lipase by added H_2O_2 was considerably reduced in the presence of catalase, whereas deoxygenated milk sealed under vacuum showed an increase in lipolytic activity over that in control milk. The continuous exposure to sunlight up to 90 minutes reduced its activity approximately 10 per cent. Fat lipolysis in milk is quite often accompanied by the development of bitter flavor, which can be traced primarily to the gravity cream layer of the milk. This could be demonstrated by draining off carefully the gravity skim milk below the cream layer of milk at the end of a 24-hour holding period at 0–5° C., in which lipolysis was stimulated by cooling and warming prior to storage. It indicated that the changes in the chemical properties both of the fat and of the fat-globules-stabilizing membrane could be responsible for the development of the bitter flavor. Not only has the milk-fat-agglutinin concentrate (gravity cream plasma, obtained by the reseparation of gravity cream forewarmed to 37–40° C. in the cream separator, *3*) a tendency to develop bitter flavor on standing at refrigeration temperatures, but the milk fat from very rancid milk is quite often bitter. The compound responsible for the bitter flavor in the fat could be readily extracted by the re-emulsification of the fat in the skim milk.

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The Origin and Evolution of Meiosis[1]

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The question of the relation of mitosis to meiosis has received as much attention, perhaps, as any in biology. The discussion has been focused, for the most part, on the mechanism responsible for the change from one type of nuclear division to the other, and the manner in which meiosis, which made sex and biparental inheritance possible, originated. Certainly, one difficulty in tracing the origin and development of meiosis from mitosis has been the failure to understand clearly the small but fundamental differences in the two processes. And, of course, the assumption by some biologists that the two processes were almost unrelated has not helped toward an understanding of them. Far too little attention has been given to the role of the centriole and the relation, in time, of its duplication to that of the chromosomes, for herein lies the key to an understanding of the manner in which a cell changes from one process to the other.

For many years I have been studying the chromosomes of 40 genera and more than 500 species of hypermastigote and polymastigote flagellates from termites and the wood-feeding roach, *Cryptocercus punctulatus* (*1*). The protozoa of *Cryptocercus* are profoundly influenced by the molting of their host (*2*). Between molts they have the haploid number of chromosomes, and division is mitotic; during molting their chromosome number is doubled, and zygotic meiosis, which follows, returns them to haploids, where they remain until their host molts again. In three genera, *Trichonympha*, *Leptospironympha*, and *Eucomonympha*, the change from haploidy to diploidy is brought about by fertilization; in others, particularly *Saccinobaculus*, it results from the autogamy. In these genera sexual processes similar to those of higher animals and plants have become fairly well established, but not permanently, for sometimes they revert to a more primitive process, such as the one that has become very well established in *Barbulanympha* and several other genera, which process will be described presently.

Of the total number of genera studied there are six which, in my opinion, are particularly important, since they serve to show the manner in which meiosis has arisen from mitosis. Among these, two processes, permanent mitotic diploidy and meiosis without gametogenesis, deserve consideration. They lie between fertilization (including autogamy) on the one hand, and mitosis on the other.

In the first process, which is seen in the genera *Holomastigotoides* and *Spirotrichosoma*, the chromosomes, in certain instances, have become permanently diploid, since these genera have not been able to develop a method for changing back to haploids. In the genus *Holomastigotoides*, which is present in many genera of termites distributed through most of the tropical and semitropical regions of the earth, the haploid number of chromosomes is 2, and most of the species have this number. However, in each of the species of termites that I have examined from the genera *Prorhinotermes*, *Psammotermes*, *Coptotermes*, and *Heterotermes*, diploids have also been present, together with a 3-chromosome form (1n, 2n); and, in *Psammotermes*, there is in addition a 5-chromosome form (2n, 3n). All of these are derived from the basic 2-chromosome form. This polyploidy is not one of recent origin, since, for example, precisely the same forms occur in widely separated species of *Prorhinotermes* (southern Florida, Java, Madagascar), which termites have been separated at least since the beginning of the Tertiary, and probably much longer. *Holomastigotoides*, then, in a few instances, has been able to survive in a permanent diploid condition.

Another example of a similar situation is found in the genus *Spirotrichosoma*, present in three species of *Stolotermes* (a very primitive termite) from Australia, one from South Africa, and one from New Zealand. The haploid number of chromosomes is 12—the number present in all the species of *Spirotrichosoma* from the Australian and South African species of *Stolotermes*. This same number also occurs in the *Spirotrichosoma* from the New Zealand species of *Stolotermes*, but polyploids with 24, 48, and 60 chromosomes are also present. Thus, with a larger number of chromosomes, the difficulty an organism encounters in permanently adapting itself to polyploidy seems to be greatly increased.

Nuclear division of these polyploids can be seen very plainly, especially those with 4 rod-shaped chromosomes. Every division is exactly alike: synapsis in the prophase, followed by formation of tetrads, and movement of the chromosomes to the poles as dyads, *i.e.* every division is exactly like the first division in meiosis. One may ask: Why isn't this followed by a second meiotic division, thus returning the chromosomes to the haploid condition? The answer is simple: the centrioles are

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not duplicated until the chromosomes have also been duplicated, and therefore reduction in chromosome number is impossible. Then, so long as the chromosomes are duplicated every time the centrioles are, diploidy is permanent. The schedule of centriole-chromosome duplication must be changed before reduction can occur.

In the second process, which is termed endomitosis, meiosis occurs, but it is neither preceded nor followed by nuclear fusion. Several genera are involved, not all of which behave in the same manner, but nearly enough so, perhaps, that only one, *Barbulanympha*, need be mentioned. This is an unusually large cell with two interphase centrioles 40–50 μ long and 3–4 μ in width, with centrosomes 5–6 μ in diameter surrounding their distal ends. It is from these ends of the centrioles that the achromatic figure is produced, while the other, or proximal, ends produce new centrioles directly and other extranuclear organelles (flagella, axostyles, and parabasals) indirectly. As a result of molting, these centrioles degenerate and, because of their size, the process may be observed step by step; but before they degenerate each produces a small, new one from its proximal end, just as in each mitotic division. Shortly after the old, or parent, centrioles degenerate, parabasals, axostyles, and flagella begin to do so, the last to disappear being the flagella. Before degeneration of these organelles has progressed very far, two small, new, intracytoplasmic, flagellated areas, produced by the new centrioles, make their appearance adjacent to the nucleus, which at this time lies more or less in the center of the cell, having migrated there together with the new centrioles. There is one new, short centriole underneath each area, and as these become longer and larger, so do the flagellated areas, until finally both are fully grown. Shortly before growth of the flagellated areas is completed, new sets of parabasals and axostyles begin to grow out from their inner margins. Thus, two complete sets of extranuclear organelles arise from the new centrioles and replace the two degenerated sets. The flagella, which are motile throughout their growth period, remain in the cytoplasm until a few hours after the roach sheds its exoskeleton and then are extroverted.

About the time the new flagellated areas begin to develop there is a duplication of the chromosomes, but, since the short, new centrioles, the only ones now present, cannot produce an achromatic figure to move the chromosomes to separate poles, they remain in a single, undivided nucleus, in which they go through all the phases of mitosis. About two days after the new centrioles attain full size, they begin to produce an achromatic figure from their distal ends and, shortly before this takes place, the chromosomes are duplicated again, so that now each chromosome is represented four times. As prophase shortening occurs, synapsis begins, and soon the plainest tetrads I have ever seen are formed. This is followed by the first meiotic division, the chromosomes going to the poles as dyads. Then the centrioles are duplicated quickly and produce an achromatic figure which functions in the second meiotic division, before duplication of the chromosomes can occur, the chromosomes, of course, going to the poles singly.

Ordinarily, in mitosis in *Barbulanympha* it is late telophase, frequently after cytoplasmic division, before the new centriole begins to elongate by the side of the old or persisting one; but by the first meiotic metaphase growth has already begun, and by late anaphase or early telophase it is almost complete. It is very easy, then, to see in *Barbulanympha*, where the centrioles are so large, that the mechanism which makes the reduction in chromosome number possible is the speeded-up duplication and function of the centrioles without duplication of the chromosomes. In other words, the centrioles are duplicated between the first and second meiotic divisions while the chromosomes are not, and in this manner the centrioles make up for the

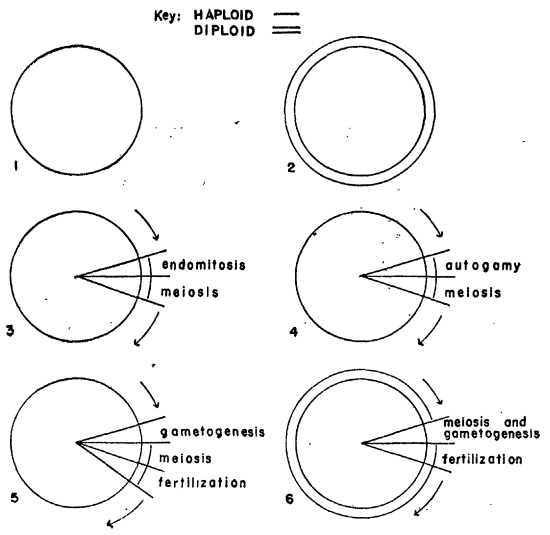

FIG. 1. Progressive stages in the origin and evolution of meiosis. (Each circle represents a life cycle.)

generation which was lost earlier (due to degeneration). In the first meiotic division the centrioles are somewhat ahead of the chromosomes and produce an achromatic figure which is ready to function before the relational coiling of the chromatids has time to come out, and poleward movement as dyads results.

It should be noted that *Barbulanympha* usually behaves in the manner just described, but sometimes the old centrioles produce an achromatic figure before they degenerate. When this happens, nuclear division occurs. The daughter nuclei fuse, and, so far as chromosomes are concerned, the end result is the same as if the nucleus had not divided. This process, termed autogamy, is the usual one in *Urinympha*, although chromosomal duplication without nuclear division also occurs. In these, and other genera too, the type of behavior depends on when a generation of centrioles is lost: if early, duplication of chromosomes without nuclear division results; if late, nuclear division occurs.

The endomitosis of *Barbulanympha* and other genera is closely related to that in several types of cells in insects, reaching its highest development in the multiple, giant chromosomes of the salivary glands of the Diptera. However, insects have developed no workable method of relieving the polyploidy and, because of the instability imposed by such a condition, these cells degenerate, while in *Barbulanympha* polyploidy is always relieved by meiosis, and no degeneration results. Since endomitosis in these protozoa is brought on by the molting fluid of their insect host, similar secretions may be responsible for the production of endomitosis in the tissues of the insects themselves, resulting eventually in degeneration followed by reorganization (metamorphosis).

In gametic meiosis, which precedes fertilization, and in zygotic meiosis, which follows fertilization, centrioles are dup-

licated without a corresponding duplication of the chromosomes, and this extra generation makes up for the one lost at fertilization by one of the gametes (each gamete has two centrioles). Briefly, then, in changing from mitosis to meiosis, the centrioles gain a generation on the chromosomes, and in changing back to mitosis, they lose a generation, although ultimately there are the same number of generations of both.

We see in *Barbulanympha* and *Holomastigotoides* the changes which occurred in the transition from mitosis to meiosis, resulting finally in the formation of gametes. The first step is diploidy, and anything which prevents the centrioles from producing an achromatic figure or the achromatic figure from functioning properly in the movement of chromosomes can bring about a change from haploidy to diploidy. This is as far as *Holomastigotoides* and *Spirotrichosoma* have been able to go. *Barbulanympha* has gone one step beyond these organisms; by throwing the centriole-chromosome duplication schedule out of line, it has evolved a method for changing from haploidy to diploidy and vice versa. The next step is seen in *Saccinobaculus* and *Urinympha*, and sometimes in *Barbulanympha*, where the loss of a generation of centrioles does not usually occur until after the nucleus divides (otherwise the nucleus would not divide). Cytoplasmic division does not occur, the nuclei fuse, the chromosomes are duplicated, and two meiotic divisions change them to haploids. The next and final step occurs in *Trichonympha* and two other genera. The advance is a small but very important one: the cytoplasm divides and thus produces gametes which are free to fuse in any manner.

Evolution of meiosis has been direct: *Holomastigotoides*, haploidy to diploidy; *Barbulanympha*, diploidy to haploidy and vice versa; *Saccinobaculus*, fusion of nuclei; *Trichonympha*, cytoplasmic division producing gametes. In each stage after the first one, the events of the preceding stage are repeated, and one additional step forward is taken. *Trichonympha*, for example, goes through all the stages that the other organisms do and, in addition, produces gametes.

If meiosis, as many observations indicate, serves to relieve the instability of polyploidy—the relief when it is zygotic usually being for a longer period than when it is gametic—one might almost say that biparental inheritance and all the evolution that it has produced resulted because of the particular method which most organisms developed to free themselves from the limitations of permanent polyploidy.

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Are Lake Salmon Hereditarily Distinct?

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Peculiar salmon found in certain lakes of Europe and eastern North America have been considered by taxonomists to be distinct species (e.g. *Salmo sebago, 1*), merely subspecies (e.g. *Salmo salar sebago* and *S. s. ouananiche, 3*), or varieties (e.g. *S. s.* var. *lacustris, 2*) of the ordinary sea salmon.

Similar, supposedly nonmigratory kinds have been found in various other species of *Salmonidae*. Without proof, there should not be unquestioning acceptance of these as being hereditarily distinct kinds rather than the effects of environment on the individuals. The utter lack of published data from experiments to distinguish the effects of heredity and environment and the difficulty of carrying out such experiments should make the following of interest.

At Grand (Shubenacadie) Lake, Nova Scotia, the young from the lake salmon, locally known as "grayling," are reared for planting to get "grayling," and the young of sea-running salmon from the River Philip of northern Nova Scotia are reared for planting to get sea salmon. Grand Lake discharges into Shubenacadie River, which contains sea-running salmon. These evidently spawn in tributaries (entering the river below Grand Lake) which drain a relatively lakeless and arable country in comparison with the rocky country, well provided with lakes, that forms the watershed of Grand Lake. There is no physical barrier to prevent the young of these "grayling" from descending to the sea or the sea salmon from ascending into the lakes, which they may do. Are the differences in appearance, structure, and migration between "grayling" and sea salmon the results of a difference in heredity, which would justify keeping the stocks separate, or are they the results of differences in the conditions they face as they grow up?

In June of both 1944 and 1945, yearling offspring of lake and sea salmon, as reared at Grand Lake, were marked distinctively and planted together in equal numbers in streams in a linear series draining into Grand Lake. This has been a cooperative experiment by the Fisheries Research Board of Canada and the Fish Culture Branch of the Department of Fisheries. Supt. W. H. Cameron reared the salmon and marked them, the "lake" salmon by removal of the adipose and right pelvic, and the "sea" salmon by removal of the adipose and left pelvic fins. The streams planted formed, with intervening lakes all tenanted by lake salmon, an ascending linear series: Grand Lake, lower Rawdon River (½ mile long), Long (Kinsac) Lake, upper Rawdon River (½ mile long), Beaverbank Lake, and Beaver River (1-mile stretch).

Very few survivors were found in September seinings, either from the 9,538 marked yearlings planted in 1944 or from the 9,240 planted in 1945. Although the streams had scarcely any bottom suitable for spawning, native parr of comparable size (yearlings or older) were present and finally predominated over the marked fish, as if they kept possession of the good places in the streams by virtue of being there first. So far as could be judged by September seining, the few parr were in both years mainly in the lower part of Beaver River, but the numbers taken were very small: 1944—9 native, 1 "sea," 1 "lake"; 1945—16 native, 1 "sea," 1 "lake." With higher water they were more numerous in 1945 than in 1944 (more taken with less seining), which afforded a better opportunity to follow their movements.

That they may have descended into the lakes shortly after planting and survived there seems negatived by the facts that (1) five lots of 50 yearlings each when planted in 1945 above traps in branches of the Petitcodiac River, N.B., failed during that season to appear in the traps or to be seined more than 200 yards from the point of planting, and (2) 175 yearlings planted in 1946 above a trap on the lower Rawdon River failed to appear in the trap and yet disappeared utterly so far as seining showed.

With so few survivors even in the first few months of stream