two, and those of quadruple size four, of these structures.[1] It is practically certain, therefore, that the double forms are due to a suppression of the second spermatocyte-division, the quadruple ones to suppression of both divisions, in respect to all the sperm-forming elements excepting the centriole and the chondriosome-apparatus. The latter have completed their allotted number of divisions and subsequent differentiations. A remarkable demonstration is here given of the genetic continuity of these structures. A result similar to this in all of its essentials has been reached in case of the insects by several later observers, including Zweiger ('06) and Buchner ('09); also by G. Smith ('12) in the case of hybrid pigeons, where the giant sperms are said to arise directly from the secondary spermatocytes. Whether such sperms may fertilize the egg is unknown.

(2) *Physiological Dimegaly or Polymegaly.* In some insects all the sperms formed in certain follicles of the testis are much larger than those from other follicles, a fact discovered by Montgomery ('98, '10) in *Euschistus*. In this insect the testis consists of six parallel tubular lobes disposed side by side in a nearly flat plate; these may be designated by numbers 1–6. In all alike the spermatogonia and the very young spermatocytes are of the same size; but as the growth-period advances the spermatocytes and their products become constantly much larger in lobes 4 and 6 than in the others while in 5 they are somewhat smaller than in 1, 2 and 3. These lobes give rise to sperms of three correspondingly different sizes, all of the same structural type and normally formed. The observations of Bowen ('22) show that conditions more or less similar are found in nearly twenty additional species and genera of Heteroptera (Pentatomidæ), some species showing only two sizes (dimegaly) of spermatocytes or sperms, others three sizes (polymegaly). In each case the size of these cells is constant for particular lobes.

Montgomery found that during the spermatocyte-divisions the chromosomes of the two sizes of spermatocytes are of nearly or quite the same size, the greater size of the sperm-nuclei in follicles 4 and 6 being due to a subsequent compensatory growth of the spermatid-nucleus. This has been confirmed in the polymegalous forms by Bowen who also found that the cytoplasmic components, including the centrioles, chondriosomes, acroblast

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[1] Analogous double spermatids have been observed in the cycads (Ikeno, '03) and mosses (M. Wilson, '11); and in the latter case both the limosphere (acroblast) and blepharoplast (central body) were likewise found to be double.

and chromatoid body, vary with the size of the cytosome (*Cf*. p. 732). What determines the various sizes is unknown, nor is it known whether all three forms of sperms are functional. Montgomery believed the size-difference to result merely from differences of nutrition in the respective follicles traceable to corresponding differences in the accessory nurse-cells; how the latter differences arise was, however, not determined, nor are we yet better informed.

5. Conjugate Sperms

A remarkable phenomenon is the regular occurrence in certain animals of "twin sperms," or "double sperms," consisting of two sperms closely united by their heads, leaving the tails more or less free (Fig. 132).[1] The meaning of this singular condition is still unknown; but Selenka and Ballowitz found the union to be secondary, the sperms being at first single and
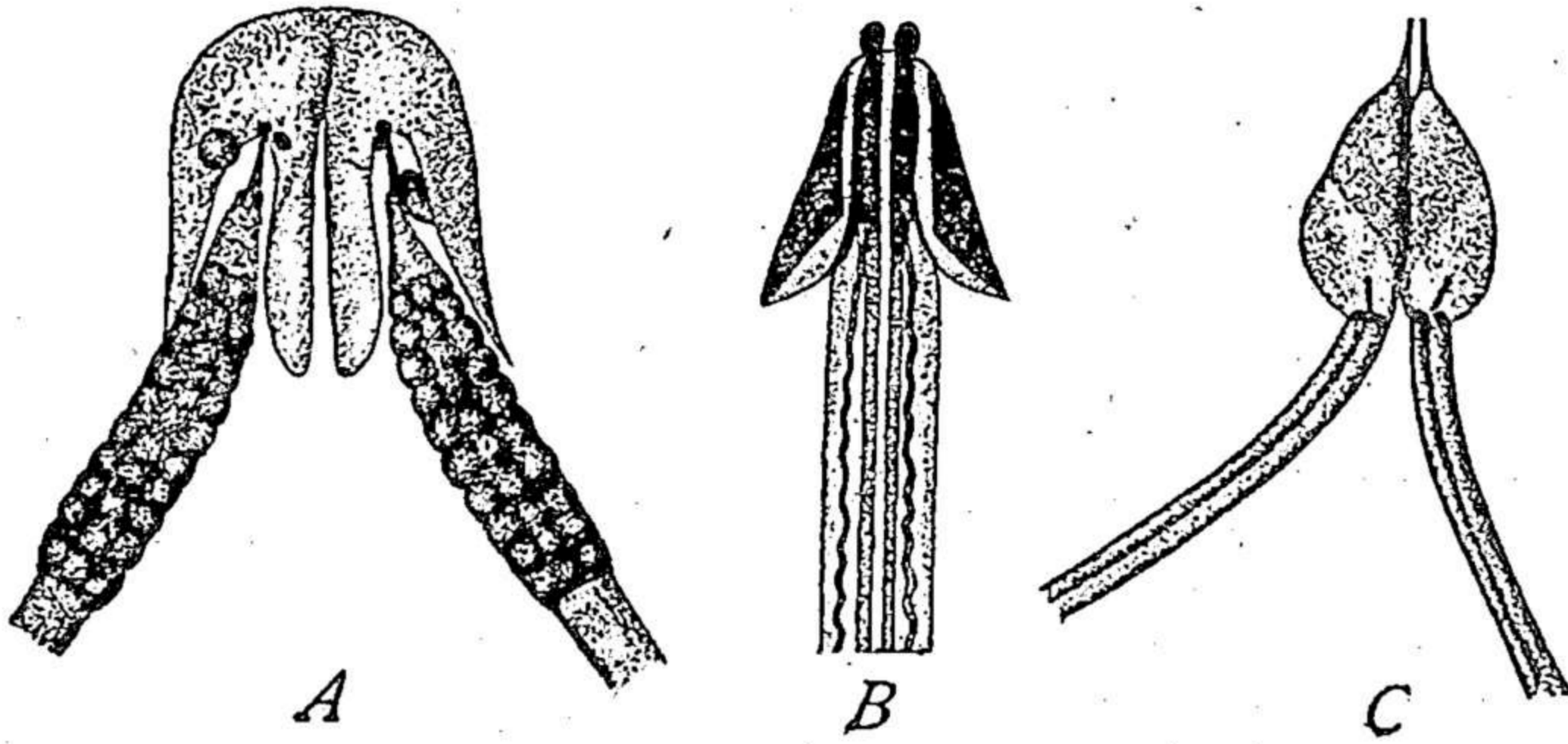

Fig. 132.—Conjugate sperms.

A, in the opossum (RETZIUS); *B* in the beetle *Dytiscus* (BALLOWITZ); *C* in the gasteropod *Turritella* (RETZIUS).

free in the duct of the testis, and only later uniting two by two. In this condition they may actively swim together in the *vas deferens*, but later separate so that single sperms are again found in the freshly discharged sperm and (in *Dytiscus*) in the *receptaculum seminis* of the female. During the period of their association (as Selenka pointed out in *Didelphys*), the two sperms are of different but corresponding shape, being mirror figures of each other, or "right" and "left" handed. This, however, seems to be a result of their mode of attachment and not of a preëxisting morphological difference. These facts still constitute an unsolved puzzle.

II. THE GAMETES OF PLANTS

The maternal and paternal gametes of plants show differences that are broadly parallel to those of animals; but non-motile sperms, so rare among Metazoa, are not uncommon among plants, being found in all the seed-

[1] In the opossum (*Didelphys*) (Selenka, '86), in the beetle (*Dytiscus*) (Ballowitz, '95), and in the gasteropod *Turritella* (Retzius, '06).

plants except the cycads and Ginkgoales, and with rare exceptions (*Mon-oblepharis*) in the fungi and red algæ. The microgametes of plants seem to be almost as diverse in structure as those of animals. The macrogametes, on the other hand, are in certain respects less varied owing to the greater uniformity of the conditions under which development of the zygote takes place. We shall attempt no more than a brief mention of a subject hardly less complicated than in the case of animals, though as yet less completely known. Some additional details concerning the gametes of lower plants will be found in Chap. VII.

1. The Ovum

In the higher plants the ovum rarely attains the dimensions or complexity of structure shown in animal ova, in part because it remains attached to and imbedded in the maternal tissues by which it is nourished and protected (Figs. 211, 214, etc.). As a rule, therefore, the egg is not provided with complex envelopes or heavily laden with reserve food-matters such as the deutoplasm of animal ova. In the second place, the history of the nucleus is not complicated by the phenomena of meiosis, since this process is completed in the sporophyte during spore-formation, long before the ovum is formed. Here, therefore, the egg-nucleus differs in no essential way from the nuclei of the tissue-cells except that it is from the beginning of haploid constitution. An interesting feature of the plant ovum in the archegoniate plants is the frequent (perhaps general) presence of plastids in the form of small colorless leucoplasts which according to the researches of Schimper, Meyer and their successors multiply by division and thus form the source of the plastids of the embryonic cells and ultimately of the tissue-cells of the mature plant. This is a point of much theoretical interest in relation to the view that the plastids are persistent morphological bodies traceable in direct genetic continuity from one generation to another through the germ-cells. In the lower plants (algæ) plastids may occur in the gametes of both sexes; in the higher forms they seem to occur in the egg alone, and in such cases the plastids of the embryonic body appear to be of purely maternal origin. In plants, as in animals, however, it is probable that both gametes contain mitochondria and as already stated (p. 47) it is possible that these may be fundamentally indentical with plastids and give rise to them.[1]

The plant ovum attains its greatest size in the gymnosperms (Figs. 213–215). In the conifers the protoplasm contains many fibrous bodies, the origin of which has been much disputed (Ferguson, '01), Miyaki, '03, Coker, '03, etc.). These bodies are more numerous in the lower half of the

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[1] See Meves, '16, '17.

egg, while near the upper pole the protoplasm is clearer and in some cases contains a vacuole which has been described as marking a kind of receptive spot, since it is at this point that the pollen tube discharges the generative nuclei into the eggs (Ferguson, Murrill, etc.). The egg is likewise very large in cycads, but seems to lack the protein vacuoles and fibrillar formations seen in the conifers. In the angiosperms the egg has at first no definite external boundary, being represented by an egg-nucleus lying in the syncytial protoplasm of the embryo-sac and accompanied by two synergid-nuclei which probably represent the vestige of an archegonium. In later stages the egg, like the synergids, acquires a definite boundary by gathering a clearly defined, spheroidal protoplasmic cytosome about it (Figs. 216–217).

2. The Sperm

The microgametes or sperms of plants have received many names, the motile forms being commonly designated as *antherozoids* or *spermatozoids*. The latter, like the sperms of animals, move by means of flagella or cilia, and a study of their development shows many analogies to animal sperms in other respects. Uniflagellate sperms seem, however, not to occur in plants, at least two flagella being present and in many cases numerous flagella or cilia.

In the lower archegoniates (bryophytes) the sperm is bi-flagellate (Fig. 134) with an elongate and somewhat spiral body near the anterior end of which are attached two long flagella directed backwards.[1] The body is occupied mainly by an elongate nucleus with a delicate cytoplasmic investment, and leaving a small purely cytoplasmic region at the anterior end and a larger one at the posterior. The development of these sperms shows that the flagella grow forth from a basal body or blepharoplast that passes into the anterior cytoplasmic region; also that this region receives a body that is comparable to the acrosome or acroblast of the
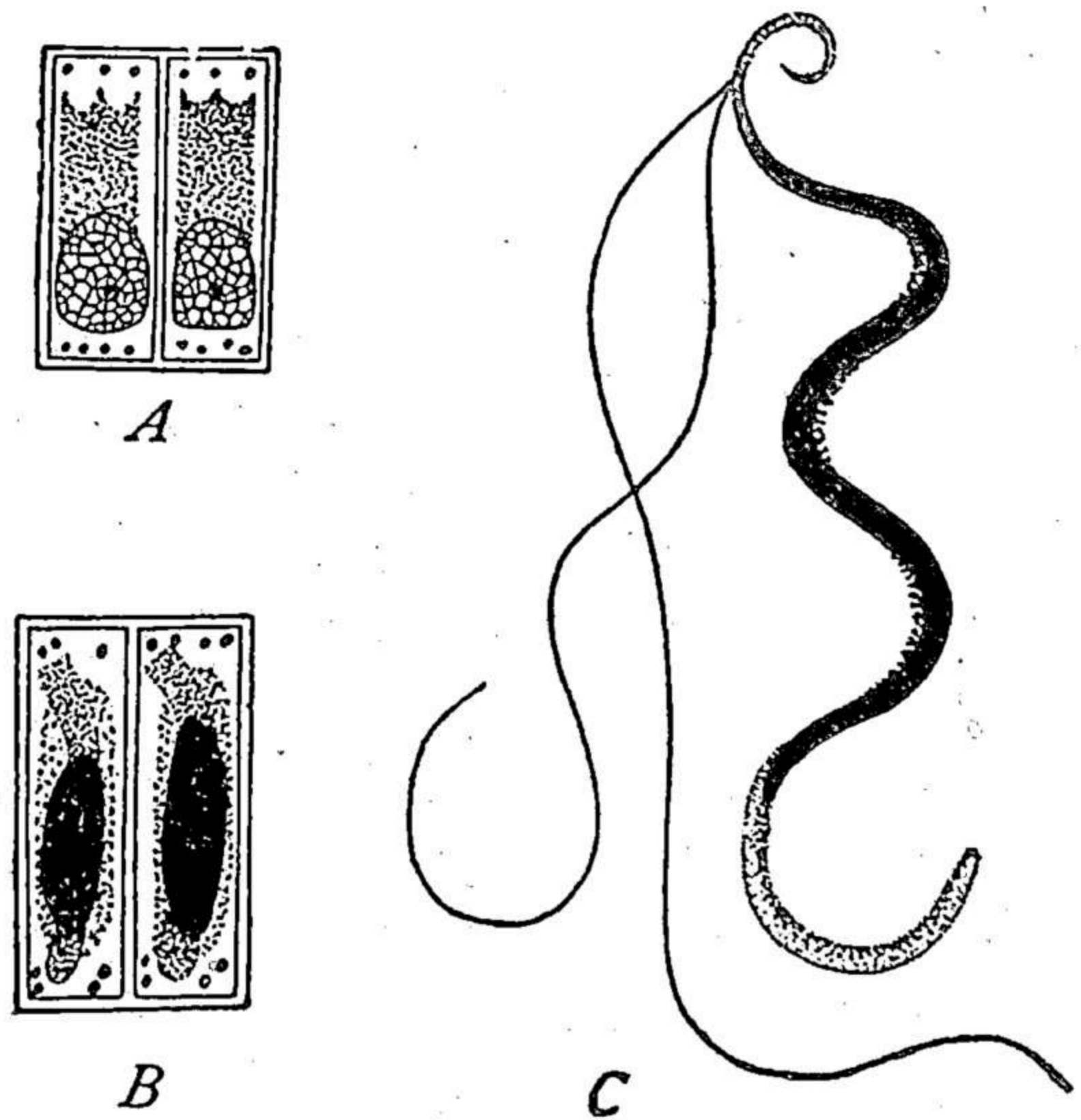

Fig. 133.—Sperms of *Chara* (BELAJEFF).

A, mother-cells with reticular nuclei; *B*, later stage, with sperms forming; *C*, mature sperms (the elongate nucleus black).

[1] *Cf.* the closely similar sperms of certain platodes, p. 295.

animal sperm (p. 391). Sperms of this type are found also in the Charales (Fig. 133).

The sperms of most pteridophytes are similar in general type to those of bryophytes but differ in the more pronounced spiral form of the cytosome and in the presence of numerous cilia arranged in a series along a considerable region of the spiral cytosome. An elongated, spiral nucleus occupies
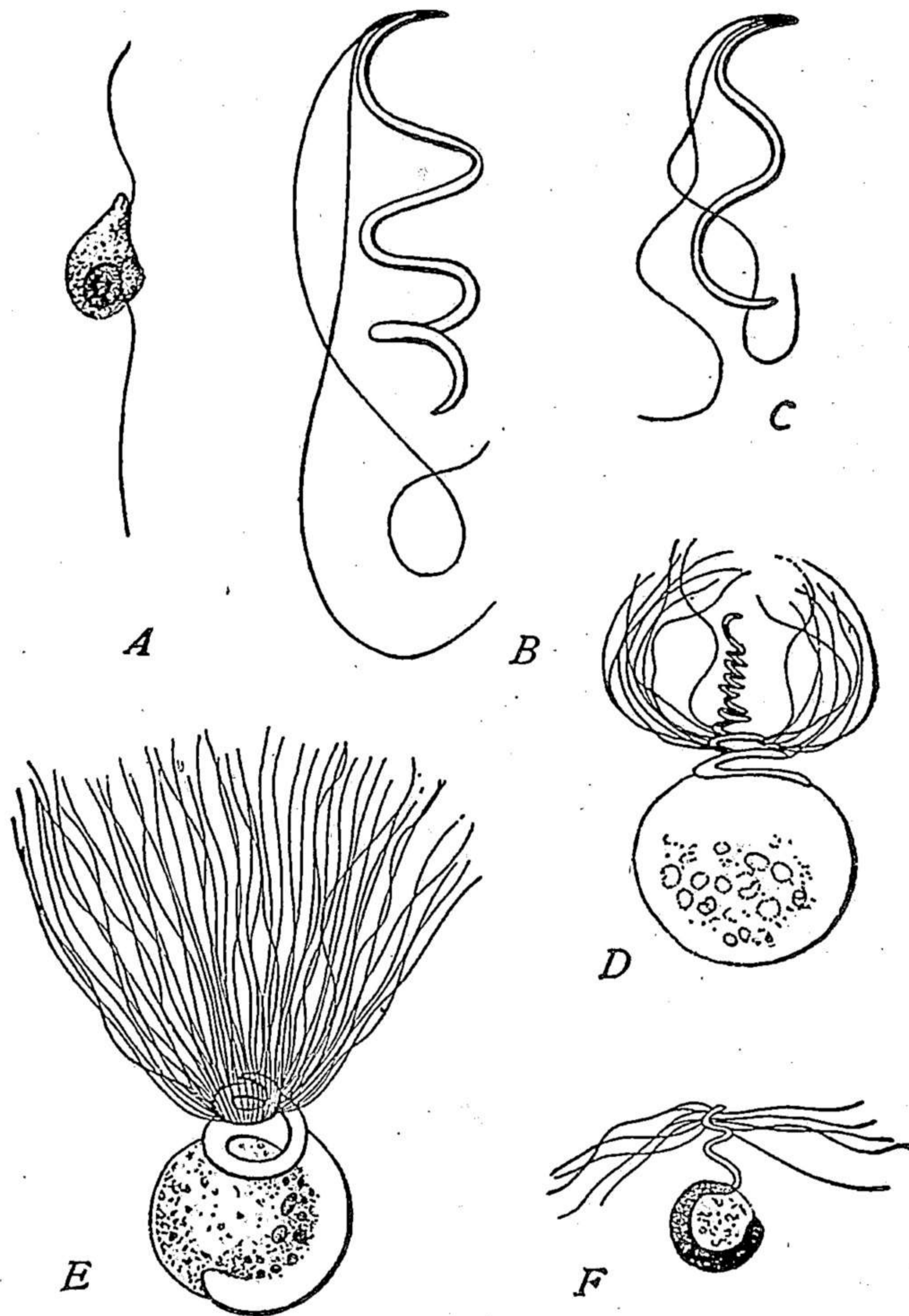

Fig. 134.—Sperms of plants. (*A, B, C, E*, after GUIGNARD; *D, F*, after STRASBURGER). *A*, of an alga (*Fucus*); a red chromatophore at the right of the nucleus; *B*, liverwort (*Pellia*); *C*, moss (*Sphagnum*); *D*, *Marsilia*; *E*, fern (*Angiopteris*); *F*, fern, *Phegopteris* (the nucleus dark).

the lower turns of the spiral, while the cilia are confined to the upper or middle turns (Figs. 134, 180), borne upon an elongated, spirally twisted blepharoplast of which they are outgrowths (p. 387). The cytosome bears a large "cytoplasmic vesicle" attached to the lower turns of the spiral which is cast off after the sperm is set free and before it enters the ovum. This structure seems to correspond exactly to the "residual protoplasm" that

is cast off from the developing animal sperm (p. 367). Sperms of this general type occur in all the pteridophytes save a few forms (*Lycopodium, Selaginella, Phylloglossum*) in which occurs a simple biflagellate sperm somewhat like that of bryophytes.

The pteridophyte type of sperm is connected by interesting intermediate forms with the non-motile sperm-cells of the higher gymnosperms and angiosperms. Sperms of this type but somewhat simplified are still present in the cycads and Ginkgoales, but reduced in number and of great relative size. In *Microcycas* their number is 16–20, in *Ceratozamia* exceptionally 4 but usually 2, in other cycads and in *Ginkgo* always 2; and in all of these cases they are carried within the tip of the pollen-tube, never being discharged to lead a free-swimming life in the water.[1] These sperms are obtusely conical in shape, with a large rounded nucleus, and a band-shaped blepharoplast which forms several spiral turns around the upper region and bears a close series of short cilia by which the sperm slowly swims (Fig. 182). These are probably the largest sperm-cells known in either plants or animals, reaching in *Zamia* a diameter of more than 300μ and readily visible to the naked eye (Webber). In the higher gymnosperms the cilia and associated structures have been lost, but in most cases the sperm, temporarily at least, is a complete cell (Figs. 214, 215) with a definitely bounded cytosome, closely similar to the young sperms of cycads (*Thuja, Sequoia, Taxus,* etc.); but no trace of blepharoplasts has yet been found in them. These cells are typically two in number, and usually equal; but in some cases (*Taxus, Torreya*) are unequal, only the larger being functional. In *Pinus* the cytosome finally breaks down, only the nucleus retaining its individuality. In the seed-plants, finally, these are but two sperms represented by two "generative nuclei" borne within the growing pollen-tube near its tip and by most observers described as not surrounded by definite cytosomes. In a few cases, however, the sperm-cytosome is said to be definitely marked off and even to enter the egg during fertilization; but little is known concerning its structure.[2] It has been supposed that at the time of fertilization these gametes (or nuclei) though not ciliated, may have some power of movement within the egg; but this is conjectural (p. 452).

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[1] *Cycas* (Ikeno, '96, '98, '04), *Ginkgo* (Hirase, '06, '98), Webber, '97, '01), *Stangeria* (Lang, '00), *Dioön* (Chamberlain, '09), *Microcycas* (Caldwell, '07), *Ceratozamia* (Chamberlain, '07).

[2] See Welsford, '14 (*Lilium*), Wylie, '22 (*Vallisneria*). For further details concerning the gametes of plants, see Chaps. V and VII.