

A PARTIAL LIST SHOWING THE NUMBER OF CHROMOSOMES CHARACTERISTIC OF THE GERM-NUCLEI AND SOMATIC NUCLEI IN VARIOUS PLANTS AND ANIMALS¹

GERM-NUCLEI.	SOMATIC NUCLEI.	NAME.	GROUP.	AUTHORITY.
1	2	<i>Ascaris megalocephala</i> , var. <i>univalens</i> .	Nematodes.	Van Beneden, Boveri.
2	4	Id. var. <i>bivalens</i> .	"	"
"	"	<i>Ophryotrocha</i> .	Annelids.	Korschelt.
"	[..]	<i>Styleopsis</i> .	Tunicates.	Julin.
4	8	<i>Coronilla</i> .	Nematodes.	Carnoy.
"	"	<i>Pallavicinia</i> .	Hepaticæ.	Farmer.
"	"	<i>Anthoceras</i> .	"	Davis.
6	12	<i>Spiroptera</i> .	Nematodes.	Carnoy.
"	"	<i>Prostheceræus</i> .	Polyclades.	Klinckoström, Francotte.
"	"	<i>Nais</i> .	Phanerogams.	Guignard.
[..]	"	<i>Spirogyra</i> .	Conjugatæ.	Strasburger.
"	[..]	<i>Grylotalpa</i> .	Insects.	Vom Rath.
"	"	<i>Caloptenus</i> .	"	Wilcox.
[..]	"	<i>Æquorea</i> .	Hydromedusæ.	Häcker.
7	14	<i>Pentatoma</i> .	Insects.	Montgomery.
8	16	<i>Filaroides</i> .	Nematodes.	Carnoy.
"	[..]	<i>Prosthiostomum</i> .	Polyclades.	Francotte.
"	[..]	<i>Leptoplana</i> .	"	"
"	[..]	<i>Cycloporus</i> .	"	"
"	"	<i>Hydrophilus</i> .	Insects.	Vom Rath.
"	"	<i>Phallusia</i> .	Tunicates.	Hill.
"	"	<i>Limax</i> .	Gasteropods.	Vom Rath.
"	[..]	Rat.	Mammals.	Moore.
"	[..]	Ox, guinea-pig, man.	"	Bardeleben.
"	"	<i>Ceratozamia</i> .	Cyads.	Overton. Guignard.
"	"	<i>Pinus</i> .	Coniferæ.	Dixon.
"	"	<i>Scilla</i> , <i>Triticum</i> .	Angiosperms.	Overton.
"	"	<i>Allium</i> .	"	Strasburger, Guignard.
"	"	<i>Podophyllum</i> .	"	Mottier.
9	18	<i>Echinus</i> .	Echinoderms.	Boveri.
"	"	<i>Thysanozoön</i> .	Polyclades.	Van der Stricht.
"	"	<i>Sagitta</i> .	Chætognaths.	Boveri.
"	"	<i>Chætopterus</i> .	Annelids.	Mead.
"	"	<i>Ascidia</i> .	Tunicates.	Boveri.
10	20	<i>Lasius</i> .	Insects.	Henking.
11	[22]	<i>Allolobophora</i> .	Annelids.	Foot.
12	24	<i>Myzostoma</i> .	"	Wheeler.

¹ This table is compiled from papers both on fertilization and maturation. Numbers in brackets are inferred.

GERM-NUCLEI.	SOMATIC NUCLEI.	NAME.	GROUP.	AUTHORITY.
12	24	Thalassema.	Annelids.	Griffin.
11 (12)	22 (24)	Cyclops strenuus.	Copepods.	Rückert.
12	24	„ brevicornis.	„	Häcker.
„	„	Helix.	Gasteropods.	Platner, Vom Rath.
„	„	Branchipus.	Crustacea.	Brauer.
„	„	Pyrrhocoris.	Insects.	Henking.
„	„	Salmo.	Teleosts.	Böhm.
„	„	Salamandra.	Amphibia.	Flemming.
„	„	Rana.	„	Vom Rath.
„	„	Mouse.	Mammals.	Sobotta.
„	„	Osmunda.	Ferns.	Strasburger.
„	„	Lilium.	Angiosperms.	Strasburger, Guignard.
„	„	Helleborus.	„	Strasburger.
„	„	Leucojum, Pæonia, Aconitum.	„	Overton.
14	28	Tiara.	Hydromedusæ.	Boveri.
„	„	Pieris.	Insects.	Henking.
16	32	Cerebratulus, Micrura.	Nemertines.	Coe.
„	„	Pterotrachea, Carinaria, Phyllirhoë.	Gastropods.	Boveri.
„	[„]	Diaptomus, Heterocope.	Copepods.	Rückert.
„	[„]	Anomalocera, Euchæta.	„	Vom Rath.
„	[„]	Lumbricus.	Annelids.	Calkins.
18	36	Torpedo, Pristiurus.	Elasmobranchs.	Rückert.
[18(19)]	36(38)	Toxopneustes.	Echinoderms.	Wilson.
30	[60]	Crepidula.	Gasteropods.	Conklin.
84	168	Artemia.	Crustacea.	Brauer.

The above data are drawn from sources so diverse and show so remarkable a uniformity as to establish the general law with a very high degree of probability. The few known exceptions are almost certainly apparent only and are due to the occurrence of plurivalent chromosomes. This is certainly the case with *Ascaris* (cf. p. 87). It is probably the case with the gasteropod *Arion*, where, as described by Platner, the egg-nucleus gives rise to numerous chromosomes, the sperm-nucleus to two only; the latter are, however, plurivalent, for Garnault showed that they break up into smaller chromatin-bodies, and that the germ-nuclei are exactly alike at the time of union. We may here briefly refer to remarkable recent observations by Rückert and others, which seem to show that not only the paternal and maternal chromatin, but also the chromosomes, may retain their individuality throughout development.¹ Van Beneden, the pioneer observer

¹ '89, pp. 10, 33.

in this direction, was unable to follow the paternal and maternal chromatin beyond the first cleavage-nucleus, though he surmised that they remained distinct in later stages as well; but Rabl and Boveri brought forward evidence that the chromosomes did not lose their identity, even in the resting nucleus. Rückert ('95, 3) and Häcker ('95, 1) have recently shown that in *Cyclops* the paternal and maternal chromatin-groups not only remain distinctly separated during the anaphase, but give rise to double nuclei in the two-cell stage (Fig. 146). Each half again gives rise to a separate group of chromosomes at the second cleavage, and this is repeated at least as far as the blastula stage. Herla and Zoja have shown furthermore that if in *Ascaris* the egg of variety *bivalens*, having two chromosomes, be fertilized with the spermatozoon of variety *univalens* having one chromosome, the three chromosomes reappear at each cleavage, at least as far as the twelve-cell stage (Fig. 145); and according to Zoja, the paternal chromosome is distinguishable from the two maternal at each step by its smaller size. We have thus what must be reckoned as more than a possibility, that every cell in the body of the child may receive from each parent not only half of its chromatin-substance, but one-half of its chromosomes, as distinct and individual descendants of those of the parents.

C. THE CENTROSOME IN FERTILIZATION

In examining more critically the history of the centrosomes we may conveniently take Boveri's hypothesis of fertilization as a point of departure, since it has long formed the focus of discussion of the entire subject. Before the hypothesis is more closely scrutinized we may first eliminate two other views, both of which are irreconcilable with it, though neither has stood the test of later research. The first of these, doubtfully suggested by Van Beneden ('87) and definitely maintained by Wheeler ('97) in the case of *Myzostoma*, is that the cleavage-centrosomes have no definite relation to the spermatozoon, but are derived from the egg—a conclusion that has the *a priori* support of the fact that in parthenogenesis the centrosomes are certainly of maternal origin.

Van Beneden's early statement may be passed by, since it was no more than a surmise. Wheeler, after a careful research, found that no sperm-aster accompanied the sperm-nucleus—a fact correlated with the absence of a middle-piece in the spermatozoon,—and reached the conclusion that after formation of the polar bodies, the egg-centrosomes persisted to become directly converted into the cleavage-centrosomes (Fig. 104). That the absence of a distinct middle-piece is not a valid argument is shown by the insect-spermatozoon, where the region

of the middle-piece is likewise not marked off from the tail, yet as we have seen (p. 165) the centrosome passes into this part of the spermatozoön. Kostanecki's later examination of the fertilization of the

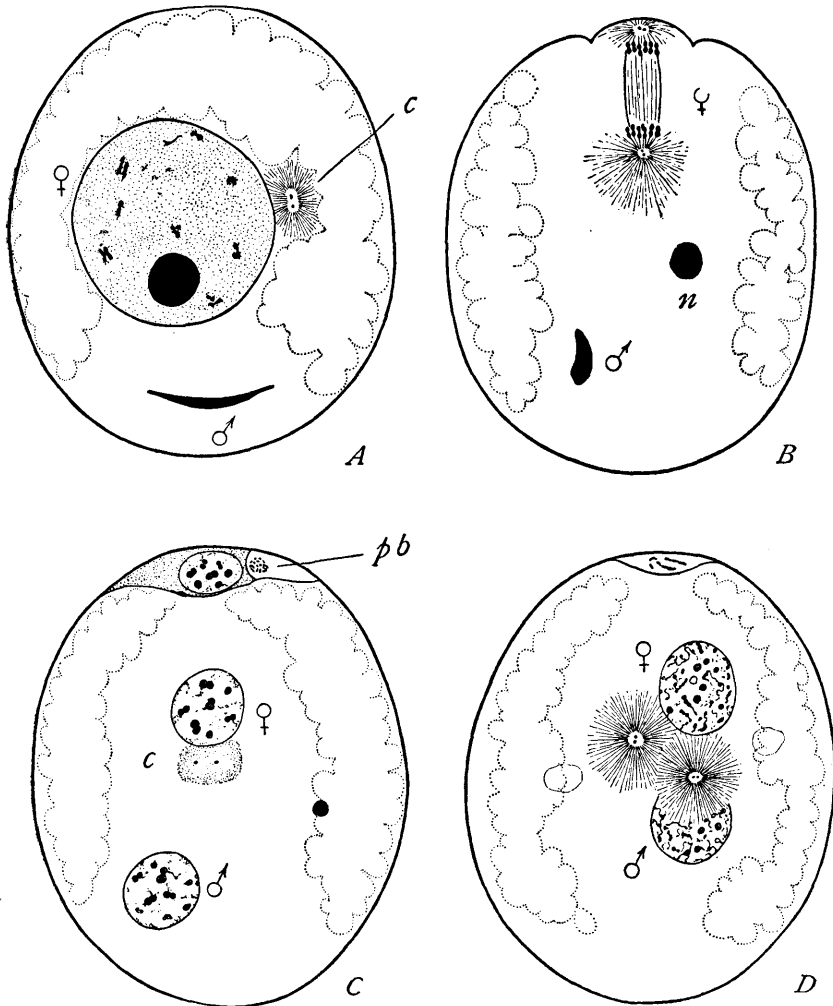


Fig. 104. — Fertilization of the egg of the parasitic annelid, *Myzostoma*. [WHEELER.]

A. Soon after entrance of the spermatozoön; the sperm-nucleus at ♂; at ♀ the germinal vesicle; at *c* the double centrosome. B. First polar body forming at ♀; *n*, the cast-out nucleolus or germinal spot. C. The polar bodies formed (*p.b.*); germ-nuclei of equal size; at *c* the centrosomes. D. Approach of the germ-nuclei; the amphiaster formed.

same animal ('98), while inconclusive on the main point, leaves little doubt that Wheeler's evidence was equally so; for he has on the one hand shown that the sperm-nucleus is often accompanied by a sperm-

aster containing a pair of centrosomes, on the other hand that these, like the egg-centrosomes, wholly disappear from view at a later period, the cleavage-centrosomes having only a conjectural origin.

The second of the views in question is that the cleavage-centrosomes are derived from both germ-cells; and this in turn has in its favour the *a priori* evidence that in the Infusoria conjugation takes place between two mitotic figures (p. 224). It appears in two forms, of which the first, though undoubtedly erroneous, has had so interesting a history as to deserve a brief review. It was predicted by Rabl in 1889 that if the centrosome be a permanent cell-organ, the conjugation of germ-cells and germ-nuclei would be found to involve also a conjugation of centrosomes. Unusual interest was therefore aroused when Fol, in 1891, under the somewhat dramatic title of the "Quadrille of Centres," described precisely such a conjugation of centrosomes as Rabl had predicted. The results of this veteran observer were very positively and specifically set forth, and were of so logical and consistent a character as to command instant acceptance on the part of many authorities. In the eggs of the sea-urchin the sperm-centrosome and egg-centrosome were asserted to divide each into two, the daughter-centrosomes then conjugating two and two, paternal with maternal, to form the cleavage-centrosomes. The same result was announced by Guignard ('91) in the lily, by Conklin ('93) in the gasteropod *Crepidula*, less definitely by Blanc ('93) in the trout, and still later by Van der Stricht ('95) in *Amphioxus*. None of these results have stood the test of later work. Fol's result was opposed to the earlier conclusions of Boveri and Hertwig, and a careful reëxamination of the fertilization of the echinoderm egg, independently made in 1894-95 by Boveri (*Echinus*), by myself (*Toxopneustes*), and Mathews (*Arbacia*, *Asterias*), and slightly later by Hill ('95) and Reinke ('95) in *Sphaerechinus*, demonstrated its erroneous character. Various attempts have been made to explain Fol's results as based on double-fertilized eggs, on imperfect method, on a misinterpretation of the double centrosomes of the cleavage-spindle, yet they still remain an inexplicable anomaly of scientific literature.

Serious doubt has also been thrown on Conklin's conclusions by subsequent research. Kostanecki and Wierzejski ('96) made a very thorough study, by means of serial sections, of the fertilization of the gasteropod *Physa*, and reached exactly the same result as that obtained in the echinoderms. Here, also, the egg-centres degenerate, their place being taken by a new pair, arising in intimate relation with the middle-piece of the spermatozoön, about which forms a sperm-amphiaster (Fig. 89). Conklin, after renewed research, himself admitted that no quadrille occurs in *Crepidula*, though he still believes that a union of paternal and maternal attraction-spheres takes place.

Guignard's results, too, have entirely failed of confirmation by later observers (p. 221), and in his own latest contribution to the subject ('99) the centrosomes are conspicuous by their absence in both the text and the figures. In like manner Van der Stricht's conclusions have been shown by Sobotta ('97) to be without substantial foundation, while Blanc's account, opposed to the earlier work of Böhm, is too incomplete to carry any weight. The entire case for the "quadriple" has thus fallen to the ground. In its second form the supposed double origin of the centrosomes rests upon a single research upon *Ascaris* by Carnoy and Le Brun ('97, 2), who assert that the cleavage-centrosomes arise *de novo* and separately, one inside of each of the germ-nuclei, to migrate thence out into the cytoplasm. At the close of mitosis they wholly disappear, to be replaced by a new pair, likewise of intranuclear origin. Since this result is totally opposed to those of Van Beneden, Boveri, Erlanger, and Kostanecki and Siedlecki on the same object, and is contradicted in the most positive manner by Fürst,¹ it may be received with some scepticism. The work of Kostanecki and Siedlecki ('96) demonstrates the division of the sperm-centrosome in *Ascaris* as described by Boveri; and while it still remains possible that the daughter-centrosomes may for a very brief period disappear (as in some of the mollusks described beyond), no ground is given for such a conclusion as Carnoy has drawn. No one familiar with the object can repress the suspicion that Carnoy and Le Brun have confused the centrosomes with the nucleoli; but only renewed research can determine the point.

The ground is now clear for a closer study of Boveri's hypothesis in the light of more recent research. It should first be pointed out that that hypothesis is based upon and forms a part of the more general theory of the autonomy of the centrosome; and if the latter theory cannot be sustained, the *a priori* side of Boveri's hypothesis assumes a different aspect. In point of fact the general outcome of recent research on fertilization has been on the whole unfavourable to the view that the cleavage-centrosomes must necessarily be individually identical with permanent preëxisting centrosomes — indeed, it is in this very field that some of the most convincing evidence against the persistence of the centrosome has been produced. The mode of origin of the cleavage-centrosomes is nevertheless a question of high interest on account of the unmistakable genetic relations existing between the centrosome of the spermatid and spermatozoön and those of the sperm-amphiaster within the egg.

There are two points of capital importance to be determined before a definite decision regarding the origin of the cleavage-centrosomes can be reached. First, are the centrosomes of the sperm-aster within

¹ '98, p. 105.

the egg identical with, or the descendants of, a centrosome or pair of centrosomes in the middle-piece of the spermatozoön? Second, do they actually persist to form those of the cleavage-amphiaster? In the present state of knowledge we are not in a position to give an affirmative answer to the first of these questions. As has been shown in Chapter III., it is no longer possible to doubt that the middle-piece either contains or is itself a metamorphosed centrosome; but, as pointed out at page 196, it does not seem possible that the extremely minute centrosome of the sperm-aster can represent the entire centrosome of the middle-piece (however we conceive the origin of the latter). At most we can only assume that a part of the latter persists as the sperm-centrosome within the egg. The exact origin of the latter still remains problematical. A large number of observers are now agreed that the sperm-aster is formed about a focus that is either in or very near the middle-piece;¹ but no one, I believe, has yet succeeded in showing that the centrosome actually is the metamorphosed middle-piece, or escapes from it.² The possibility therefore remains that the centrosome of the sperm-aster is not actually imported as such into the egg, but is either only a portion of the original spermatid-centrosome, or, as was first suggested by Miss Foot ('97) and further discussed by Mead ('98, 2), is, like the aster, formed anew in the egg-cytoplasm. If the latter alternative be the case, the original form of Boveri's hypothesis would have to be abandoned;

¹ For example, in echinoderms (Flemming, '81, O. and R. Hertwig, '86, Boveri, '95, Wilson and Mathews, '95, Hill, '95, Reinke, '95, R. Hertwig, '96, Doflein, '97, 2, Erlanger, '98), in *Pterotrachea* and *Pteris* (Henking, '91, '92), in the axolotl (Fick, '93), and *Triton* (Michaelis, '97), in *Phallusia* (Hill, '95), in *Ophryotrocha* (Korschelt, '95), in *Physa* (Kostanecki and Wierzejski, '96), in *Strongylus* (Meyer, '95), in *Thysanozöön* (Van der Stricht, '98), and *Prosthiostomum* (Francotte, '98). In a large number of other cases the sperm-aster is found near the sperm-nucleus, but its relation to the middle-piece has not been demonstrated.

² I myself formerly concluded ('95, 2) that the entire middle-piece of echinoderms is the centrosome — a result apparently confirmed in a most positive manner by Erlanger ('98), as well as by R. Hertwig ('96) and Doflein ('97, 2). I have, however, demonstrated this to be an error, showing that the extremely minute centrosome is quite distinct from the middle-piece, the latter being thrown aside and degenerating in the egg-cytoplasm outside of the newly formed sperm-aster (Figs. 12, 94). This fact, of which the phenomena in *Toxopneustes* leave no doubt (see Wilson, '97, '99), is, I think, fatal to Kostanecki's and Wierzejski's theory of fertilization ('96, pp. 374-375), according to which the archoplasm of the middle-piece gives rise to the new astral system and is thus the essential fertilizing substance (the centrosome being merely a mechanical centre for the attachment of the rays); but the most careful examination has still failed to show whether the centrosome actually escapes from the middle-piece, nor have other observers had better success with any animal. Erlanger ('96, 2, '97, 4) believes he has seen the centrosome in the *Ascaris* spermatozoön as a distinct body lying behind the nucleus, and that it can be traced continuously into the egg and after its division into the two poles of the cleavage-figure. Neither the schematic figures of his preliminary nor the photographic ones of his final paper seem sufficient to establish either the identity or the subsequent history of the granule in question.

though in substance it would still retain an element of truth, as pointed out beyond.

We may now examine the question whether the sperm-centrosomes are actually identical with the cleavage-centrosomes. That such is the case is positively maintained in the case of *Ascaris* by Boveri, Kostanecki, and Erlanger, in *Physa* by Kostanecki and Wierzejski ('96), in *Thalassema* by Griffin ('96, '99), and in *Chatopterus* by Mead ('95, '98). The two last-mentioned observers, who have followed the phenomena with especial care, produce very strong evidence that at no time do the sperm-centrosomes and asters disappear, and that the former may be traced in unbroken continuity from the time of their first appearance to the daughter-cells resulting from the first cleavage (Figs. 99, 155). On the other hand, a considerable number of observers, beginning with Hertwig (*Phyllirrhoë*, *Pterotrachea*, '75), have found that as the sperm-nucleus enlarges the sperm-asters diminish in size, until, in many cases, they nearly or quite disappear; for example, in *Prostheceræus* (Klinckowström, '97), in the mouse (Sobotta, '95), in *Pleurophyllidia* (MacFarland, '97), *Physa* (Kostanecki and Wierzejski, '96), *Arenicola* (Child, '97), *Unio* (Lillie, '97), *Myzostoma* (Kostanecki, '98), and *Cerebratulus* (Coe, '98).¹ Several of these observers (Klinckowström, MacFarland, Lillie, Child) have found that not only the asters *but also the centrosomes* totally disappear about the time the germ-nuclei come together, a new pair of cleavage-centrosomes and asters being afterward developed at the poles of the united nuclei. These conclusions, if correct, place in a new light the disappearance of the egg-centrosomes; for this process

¹ Coe has pointed out that the eggs of various animals may be arranged in a series showing successive gradations in the disappearance of the sperm-asters. "At the head of the series we must place the eggs of *Ascaris* and *Myzostoma* (according to Kostanecki) and similar ones in which the sperm-asters make their appearance only a short time before the formation of the cleavage-spindle, and which, consequently, suffer no diminution in size. Following these are the eggs of *Chatopterus* (Mead) and *Ophryotrocha* (Korschelt) and of some echinoderms in which the sperm-asters develop very early, but are not described as decreasing in size before the formation of the cleavage-spindle. Then come the eggs of *Toxopneustes* (Wilson) and *Thalassema* (Griffin), where the sperm-asters appear early and develop to a very considerable size, but nevertheless become very much smaller and less conspicuous after the germ-nuclei have come together. After these we must place the eggs of *Physa* (Kostanecki and Wierzejski), for here the sperm-asters, after becoming very large and conspicuous, degenerate to such an extent that only a very few exceedingly delicate fibres remain. Those of *Cerebratulus* follow next.

"Here the sperm-asters increase in size until they extend throughout the whole body of the cell, but at the time of fusion of the germ-nuclei they degenerate completely. The peripheral portions of their fibres, however, may be followed, as stated above of *Pleurophyllidia*, *Prostheceræus*, etc., where the sperm-asters degenerate soon after their formation, so that for a considerable period the egg is without trace of aster-fibres. Yet in all of those cases where the sperm-asters disappear and their centrosomes become lost among the other granules of the cell, we are justified in believing that the sperm-centrosomes nevertheless retain their identity, and later reappear in the cleavage-asters" ('98, p. 455).

would thus seem to be of the same nature as the disappearance of the sperm-centrosomes, and both Boveri's theory of fertilization and the general hypothesis of the permanence of the centrosomes would receive a serious blow.

The investigators to whom these observations are due have ranged themselves in two groups in the interpretation of the phenomena. On the one hand, Lillie and Child do not hesitate to maintain that the centrosomes actually go out of existence as such, to be re-formed like the asters out of the egg-substance; and that such a new formation of centrosomes is possible seems to be conclusively shown by the experiments of Morgan and Loeb described at pages 215 and 307. On the other hand, Sobotta, MacFarland, Kostanecki, and Coe, relying partly on the analogy of other forms, partly on the occasional presence of the centrosomes during the critical stage, urge that the disappearance of the sperm-centrosomes is only apparent, and is due to the disappearance of the asters, which renders difficult or impossible the identification of the centrosomes among the other protoplasmic granules of the egg. These authors accordingly still uphold Boveri's theory.

It is difficult to sift the evidence at present, for it has now become very important to reëxamine, in the light of these facts, those cases in which the absolute continuity of the centrosome has been maintained — for example, in *Ascaris*, *Chætopterus*, and *Thalassema* — in order to determine whether there may not be here also a brief critical period in which the centrosomes disappear. There are, however, some facts which tend to sustain the conclusion that even though the sperm-centrosomes disappear from view, there is some kind of genetic continuity between them and the cleavage-centrosomes. First, both Kostanecki and Wierzejski ('96) and Coe ('98) have found that there is some variation in eggs apparently equally well preserved, a few individuals showing the sperm-centrosomes at the poles of the united nuclei at the same period when they are invisible in other individuals. Second, both these observers, Coe most clearly, have shown that the egg-centrosomes disappear considerably earlier than the sperm-centrosomes, and Coe has traced the sperm-centrosomes continuously *to the exact points (the poles of the united nuclei) at which the cleavage-centrosomes afterward appear* (Fig. 155). This important observation leads to the suspicion that the apparent disappearance of the centrosomes may be due to a loss of staining-capacity at the critical period, or that even though the formed centrosome disappears its substance reappears in its successor. Here again we come to the view suggested at page 111, that the centrosome may be regarded as the vehicle of a specific chemical substance which is transported to the nuclear poles by its division, and may there persist even though the body of the

centrosome be no longer visible. On such a basis we may perhaps find a reconciliation between these observations and Boveri's theory, and may even bring the fertilization of plants into relation with it (p. 221). Even in case of the nucleus, universally recognized as a permanent cell-organ, it is not the whole structure that persists as such during division, but only the chromatin-substance—in some cases only a small fraction of that substance. The law of genetic continuity therefore would not fail in case of the centrosome, though only a portion of its substance were handed on by division; and even if we take the most extreme negative position, assuming that the sperm-centrosome is wholly formed anew under the stimulus of the spermatozoon, we should still not escape the causal *nexus* between it and the centrosome of the spermatid.

Boveri himself has suggested¹ that the egg may be incited to development by a specific chemical substance carried by the spermatozoon, and the same view has been more recently urged by Mead,² while Loeb's recent remarkable experiments on sea-urchins ('99) show that the egg may in this case (*Arbacia*) undergo complete parthenogenetic development as the result of artificial chemical stimulus.³ Assuming such a substance to exist, by what part of the spermatozoon is it carried? It is possible that the vehicle may be the nucleus, which forms the main bulk of that which enters the egg; and this view seems to be supported by what is at present known of fertilization in the plants (p. 221). Yet when we regard the facts of fertilization in animals, taken in connection with the mode of formation of the spermatozoon, we find it difficult to avoid the conclusion that the substance by which the stimulus to development is normally given is originally derived from the spermatid-centrosome, is conveyed into the egg by the middle-piece, and is localized in the sperm-centrosomes which are conveyed to the nuclear poles during the amphister-formation. Accepting such a view, we could gain an intelligible view of the genetic relation between spermatid-centrosome, middle-piece, sperm-centrosome, and cleavage-centrosomes, without committing ourselves to the morphological hypothesis of the persistence of the centrosome as an individualized cell-organ. Such a conclusion, I believe, would retain the substance of Boveri's theory while leaving room for the abandonment of the too simple morphological form in which it was originally cast.

D. FERTILIZATION IN PLANTS

The investigation of fertilization in the plants has always lagged somewhat behind that of the animals, and even at the present time

¹ '91, p. 431.

² '98, 2, p. 217.

³ Cf. p. 111.

our knowledge of it is rather incomplete. It is, however, sufficient to show that the essential fact is everywhere a union of two germ-nuclei—a process agreeing fundamentally with that observed in animals. On the other hand, almost nothing is known regarding the centrosome and the archoplasmic or kinoplasmic structures; and most recent observations point to the conclusion that in the lowering plants and pteridophytes no centrosomes are concerned in fertilization.

Many early observers from the time of Pringsheim ('55) onward described a conjugation of cells in the lower plants, but the union of *germ-nuclei*, as far as I can find, was first clearly made out in the flowering plants by Strasburger in 1877-78, and carefully described by him in 1884. Schmitz observed a union of the nuclei of the

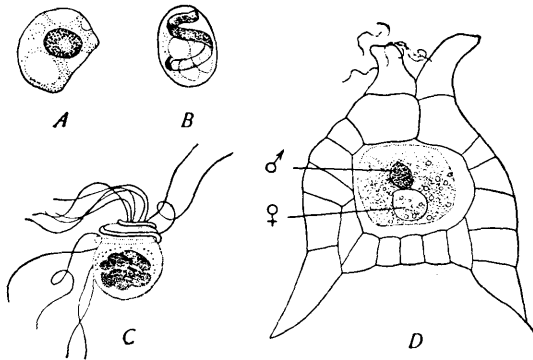


Fig. 105. — Fertilization in *Pilularia*. [CAMPBELL.]

A, B. Early stages in the formation of the spermatoid. C. The mature spermatoid; the nucleus lies above in the spiral turns; below is a cytoplasmic mass containing starch-grains (cf. the spermatoids of ferns and of *Marsilia*, Fig. 71). D. Archegonium during fertilization. In the centre the ovum containing the apposed germ-nuclei (♂, ♀).

conjugating cells of *Spirogyra* in 1879, and made similar observations on other algæ in 1884. Among other forms in which the same phenomenon has been described may be mentioned *Edigonium* (Klebahn, '92), *Vaucheria* (Oltmanns, '95), *Cystopus* (Wager, '96), *Sphærotheca* and *Erysiphe* (Harper, '96), *Fucus* (Farmer and Williams, '96, Strasburger, '97), *Basidiobolus* (Fairchild, '97), *Pilularia* (Fig. 105, Campbell, '88), *Onoclea* (Shaw, '98, 2), *Zamia* (Webber, '97, 2), and *Lilium* (Guignard, '91, Mottier, '97), *Ginkgo* (Hirase, '97).¹ In all of these forms and many others fertilization is effected by the union of a single paternal and a single maternal uninucleated cell, such as occurs throughout the animal kingdom. There are, however, some apparently well-determined exceptions to this rule occurring in the "compound" multinucleate oöospheres of some of the lower

¹ For unicellular forms see pp. 228, 280.

plants. In *Albugo bliti* (one of the Peronosporæ), for example, as shown by the recent work of Stevens ('99), the mature ovum contains about a hundred nuclei, and is fertilized by a multinucleate protoplasmic mass derived from the antheridium, each nucleus of the latter conjugating with one of the egg-nuclei. But although the conjugating bodies are here multinucleate, the germ-nuclei conjugate two and two (as is also the case in the multinucleate cysts of *Actinosphaerium*, p. 279); and the case therefore forms no real exception to the general rule that one paternal nucleus unites with one maternal.

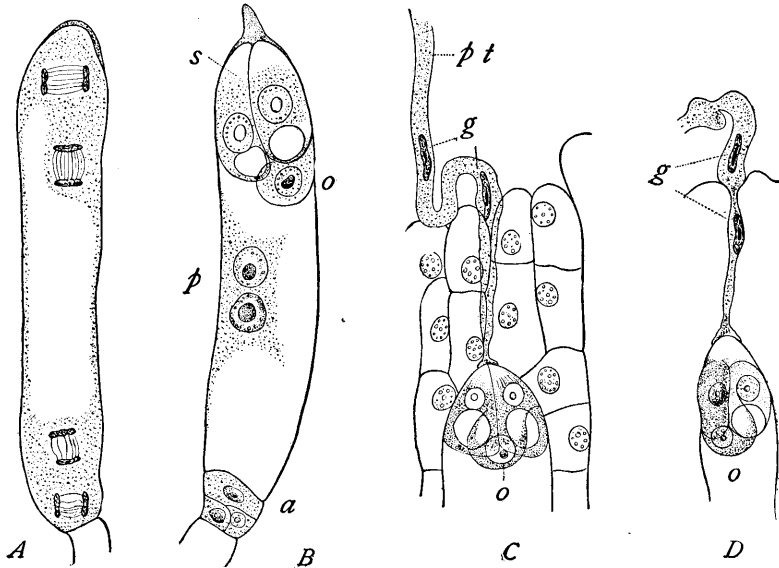


Fig. 106.—Formation of the ovum and penetration of the pollen-tube in flowering plants. [STRASBURGER.]

A. Embryo-sac of *Monotropa*, showing the division that follows the two maturation-divisions and produces the upper and lower "tetrads." B. The same, ready for fertilization, showing ovum (*o*), synergids (*s*), upper and lower polar cells (*p*), and antipodal cells (*a*). C. Penetration of the pollen-tube (*p.t.*) in *Orchis*; *o*, ovum, with synergids at either side, *g.n.* generative nuclei in the pollen-tube. D. Slightly later stage with generative nuclei entering the micropyle.

Whether a union of more than two germ-nuclei occurs in any of the lower plants is a question still disputed by botanists.¹ Such plural fusion is rendered *a priori* improbable by the observations thus far made upon the one-celled forms both in plants and in animals; and the known facts are sufficient to show that it must be, to say the least, an exceptional process.

In cases where the paternal germ-cell is a ciliated spermatozoid, as in *Fucus*, *Pilularia*, and the ferns and cycads, the germ-nuclei differ

¹ Cf. Hartog, '91, '96, Trow, '95, Stevens, '99, Zimmerman, '96, and literature there cited.

more or less widely at the time of union, the sperm-nucleus being smaller, more compact, and deeply staining (Figs. 105, 108), as is the case in such forms of fertilization as the echinoderm-egg. In the case of angiosperms all earlier observers, including Strasburger ('78, '84), Guignard ('91, 1), and Mottier ('97, 1), found the conjugating nuclei to be closely similar at the time of union. The recent observations of Guignard ('99) and Nawaschin ('99) show, however, that even here the sperm-nucleus is smaller, more compact, and of different form (spindle-shaped) from the egg-nucleus (Fig. 107).

The ovum or oösphere of the flowering plant is a large, rounded cell containing a large nucleus and numerous minute colourless plastids from which arise, by division, the plastids of the embryo (chromatophores, amyloplasts). In the angiosperms the ovum forms one of the eight cells constituting the embryo-sac which morphologically represents the female prothallium or sexual generation of the pteridophyte and is itself embedded in the ovule within the ovary.¹ The male germ-cells are represented in the cycads by two ciliated spermatozoids (p. 175), in the angiosperms by two spindle-shaped "generative nuclei" which are suspected by Guignard and Nawaschin to be motile bodies, though no cilia were seen. These lie near the tip of the pollen-tube (Fig. 107), which is developed as an outgrowth from the pollen-grain and represents a rudimentary male prothallium or sexual generation.²

The formation of the pollen-tube, and its growth down through the tissue of the pistil to the ovule, was observed by Amici ('23), Brongniart ('26), and Robert Brown ('31); and in 1833-34 Corda was able to follow its tip through the micropyle into the ovule.³ Strasburger first demonstrated the fact that the generative nucleus, carried at the tip of the pollen-tube, enters the ovum and unites with the egg-nucleus, and the facts have been since carefully studied by himself, by Guignard, Mottier, Webber, Ikeno, Hirase, and a number of others. In the cycads, according to the last-named two observers, a single spermatozoid enters the egg, its nucleus soon fusing with that of the

¹ The eight cells are at first arranged in an upper and a lower "tetrad" of four cells each, the former including the ovum, two synergidae, and an "upper polar cell," the latter a "lower polar cell" and three antipodal cells (Figs. 106, 107); *cf.* p. 263.

² *Cf.* p. 264.

³ It is interesting to note that the botanists of the eighteenth century engaged in the same fantastic controversy regarding the origin of the embryo as that of the zoologists of the time. Moreland (1703), followed by Etienne François Geoffroy, Needham, and others, placed himself on the side of Leeuwenhoek and the spermatists, maintaining that the pollen supplied the embryo which entered the ovule through the micropyle (the latter had been described by Grew in 1672); and even Schleiden adopted a similar view. On the other hand, Adanson (1763) and others maintained that the ovule contained the germ which was excited to development by an aura or vapour emanating from the pollen and entering through the tracheæ of the pistil.

egg (Fig. 108); and the earlier observers of the angiosperms, including Strasburger ('84, '88) and Guignard ('91, 1), likewise found that only one of the generative nuclei entered the embryo-sac. Guignard

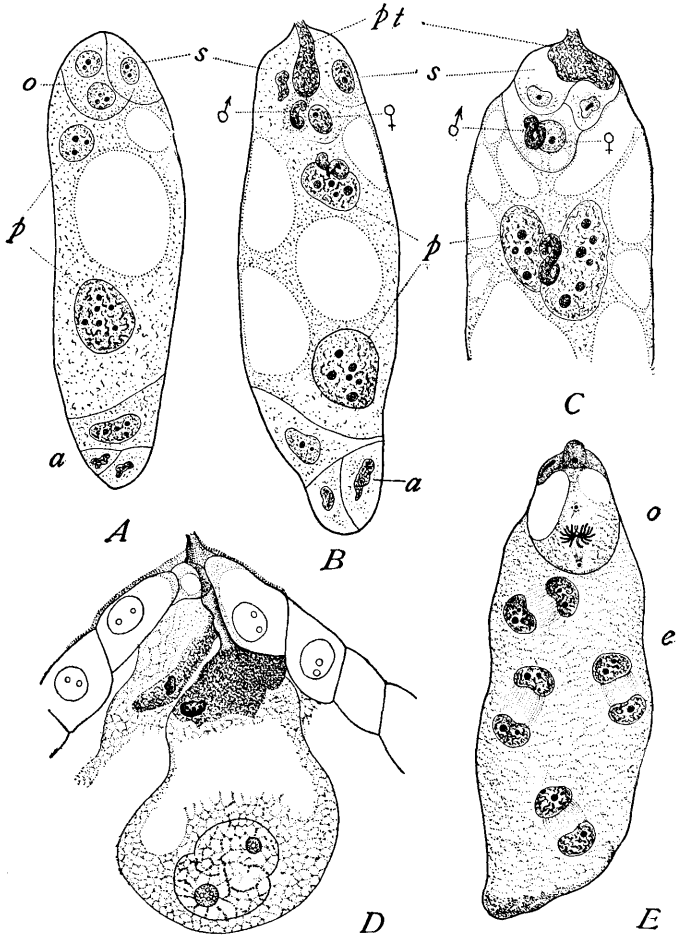


Fig. 107.—Fertilization in the lily. [D from MOTTIER, the others from GUIGNARD.]

A. Embryo-sac, ready for fertilization. B. Both generative nuclei have entered the embryo-sac; one is approaching the egg-nucleus, the other uniting with the upper polar nucleus. C. Union of the germ-nuclei; below, union of the second generative nucleus and the two polar nuclei. D. The fertilized egg, showing fusion of the germ-nuclei. E. The fertilized egg dividing; below, division of the endosperm-nuclei. a. antipodal cells; e. endosperm-nuclei; o. the oösphere or ovum; p. polar nuclei; p. t. pollen-tube.

and Nawaschin have, however, recently made the remarkable discovery that in *Lilium* and *Fritillaria* both generative nuclei enter the embryo-sac. One of these conjugates with the egg-nucleus and

thus effects fertilization (Fig. 107). *The other conjugates with one of the polar nuclei* (usually the upper), which then unites with the other polar nucleus (*cf.* p. 264). By division of the fertilized egg arises the embryo; while by division of the compound nucleus resulting from the

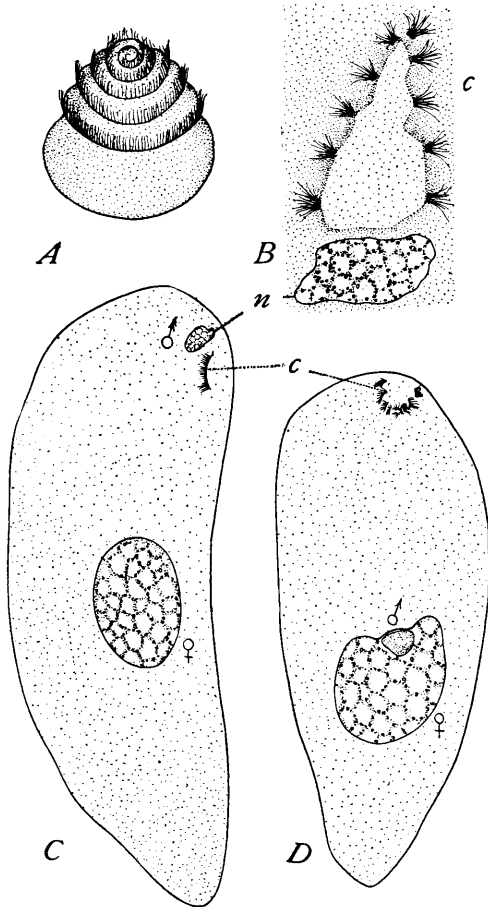


Fig. 108. — Fertilization in a cycad, *Zamia*. [WEBBER.]

A. Spermatozoid. B. The same after entrance into the egg, showing nucleus (*n*) and cilia-bearing band (*c*). C. The ovum shortly after entrance of the spermatozoid. D. Union of the germ-nuclei, cilia-bearing band near periphery (*c*).

fusion of the polar nuclei and the second sperm nucleus are formed the endosperm-cells, which serve for the nourishment of the embryo. This remarkable double copulation within the embryo-sac is without a parallel and is of wholly problematical meaning, but in no way contradicts the general rule regarding the union of two germ-nuclei to produce the embryo.¹

¹ As in the case of animals (p. 176), the germ-nuclei of phanerogams also show marked differences in structure and staining-reaction before their union, though they ultimately become exactly equivalent. Thus, according to Rosen ('92, p. 443), on treatment by fuchsin-methyl-blue the male germ-nucleus is "cyanophilous," the female "erythrophilous," as described by Auerbach in animals. Strasburger, while confirming this observation in some cases, finds the reaction to be inconstant, though the germ-nuclei usually show marked differences in their staining-capacity. These are ascribed by Strasburger ('92, '94) to differences in the conditions of nutrition; by Zacharias and Schwarz to corresponding differences in chemical composition, the male nucleus being in general richer in nuclein, and the female nucleus poorer. This distinction disappears during fertiliza-

The nature and origin of the achromatic elements involved in the fertilization of plants is still almost wholly in the dark. No observer has yet succeeded in observing either centrosomes or asters in the fertilization of the thallophytes, despite the fact that in some of these forms mitosis takes place with both these structures in a manner nearly analogous to that observed in animals.¹ In the cycads *Zamia* and *Cycas*, Webber and Ikeno ('98) agree that the entire spermatozoid enters, but only the nucleus appears to be concerned in fertilization. The cilia-bearing band — a product of the blepharoplast, and, as described at page 175, probably the analogue of the middle-piece of the animal spermatozoön — remains near the egg-periphery, gives rise to no astral or other fibrillar formations, and apparently remains quite passive (Fig. 108).

In angiosperms, too, the evidence seems to show that no centrosomes are concerned in fertilization. Guignard ('91, 1), in a very detailed and clearly illustrated paper, gave an account of the centrosomes in the lily agreeing almost exactly with the "quadrille of centres" as described by Fol,² paternal and maternal centrosomes conjugating two by two. The later and very careful studies of Motter and others have, however, entirely failed to confirm Guignard's results, the germ-nuclei fusing without the participation of centrosomes or astral formations, and after a time dividing, without centrosomes, in the manner characteristic of the higher plants.³ Neither in the cryptogams has any one thus far succeeded in finding fertilization-centrosomes or asters at the time the germ-nuclei unite. Strasburger contributes, however, the interesting observation that in *Fucus* the cleavage-centrosomes afterward appear on that side of the cleavage-nucleus derived from the sperm-nucleus, which he believes from analogy may indicate the importation of a "new dynamic centre" into the egg by the spermatozoid.⁴ Combining these facts with the phenomena involved in the origin of the spermatozoids, Strasburger suggests that the sperm-nucleus may import into the egg either a formed centrosome (probably thus in *Fucus*) or a certain quantity of "kinoplasm," which incites the mitotic phenomena in the absence of individualized centrosomes.⁵ This view harmonizes with that suggested at pages 111 and 214, and we may perhaps here in the end find a reconciliation between the various types, not only of fertilization but also of mitosis, in plants and animals.

On their face the facts of fertilization in plants, especially in the phanerogams, seem to indicate that the stimulus to development is given by the paternal germ-nucleus. Nevertheless, the analogy of animal fertilization would lead us to expect that the fertilizing sub-

¹ Cf. p. 82.

² Cf. p. 210.

³ Cf. p. 82.

⁴ '97, p. 418.

⁵ '97, p. 420.

stance is contained not in the nucleus but in the cytoplasm — more specifically, in the case of spermatozoids, in the cilia-bearing body derived from the blepharoplast, which in its development so strongly suggests a centrosome (p. 172). Webber's and Ikeno's observations on the cycads are not necessarily fatal to this view; for, as I have shown (p. 188), the middle-piece in the echinoderm is likewise cast off and degenerates near the periphery of the egg, and the centrosome is a body far more minute. The possibility has been admitted that this centrosome may be formed *de novo* under the influence of the middle-piece, which itself perishes. In like manner it may also be possible that the primary stimulus in *Zamia* and like cases is given by the cilia-bearing body, even though this body itself disappears and the mitotic apparatus is not formed until long afterward.

E. CONJUGATION IN UNICELLULAR FORMS

The conjugation of unicellular organisms possesses a peculiar interest, since it is undoubtedly a prototype of the union of germ-cells in the multicellular forms. Bütschli and Minot long ago maintained that cell-divisions tend to run in cycles, each of which begins and ends with an act of conjugation. In the higher forms the cells produced in each cycle cohere to form the multicellular body; in the unicellular forms the cells separate as distinct individuals, but those belonging to one cycle are collectively comparable with the multicellular body. The validity of this comparison, in a morphological sense, is generally admitted.¹ No process of conjugation, it is true, is known to occur in many unicellular and in some multicellular forms, and the cyclical character of cell-division still remains *sub judice*.² It is none the less certain that a key to the fertilization of higher forms must be sought in the conjugation of unicellular organisms.

The difficulties of observation are, however, so great that we are as yet acquainted with only the outlines of the process, and have still no very clear idea of its finer details or its physiological meaning. The phenomena have been most closely followed in the Infusoria by Bütschli, Engelmann, Maupas, and Richard Hertwig, though many valuable observations on the conjugation of unicellular plants have been made by De Bary, Schmitz, Klebahn, and Overton. All these observers have reached the same general result as that attained through study of the fertilization of the egg; namely, that an essential phenomenon of conjugation is *a union of the nuclei of the conjugating cells*. Among the unicellular plants both the cell-bodies and the nuclei completely fuse. Among animals this may occur; but in

Cf. p. 58.

² *Cf.* p. 178.

many of the Infusoria union of the cell-bodies is only temporary, and the conjugation consists of a mutual exchange and fusion of nuclei. It is impossible within the limits of this work to attempt more than a sketch of the process in a few forms.

We may first consider the conjugation of Infusoria. Maupas's beautiful observations have shown that in this group the life-history

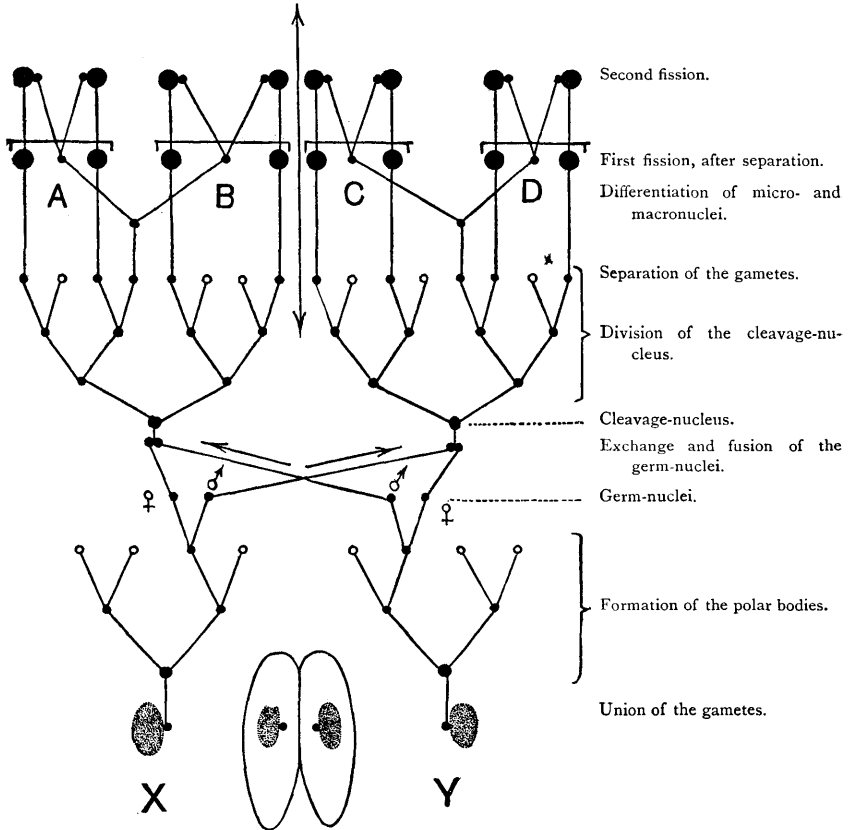


Fig. 109. — Diagram showing the history of the micronuclei during the conjugation of *Paramecium*. [Modified from MAUPAS.]

X and Y represent the opposed macro- and micronuclei in the two respective gametes; circles represent degenerating nuclei; black dots, persisting nuclei.

of the species runs in cycles, a long period of multiplication by cell-division being succeeded by an "epidemic of conjugation," which inaugurates a new cycle, and is obviously comparable in its physiological aspect with the period of sexual maturity in the Metazoa. If conjugation does not occur, the race rapidly degenerates and dies out; and Maupas believes himself justified in the conclusion that conju-

gation counteracts the tendency to senile degeneration and causes rejuvenescence, as maintained by Bütschli and Minot.¹

In *Stylonychia pustulata*, which Maupas followed continuously from the end of February until July, the first conjugation occurred on April 29th, after 128 bi-partitions; and the epidemic reached its height three weeks later, after 175 bi-partitions. The descendants of individuals prevented from conjugation died out through "senile degeneracy," after 316 bi-partitions. Similar facts were observed in many other forms. The degeneracy is manifested by a very marked reduction in size, a partial atrophy of the cilia, and especially by a more or less complete *degradation of the nuclear apparatus*. In *Stylonychia pustulata* and *Onychodromus grandis* this process especially affects the micronucleus, which atrophies, and finally disappears, though the animals still actively swim, and for a time divide. Later, the macronucleus becomes irregular, and sometimes breaks up into smaller bodies. In other cases, the degeneration first affects the macronucleus, which may lose its chromatin, undergo fatty degeneration, and may finally disappear altogether (*Stylonychia mytilus*), after which the micronucleus soon degenerates more or less completely, and the race dies. It is a very significant fact that toward the end of the cycle, as the nuclei degenerate, the animals become incapable of taking food and of growth; and it is probable, as Maupas points out, that the degeneration of the cytoplasmic organs is due to disturbances in nutrition caused by the degeneration of the nucleus.

The more essential phenomena occurring during conjugation are as follows. The Infusoria possess two kinds of nuclei, a large *macronucleus* and one or more small *micronuclei*. During conjugation the macronucleus degenerates and disappears, and the micronucleus alone is concerned in the essential part of the process. The latter divides several times, one of the products, the *germ-nucleus*, conjugating with a corresponding germ-nucleus from the other individual, while the others degenerate as "corpuscules de rebut." The dual nucleus thus formed, which corresponds with the cleavage-nucleus of the ovum, then gives rise by division to both macronuclei and micronuclei of the offspring of the conjugating animals (Fig. 109).

These facts may be illustrated by the conjugation of *Paramecium caudatum*, which possesses a single macronucleus and micronucleus, and in which conjugation is temporary and fertilization mutual. The two animals become united by their ventral sides and the macronucleus of each begins to degenerate, while the micronucleus divides twice to form four spindle-shaped bodies (Fig. 110, *A, B*). Three of these degenerate, forming the "corpuscules de rebut," which play no further part. The fourth divides into two, one of which, the "female pronucleus," remains in the body, while the other, or "male pronucleus," passes into the other animal and fuses with the female pronucleus (Fig. 110, *C-H*). Each animal now contains a cleavage-nucleus equally derived from both the conjugating animals, and the latter soon separate. The cleavage-nucleus in each divides three

¹ Cf. p. 179.

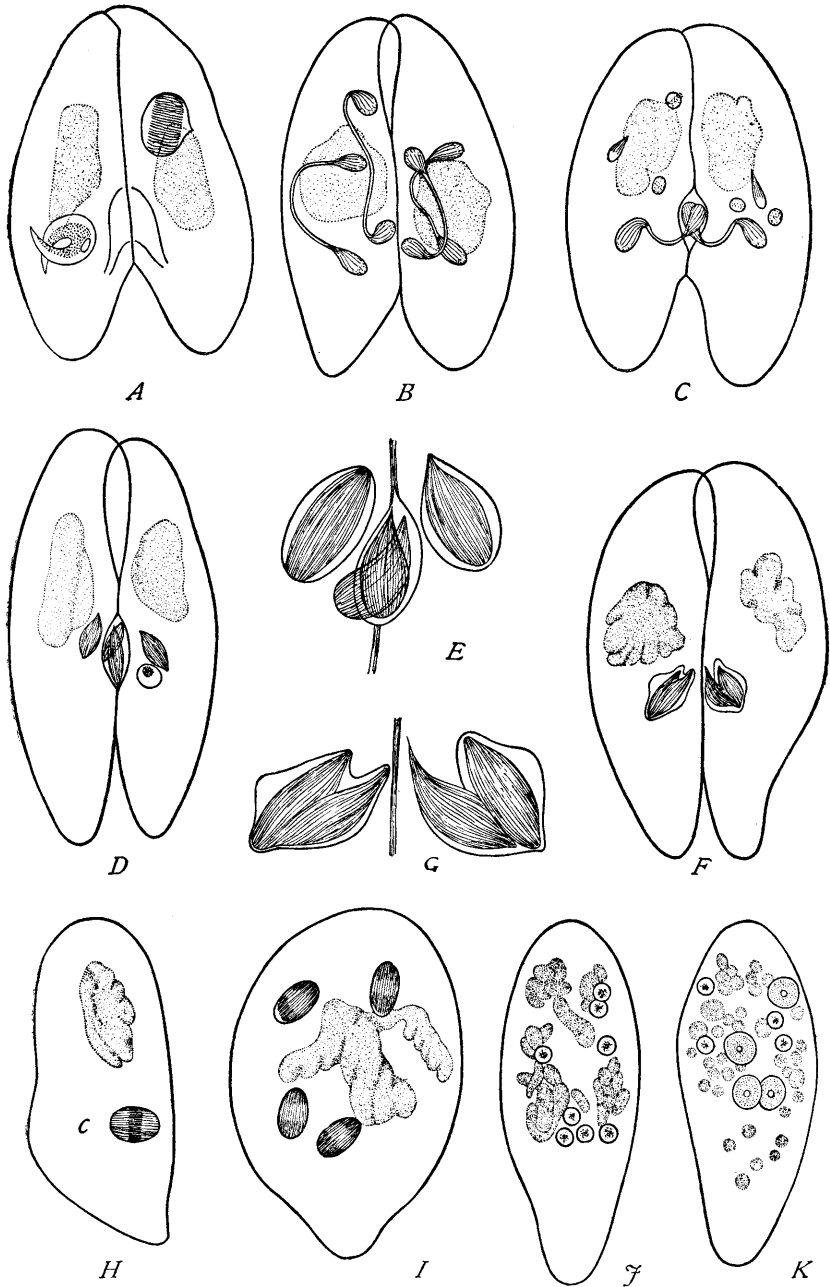


Fig. 110.—Conjugation of *Paramaecium caudatum*. [A–C, after R. HERTWIG; D–K, after MAUPAS.] (The macronuclei dotted in all the figures.)

A. Micronuclei preparing for their first division. B. Second division. C. Third division; three polar bodies or "corpuscules de rebut," and one dividing germ-nucleus in each animal. D. Exchange of the germ-nuclei. E. The same, enlarged. F. Fusion of the germ-nuclei. G. The same, enlarged. H. Cleavage-nucleus, (c) preparing for the first division. I. The cleavage-nucleus has divided twice. J. After three divisions of the cleavage-nucleus; macronucleus breaking up. K. Four of the nuclei enlarging to form new macronuclei. The first fission soon takes place.

times successively, and of the eight resulting bodies four become macronuclei and four micronuclei (Fig. 110, *H-K*). By two succeeding fissions the four macronuclei are then distributed, one to each of the four resulting individuals. In some other species the micronuclei are equally distributed in like manner, but in *P. caudatum* the process is more complicated, since three of them degenerate, and the fourth divides twice to produce four new micronuclei. In either case at the close of the process each of the conjugating individuals

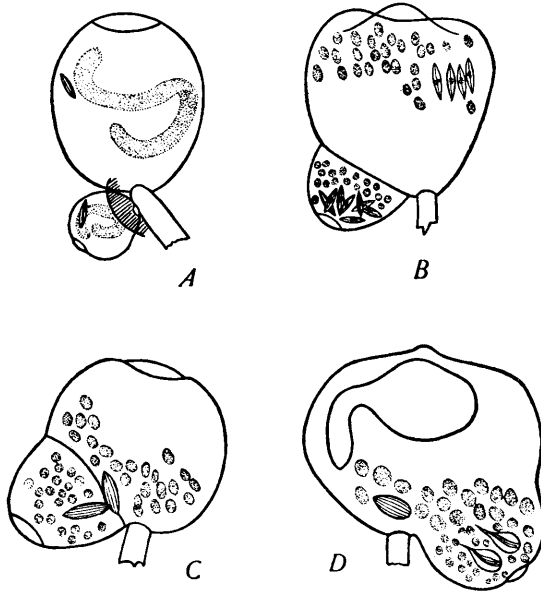


Fig. III. — Conjugation of Vorticellids. [MAUPAS.]

A. Attachment of the small free-swimming microgamete to the large fixed macrogamete; micronucleus dividing in each (*Carchesium*). *B.* Microgamete containing eight micronuclei; macrogamete four (*Vorticella*). *C.* All but one of the micronuclei have degenerated as polar bodies or "corpuscules de rebut." *D.* Each of the micronuclei of the last stage has divided into two to form the germ-nuclei; two of these, one from each gamete, have conjugated to form the cleavage-nucleus seen at the left; the other two, at the right, are degenerating.

has given rise to four descendants, each containing a macronucleus and micronucleus derived from the cleavage-nucleus. From this time forward fission follows fission in the usual manner, both nuclei dividing at each fission, until, after many generations, conjugation recurs.

Essentially similar facts have been observed by Richard Hertwig and Maupas in a large number of forms. In cases of permanent conjugation, as in *Vorticella*, where a smaller *microgamete* unites with a larger *macrogamete*, the process is essentially the same, though the details are still more complex. Here the germ-nucleus derived from each gamete is in the macrogamete one-fourth and in the microgamete

one-eighth of the original micronucleus (Fig. 111). Each germ-nucleus divides into two, as usual, but one of the products of each degenerates, and the two remaining pronuclei conjugate to form a cleavage-nucleus.

The facts just described show a very close parallel to those observed in the maturation and fertilization of the egg. In both cases there is a union of two similar nuclei to form a cleavage-nucleus or its equivalent, equally derived from both gametes, and this is the progenitor of all the nuclei of the daughter-cells arising by subsequent divisions. In both cases, moreover (if we confine the comparison to the egg), the original nucleus does not conjugate with its fellow until it has by division produced a number of other nuclei all but one of which degenerate. Maupas does not hesitate to compare

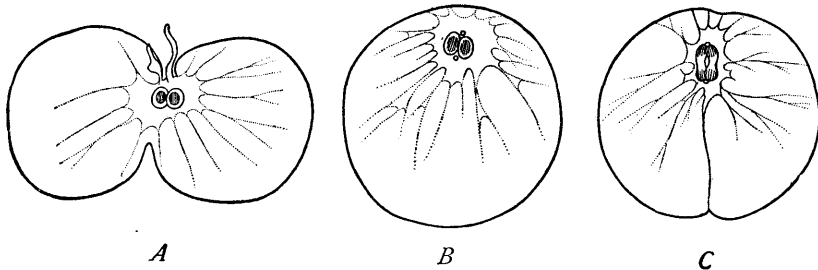


FIG. 112. — Conjugation of *Noctiluca*. [ISHIKAWA.]

A. Union of the gametes, apposition of the nuclei. *B.* Complete fusion of the gametes. Above and below the apposed nuclei are the centrosomes. *C.* Cleavage-spindle, consisting of two separate halves.

these degenerating nuclei or “corpuscules de rebut” with the polar bodies (p. 181), and it is a remarkable coincidence that their number, like that of the polar bodies, is often three, though this is not always the case.

A remarkable peculiarity in the conjugation of the Infusoria is the fact that *the germ-nuclei unite when in the form of spindles or mitotic figures*. These spindles consist of achromatic fibres, or “archoplasm,” and chromosomes, but no asters or undoubted centrosomes have been thus far seen in them. During union the spindles join side by side (Fig. 110, *G*), and this gives good reason to believe that the chromatin of the two gametes is equally distributed to the daughter-nuclei as in Metazoa. In the conjugation of some other Protozoa the nuclei unite while in the resting state; but very little is known of the process save in the cystoflagellate *Noctiluca*, which has been studied with some care by Cienkowsky and Ishikawa (Fig. 112). Here the conjugating animals completely fuse, but the nuclei are merely apposed and give rise each to one-half of

the mitotic figure. At either pole of the spindle is a centrosome, the origin of which remains undetermined.

It is an interesting fact that in *Noctiluca*, in the gregarines, and probably in some other Protozoa, conjugation is followed by a very rapid multiplication of the nucleus followed, by a corresponding division of the cell-body to form "spores," which remain for a time closely aggregated before their liberation. The resemblance of this

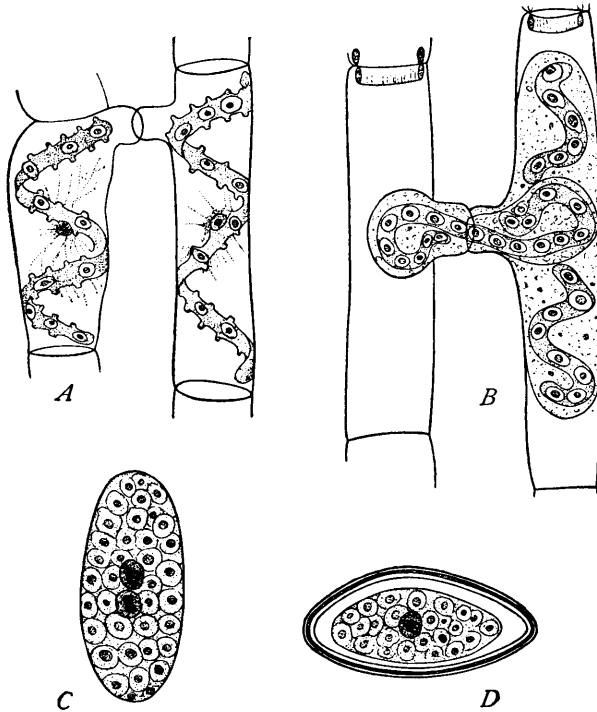


Fig. 113.—Conjugation of *Spirogyra*. [OVERTON.]

A. Union of the conjugating cells (*S. communis*). B. The typical, though not invariable, mode of fusion in *S. Weberi*; the chromatophore of the "female" cell breaks in the middle, while that of the "male" cell passes into the interval. C. The resulting zygospore filled with pyrenoids, before union of the nuclei. D. Zygospore after fusion of the nuclei and formation of the membrane.

process to the fertilization and subsequent cleavage of the ovum is particularly striking.

The conjugation of unicellular plants shows some interesting features. Here the conjugating cells completely fuse to form a "zygospore" (Figs. 113, 140), which as a rule becomes surrounded by a thick membrane, and, unlike the animal conjugate, may long remain in a quiescent state before division. Not only do the nuclei

unite, but in many cases the plastids also (chromatophores). In *Spirogyra* some interesting variations in this regard have been observed. In some species De Bary has observed that the long band-shaped chromatophores unite end to end so that in the zygote the paternal and maternal chromatophores lie at opposite ends. In *S. Weberi*, on the other hand, Overton has found that the single maternal chromatophore breaks in two in the middle and the paternal chromatophore is interpolated between the two halves, so as to lie in the middle of the zygote (Fig. 113). It follows from this, as De Vries has pointed out, that the origin of the chromatophores in the daughter-cells differs in the two species, for in the former case one receives a maternal, the other a paternal, chromatophore, while in the latter, the chromatophore of each daughter-cell is equally derived from those of the two gametes. The final result is, however, the same; for, in both cases, the chromatophore of the zygote divides in the middle at each ensuing division. In the first case, therefore, the maternal chromatophore passes into one, the paternal into the other, of the daughter-cells. In the second case the same result is effected by two succeeding divisions, the two middle-cells of the four-celled band receiving paternal, the two end-cells maternal, chromatophores. In the case of a *Spirogyra* filament having a single chromatophore it is therefore "wholly immaterial whether the individual cells receive the chlorophyll-band from the father or the mother" (De Vries).¹

F. SUMMARY AND CONCLUSION

All forms of fertilization involve a conjugation of cells by a process that is the exact converse of cell-division. In the lowest forms, such as the unicellular algæ, the conjugating cells are, in a morphological sense, precisely equivalent, and conjugation takes place between corresponding elements, nucleus uniting with nucleus, cell-body with cell-body, and even, in some cases, plastid with plastid. Whether this is true of the centrosomes is not known, but in the Infusoria there is a conjugation of the achromatic spindles which certainly points to a union of the centrosomes or their equivalents. As we rise in the scale, the conjugating cells diverge more and more, until in the higher plants and animals they differ widely not only in form and size, but also in their internal structure, and to such an extent that they are no longer equivalent either morphologically or physiologically. Both in animals and in plants the paternal germ-

¹ De Vries's conclusion is, however, not entirely certain; for it is impossible to determine, save by analogy, whether the chromatophores maintain their individuality in the zygote.

cell loses most of its cytoplasm, the main bulk of which, and hence the main body of the embryo, is now supplied by the egg; and in the higher plants, the egg alone retains the plastids which are thus supplied by the mother alone. On the other hand, the paternal germ-cell is the carrier of something which incites the egg to development, and thus constitutes the fertilizing element in the narrower sense. There is strong ground for the conclusion that in the animal spermatozoön this element is, if not an actual centrosome, a body or a substance directly derived from a centrosome of the parent body and contained in the middle-piece. Boveri's theory, according to which fertilization consists essentially of the replacement of a missing or degenerating egg-centrosome by the importation of a sperm-centrosome, was stated in too simple and mechanical a form; for the facts of spermatogenesis show conclusively that the spermatid-centrosome is not simply handed on unmodified by the spermatozoön to the egg, and the theory wholly breaks down in the case of the higher plants. But although the theory probably cannot be sustained in its morphological form, it may still contain a large element of truth when recast in physiological terms. Like mitosis, fertilization is perhaps at bottom a chemical process, the stimulus to development being given by a specific chemical substance carried in some cases by an individualized centrosome or one of its morphological products, in other cases by less definitely formed material. In the case of animals, we cannot ignore the historical continuity shown in the origin of the spermatid-centrosomes, the formation of the middle-piece, and the origin of the sperm-centrosomes and sperm-amphiaster in the egg, even though we do not yet know whether the sperm-centrosome is as such imported into the egg. And this chain of phenomena suggests that even in the higher plants, where no centrosomes seem to occur, the fertilizing substance, even if brought into the egg in an unformed state, may still be genetically related to the mitotic apparatus of the preceding division.¹

Through the differentiation between the paternal and germ-cells in the higher forms indicated above, their original morphological equivalence is lost and only the nuclei remain of exactly the same value. This is shown by their history in fertilization, each giving rise to the same number of chromosomes exactly similar in form, size, and staining-reactions, equally distributed by cleavage to the daughter-cells, and probably to all the cells of the body. *We thus find the essential fact of fertilization and sexual reproduction to be a union of equivalent nuclei; and to this all other processes are tributary.*

As regards the most highly differentiated type of fertilization and

¹ Cf. Strasburger's view, p. 221.

development we reach therefore the following conception. From the mother comes in the main the cytoplasm of the embryonic body which is the principal substratum of growth and differentiation. From both parents comes the hereditary basis or chromatin by which these processes are controlled and from which they receive the specific stamp of the race. From the father comes the stimulus inducing the organization of the machinery of mitotic division by which the egg splits up into the elements of the tissues, and by which each of these elements receives its quota of the common heritage of chromatin. Huxley hit the mark two score years ago when in the words that head this chapter he compared the organism to a web of which the warp is derived from the female and the woof from the male. Our principal advance upon this view is the knowledge that this web is probably to be sought in the chromatic substance of the nuclei; and perhaps we shall not push the figure too far if we compare the amphiasier to the loom on which the fabric is woven.

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¹ See also Literature, V., p. 287.

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