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CHROMOSOMA

Meiosis in *Mesostoma ehrenbergii ehrenbergii* (Turbellaria, Rhabdocoela)

II. Synaptonemal Complexes, Chromosome Pairing and Disjunction in Achiasmate Oogenesis

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Abstract. Female meiosis in *Mesostoma ehrenbergii ehrenbergii* is achiasmate. Electron microscope serial section reconstructions of nuclei from the germarium region of the ovary have shown that synaptonemal complex (SC) is present during the early prophase stages. The greatest amounts present were in two nuclei containing 389 and 401 μ respectively. The reconstructions showed that discontinuities in the SC existed along the lengths of the bivalents in these two nuclei which were taken to represent the maximally paired stage, i.e., pachytene. – Reconstructions of post pachytene nuclei showed that SC was absent from the bivalents and therefore retention of SC until metaphase I is not the mechanism used by this achiasmate species to ensure homologous chromosome segregation. An alternative mechanism for this function is proposed based on observations made on the later stages of meiosis in maturing oocytes.

Introduction

Female meiosis is less frequently investigated than male meiosis mainly because of the technical difficulties involved in studying oogenesis. However, when comparative studies within a species have been made, sex differences in the meiotic process have frequently been observed (e.g., Pastor and Callan, 1952; Fogwill, 1958; Perry and Jones, 1974). In view of the unusual meiosis found in spermatogenesis of *M.e. ehrenbergii* (Oakley and Jones, 1982) oogenesis was also investigated to compare the two meiotic processes in this species.

Preliminary studies on the later stages of the first meiotic division of oogenesis in *M.e. ehrenbergii* suggested that this division is achiasmate (C. Tease, pers. comm.). The phenomenon of achiasmate meiosis is now well known and has been recorded in many phyla (John and Lewis, 1965; White, 1973). In chiasmate meiosis, synaptonemal complex (SC) is almost invari-

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ably associated with the intimate pairing of homologous chromosomes at pachytene which allows crossing over to occur and chiasmata to form. Ultrastructural studies have revealed that SC is also present during prophase I of some but not all cases of achiasmate meiosis, for example, in spermatogenesis of *Bolbe nigra* (Gassner, 1969) and *Panorpa communis* (Welsch, 1973) and in oogenesis of *Bombyx mori* (Rasmussen, 1976) and *Ephestia kuehniella* (Traut, 1977). In some cases the SC, or a modified SC, has been shown to persist in the bivalents until metaphase I and is thought to have taken over the mechanical role of chiasmata in maintaining the homologous association until anaphase I (Gassner, 1969; Rasmussen, 1976).

The extent of SC formation and its duration in the bivalents during oogenesis of *M.e. ehrenbergii* have been studied through electron microscope (EM) serial section reconstructions. The later meiotic stages have been thoroughly reinvestigated by light microscopy (LM) to confirm the achiasmate nature of oogenesis.

Materials and Methods

Laboratory cultures of M.e. ehrenbergii were raised in filtered pond water at a temperature of about 21° C. For EM studies on the ovary, animals were used both before and after the onset of winter egg production (about 4 weeks).

EM Preparation, Serial and Survey Sectioning. This was carried out as described previously, for male meiosis (Oakley and Jones, 1982).

Squash Preparations of Maturing Oocytes from Winter Eggs. Oocytes are released one at a time from the ovary and are surrounded by a large quantity of yolk. They first appear as white immature eggs in the body of the animal as the hard protective shell does not form immediately. In order to study the later stages of meiosis in the maturing winter egg oocytes, animals containing immature eggs were fixed in fresh absolute ethanol:glacial acetic acid (3:1) for at least 30 min. Each egg was then dissected out carefully onto a glass slide and broken open with tungsten wire needles, being careful not to allow the fixative to dry out. A drop of lacto-propionic orcein or iron-mordanted aceto-carmine was placed over the egg and the preparation covered with a watch glass and left for at least 10 min to absorb stain. A coverslip was then gently lowered onto the preparation and the slide viewed under low power to locate the egg nucleus. The preparation was gently squashed, with frequent checks under the microscope to make sure the egg nucleus configuration was not being disrupted. The coverslip was sealed with rubber solution to prevent drying out.

Results

1. Organisation of the Ovary

The ovary is located posterior and ventral to the pharynx on the left side of the animal. It is quite a large structure approximately 250 μ in length. When seen in LM and EM sections it divides naturally into three distinct regions which have been called the germarium, elongate oocyte and oviduct regions (Fig. 1).

The germarium region contains gonial and early meiotic stages. Unlike the testes, the stages occur sequentially with the gonial mitotic divisions at the anterior end of the germarium. There are usually at least two oogonial

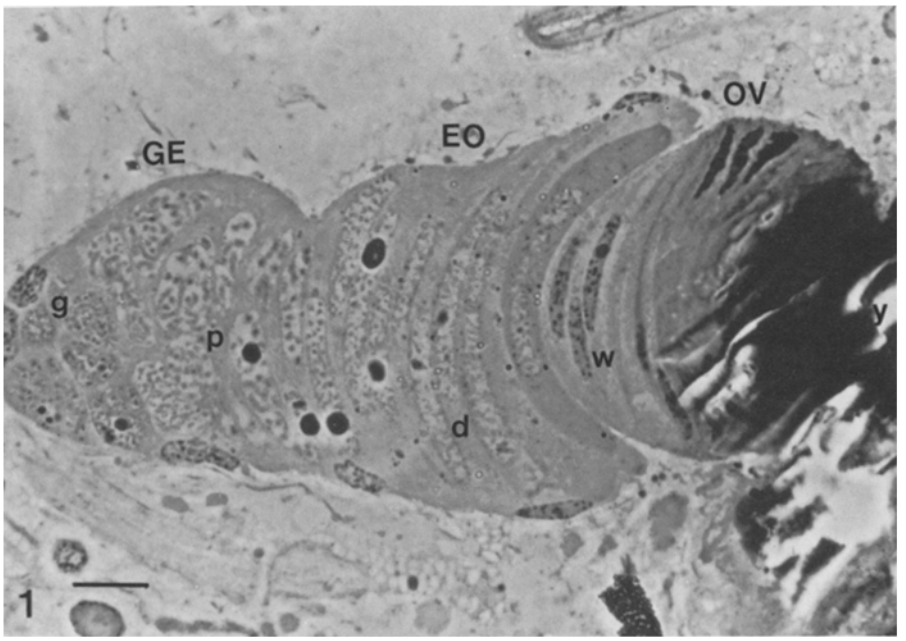


Fig. 1. LM 2 μ epon section of the ovary post stained with 4% Giemsa, pH 8.4. The division into germarium (*GE*), elongate oocyte (*EO*) and oviduct (*OV*) regions can be clearly seen. *g*, gonial and PMI nuclei; *p*, early meiotic nuclei; *d*, diplotene elongate oocytes; *w*, wall cell and oviduct nuclei; *y*, yolk. Bar = 20 μ

cells undergoing mitotic divisions in a germarium. Posterior to the oogonial cells are the premeiotic interphase (PMI) cells. There are three or four of these cells in a germarium and they have nuclei which are similar in EM appearance to PMI nuclei from the testis (see Oakley and Jones, 1982), having a highly invaginated outline, densely staining chromatin and two nucleoli. Progressing down the ovary, the next cells are the early meiotic prophase stages. Leptotene, zygotene and pachytene nuclei have been found in EM survey sections. The chromatin in these early meiotic prophase nuclei resembles that of the male SC (synaptonemal complex) and PC (polycomplex) nuclei in both appearance and distribution throughout the nucleus. All have smooth contours in contrast to the PMI and gonial nuclei.

Leptotene stage nuclei have the characteristics of early meiotic prophase nuclei and are found immediately posterior to the PMI nuclei. However, no clear unpaired axial cores have been found at this stage but the lack of visible axial cores may be due to the diffuse nature of the lateral elements of the SC. Two nucleoli are present. Leptotene nuclei were not found in every germarium studied suggesting that this stage is of short duration.

Up to six nuclei containing SC and representing zygotene and pachytene are found in a germarium. The SC is found throughout each nucleus and is not confined to a specialised region of the nucleus as in male meiosis (Fig. 2). The amount of SC present and the size of the nucleus both increase

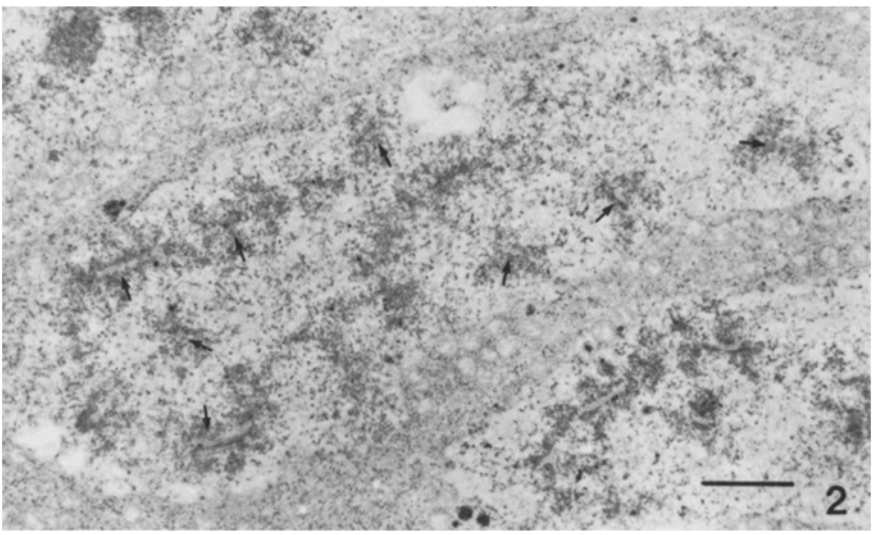


Fig. 2. EM survey section of a zygotene/pachytene nucleus from the germarium region of the ovary. The synaptonemal complex (*arrows*) is well distributed throughout the nucleus. Bar = 2.5 μ

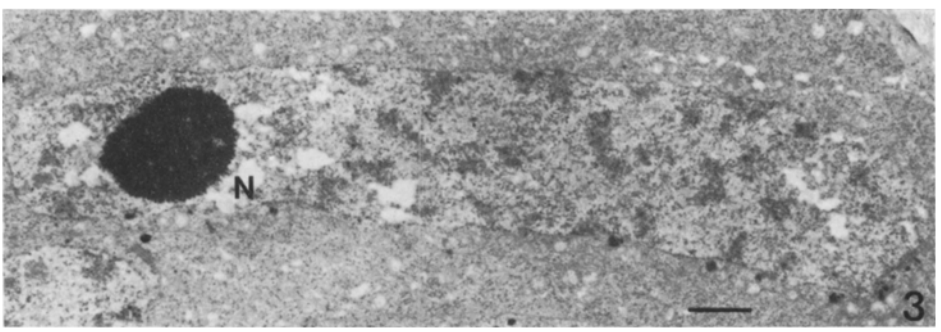


Fig. 3. EM survey section of a young elongate oocyte (close to germarium region). The nuclear outline is smooth and regular. *N*, nucleolus. Bar = 2.5 μ

as the stages progress. The last nucleus in a germarium does not contain SC and is thought to be a postpachytene stage. These nuclei will be more fully described in section 2.

The next region of the ovary contains the elongate oocytes. These cells are large and greatly elongated in a lateral direction. Successive oocytes pass down on opposite sides of the ovary, interdigitating in the centre. The youngest elongate oocytes have a very smooth nuclear outline (Fig. 3), but as these cells progress further down the ovary, the outline becomes increasingly irregular. The most mature elongate oocytes in each ovary, found, just anterior to the oviduct, are less elongated and more spherical in shape (Fig. 4). The elongate oocytes contain no SC and are thought to represent a post-pachytene diffuse stage.

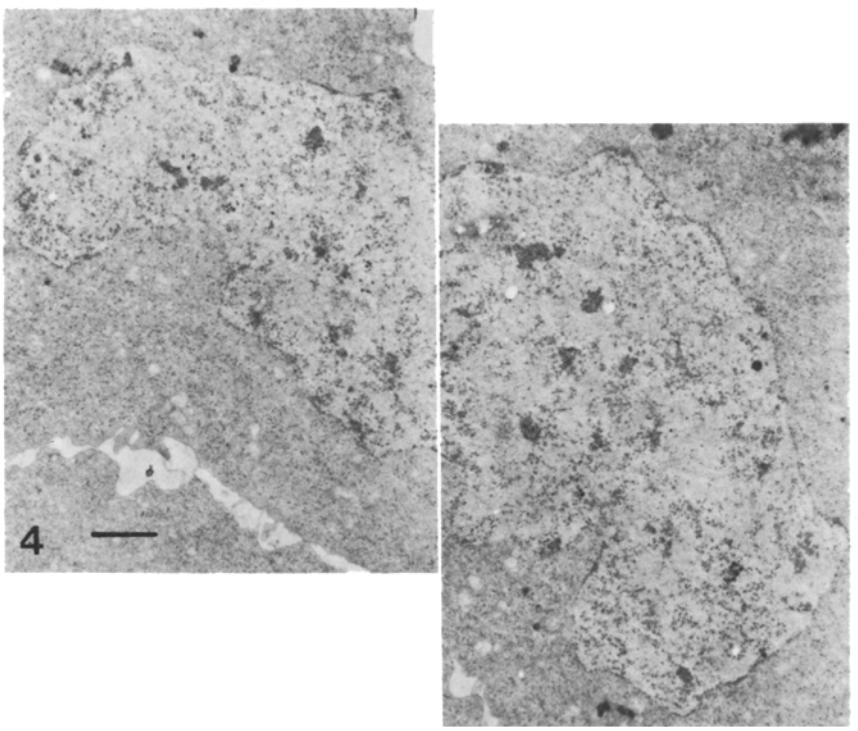


Fig. 4. EM survey section of the most mature elongate oocyte found immediately anterior to the oviduct. This oocyte has an irregular nuclear outline and is less elongated than younger ones. Bar = 2.5 μ

The oviduct comprises the last part of the ovary. The oviduct cell nuclei are small with densely staining chromatin in EM sections, and resemble wall cell nuclei from other parts of the ovary. The oviduct cells form a duct to convey oocytes down to a seminal vesicle for fertilisation. A newly released and fertilised oocyte beginning to collect its yolk cells is often found at the bottom of the oviduct (Fig. 1).

2. Reconstruction Analysis of Oocyte Prophase I Nuclei

Three dimensional reconstructions of entire nuclei from serial EM sections have been made from two ovaries. Ovary 1 had five nuclei containing SC in the germarium and all of these as well as the first elongate oocyte were reconstructed. There were only three nuclei containing SC in ovary 2 and of these the two youngest as well as the most advanced nucleus in the germarium and the second elongate oocyte were reconstructed. The position in the ovaries of the reconstructed nuclei are shown in Figure 5a, b.

The results obtained from the two ovaries have been combined and it was possible to place all the nuclei in sequential order based on position in the germaria and the amount of SC present. It was found generally that the sizes of the nuclei increased as the stages progressed, and this

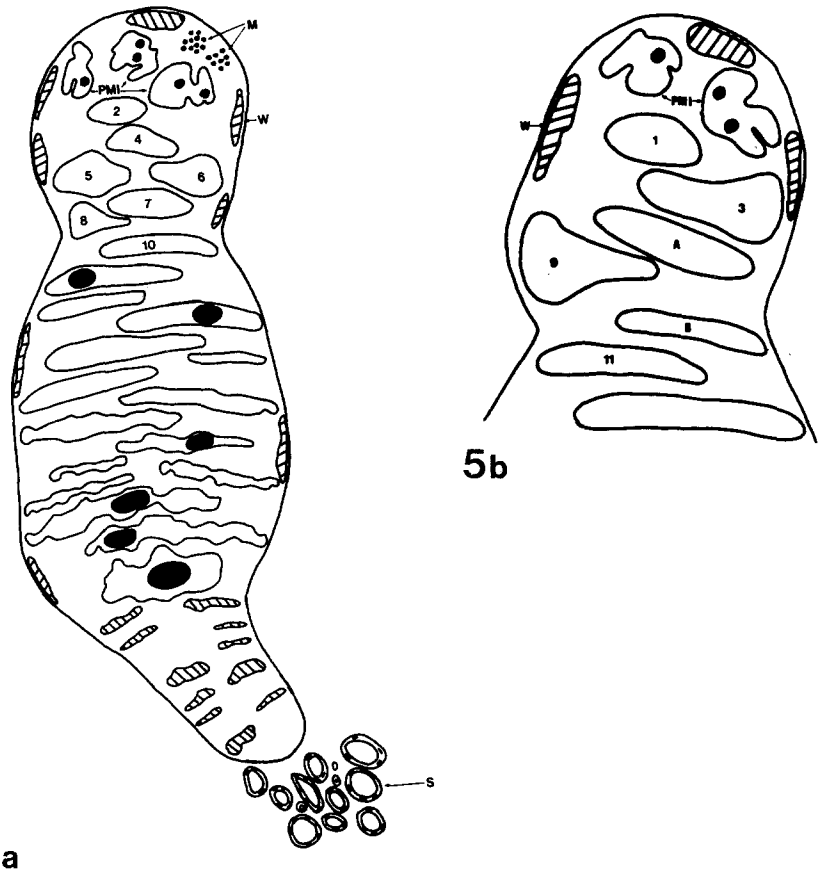


Fig. 5a, b. Diagram of **a** ovary 1 and **b** the germarium of ovary 2 showing the positions of the reconstructed nuclei. In ovary 2, A. is a nucleus containing SC and B is the first elongate oocyte, neither of which were reconstructed. *M*, mitotic divisions; *PMI*, premeiotic interphase nuclei; *w*, wall cell nuclei; *s*, sperm

is expressed by the greatest lateral dimension and the number of sections occupied by each nucleus. A summary of the results from the reconstructions is given in Table 1.

Nuclei 5 and 6 contain the greatest amounts of SC and are taken to represent a pachytene stage when homologous chromosomes are most fully paired. In both of these nuclei long stretches of SC can be joined up although discontinuities are present. The complex is well distributed throughout each nucleus. The distribution of the lengths of SC stretches present in the two pachytene nuclei is shown in Table 2. Both of these nuclei also contain polycomplex, nucleus 5 has one stack and nucleus 6 has two stacks. The reconstruction of ooycte 6 is shown in Figure 6.

Nuclei 1–4 all contain much less SC than nuclei 5 and 6 and are found anterior to them in the germaria. These nuclei are assumed to be in the

Table 1. Summary of the results obtained from oocyte reconstruction studies

Nucleus (from Fig. 5)	Amount SC in μ	Size of nucleus	Probable stage
1	36.76	24 μ 76 sections	Early zygotene
2	63.84	26 μ 96 sections	Zygotene
3	82.43	26.5 μ 113 sections	Zygotene
4	192.3	30.5 μ 105 sections	Zygotene
5	389.25	30 μ 145 sections	Pachytene
6	401.82	28 μ 154 sections	Pachytene
7	187.58	31 μ 171 sections	Late pachytene/early diplotene
8	4.87	–	Diplotene
9	–	28 μ 112 sections	Diplotene
10 11	–	35 μ 178 sections	Diplotene diffuse stage

Table 2. The distribution of the lengths of SC stretches in nuclei 5 and 6

	Lengths of SC stretches				
	>10 μ	5–10 μ	2–5 μ	<2 μ	Total
Nucleus 5	1	11	30	25	67
Nucleus 6	4	10	35	26	75

zygotene stage of prophase when homologous pairing occurs. The amounts of SC in these nuclei range from 36–192 μ showing progressive pairing of the bivalents. SC is found well distributed throughout all the nuclei suggesting that each bivalent contains many synaptic initiation sites rather than pairing proceeding sequentially from one point.

Nucleus 7 contains about half the amount of SC found in nucleus 6 and from its position posterior to the pachytene nuclei is taken to be at the end of the pachytene when the SC is being lost from the bivalents.

Nuclei 8 and 9 are in equivalent positions in the two germaria and are found immediately anterior to the elongate oocyte region. A small remnant of SC is present in nucleus 8, but no SC is found in nucleus 9. These nuclei are probably in diplotene when all SC has been lost from the bivalents.

Nuclei 10 and 11, the two elongate oocytes reconstructed, contain no

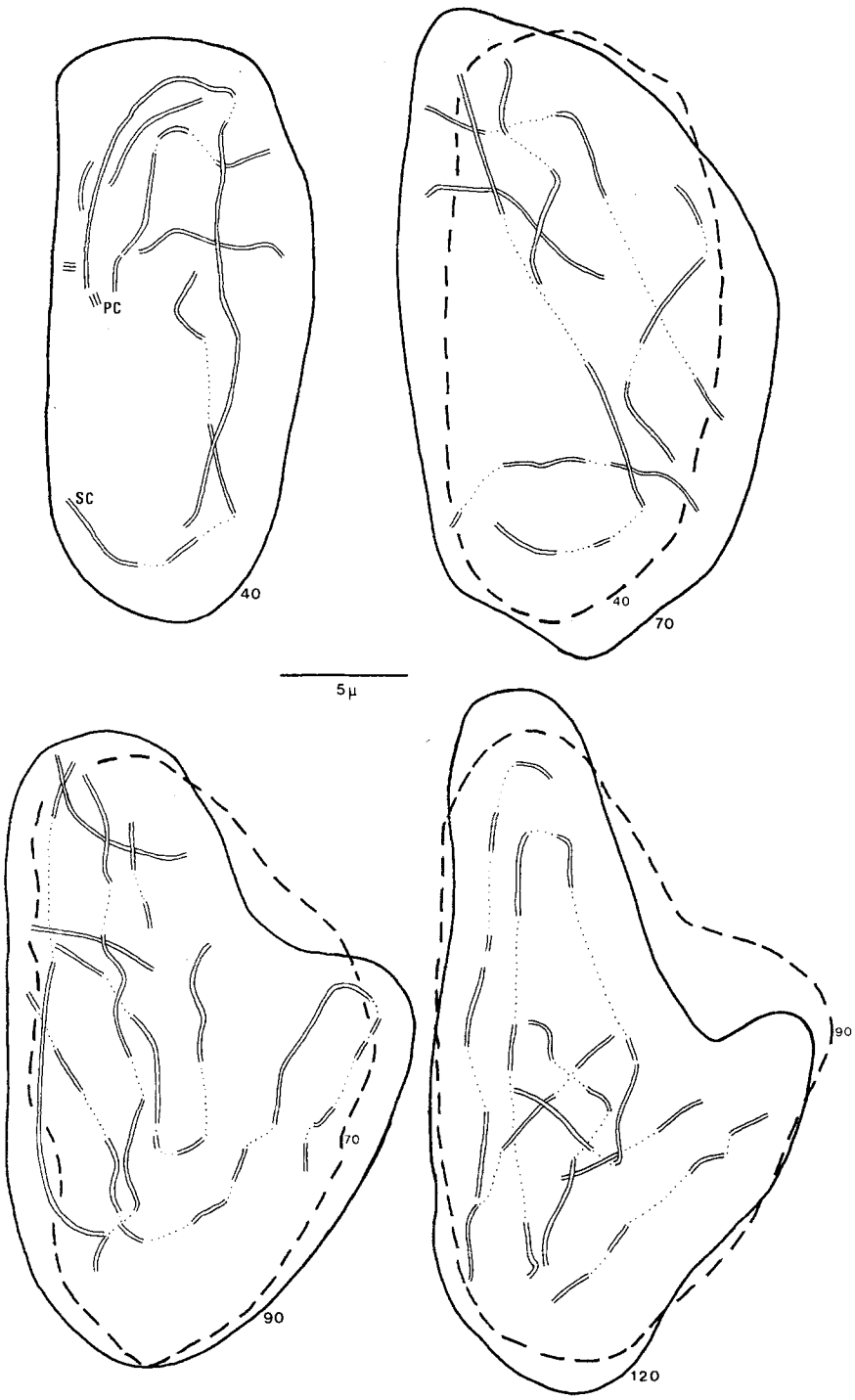


Fig. 6. Reconstruction of nucleus 6. The numbers indicate which section the outlines show. *SC*, synaptonemal complex; *PC*, polycomplex. Dotted lines show possible connections. Bar = 5 μ

SC in either a normal or modified form. These may represent a diplotene diffuse stage. The morphology of all the elongate oocytes is very similar suggesting that they remain at the same stage until released from the ovary.

3. Oocyte Maturation in the Winter Eggs

When the maturing oocytes in the form of winter eggs become visible to the naked eye they appear as white spheres about 1 mm in diameter close to the ovary/pharynx region of the animal. Squash preparations of winter eggs have shown that there are several layers of yolk cells around the oocyte which is recognisable by its large size.

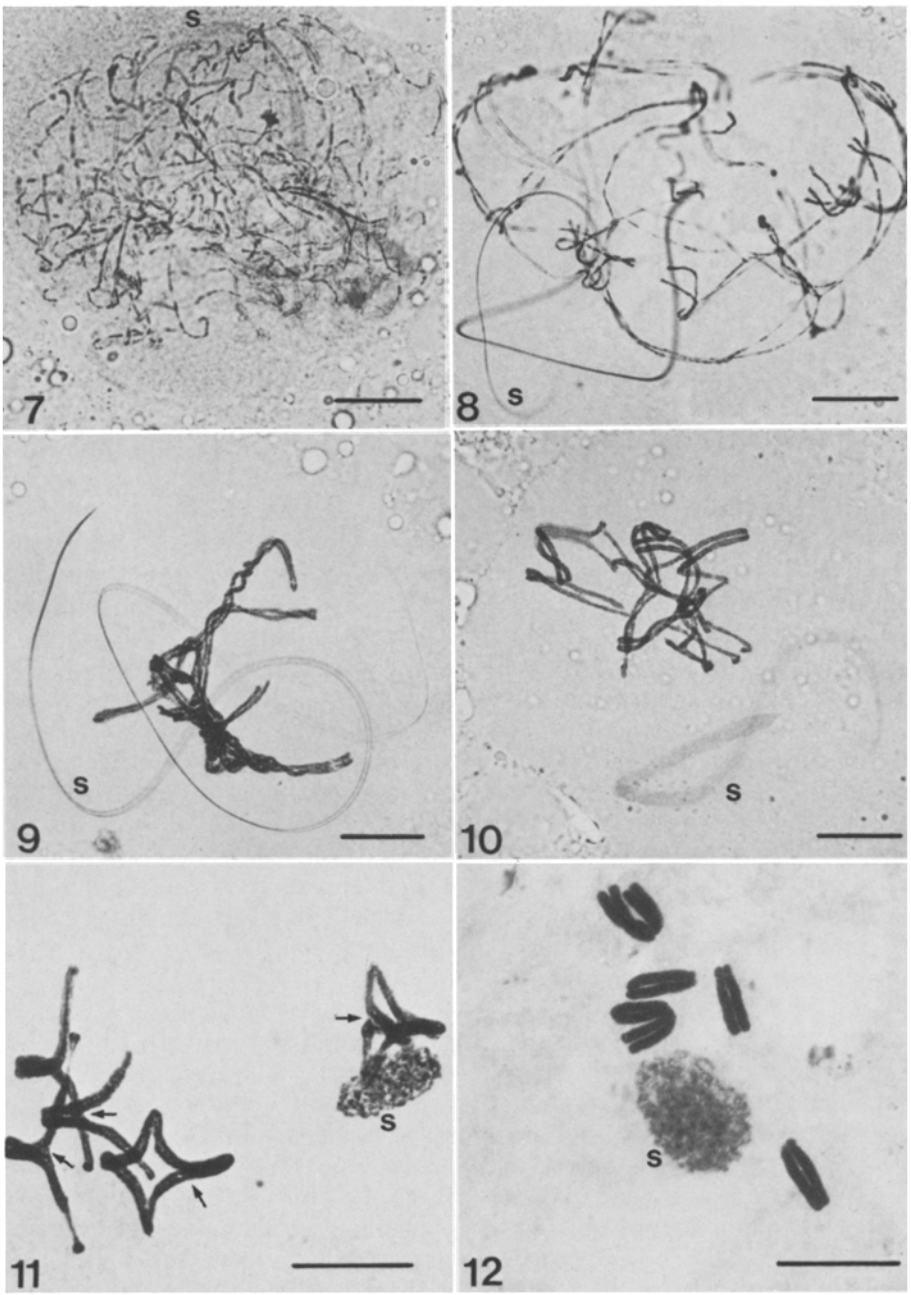
Over 100 maturing winter eggs have been studied. The meiotic stages found in these are all post-synaptic i.e. post-pachytene, but the typical diplotene and diakinesis stages of chiasmate systems are absent. To aid identification arbitrary divisions have been made in the pre-metaphase I part of the sequence and these have been called diplotene stages 1–3 and premetaphase stage.

During the diplotene stages the oocyte chromosomes which initially appear as very long thin threads tangled together gradually condense and become much shorter and thicker. In diplotene stage 1 (Fig. 7) the threads appear single along much of their length, although a doubleness visible in a few places may represent sister chromatids. In diplotene stages 2 and 3 (Figs. 8, 9) it can be clearly seen that each chromosome consists of two sister chromatids. In these stages it is also possible to see that homologous chromosomes are lying parallel and are twisted around one another. No cross connections between the separated parts of the homologues can be seen. All five pairs of chromosomes remain closely associated in a 'knot'. A single large nucleolus is present in diplotene stages 1 and 2, but has broken down before diplotene stage 3 is reached. In all the diplotene stages the sperm nucleus is present as a long thin thread curled around the oocyte chromosomes.

In the premetaphase stage the chromosomes have condensed still further and it is possible to trace all five pairs although they are still associated in a knot (Fig. 10). Homologues are still twisted around one another but to a much lesser degree than in the previous stages. No physical connections between the separated parts of the homologues are visible. The sperm nucleus is also beginning to condense and appears much thicker and shorter.

Metaphase I is reached between 3.5 and 5 h after the egg first becomes visible. The homologous pairs of chromosomes are now well spread out on a metaphase plate (Fig. 11). No chiasmata are present and separation of homologues to opposite poles has already begun with the centromeres pulling apart. The homologous chromosomes are only associated at one or two places distally and some show a remnant of the homologous twisting present during the premetaphase stages. The sperm nucleus now has an elliptical shape.

The post-metaphase I stages proceed as normal with polar bodies being produced. However, during anaphase I and metaphase II (Fig. 12) the sister



Figs. 7–12. Post pachytene stages of meiosis from squash preparations of winter eggs. *s*, sperm nucleus, bars = 20 μ. **7** Diplotene stage 1. **8** Diplotene stage 2. **9** Diplotene stage 3 showing the twisting of homologous chromosomes. **10** Premetaphase stage. **11** Metaphase I – the homologous chromosomes appear to be associated in localised distal regions (*arrows*). **12** Metaphase II showing the continued close association of sister chromatids at this stage

chromatids of each chromosome remain closely associated along their length which was also observed during these stages in spermatogenesis. The sperm nucleus continues to condense and by anaphase II it can be seen that this now consists of discrete chromosomal threads. At the first cleavage stage which is reached about 8 hours after the egg first appears, two haploid sets of chromosomes are present. After this stage the thick protective shell is fully formed and the egg passes down into the uterus where it is stored.

Discussion

Oocyte Reconstruction Analysis

An attempt has been made to reconstruct the SC stretches to show the complement of bivalents as already done for several species, for example *Locusta migratoria* (Moens, 1969), *Neurospora crassa* (Gillies, 1972) *Zea mays* (Gilles, 1973) and man (Holm and Rasmussen, 1977). However this proved impossible to do for *Mesostoma.* It was possible to join up some fairly long stretches of SC which were lying in the chromatin in the pachytene nuclei, but both the SC and chromatin were discontinuous. This resulted in gaps between the stretches of SC with no clear indication of which stretch of SC joined to which, as shown in Figure 6 and Table 2. A similar discontinuous pattern has been found in *Pales ferruginea* spermatocytes (Fuge, 1979). In this case, the explanation offered was that the bivalents were only partially synapsed at intervals along their lengths at pachytene. This may also be the case in *M.e. ehrenbergii* and the gaps found in the reconstructions may represent real discontinuities of the SC. Alternatively, it may be that by chance a full pachytene stage is absent from the two germaria studied. This, however, is unlikely. Pachytene is usually of long duration (Rhoades, 1961) and this stage appears to be of reasonably long duration in the testis of *M.e. ehrenbergii* as many nuclei in this stage were found. It would be expected, therefore, that at least one nucleus in this stage would be present in a germarium even though these do not contain many nuclei. In the only other complete reconstruction made of an ovary, Carpenter (1975) found that 11 of 13 oocyte nuclei in the germarium of a *Drosophila melanogaster* ovariole were in pachytene. This suggests that a full pachytene in the germarium of *M.e. ehrenbergii* would have to be of unusually short duration for one not to be found in the reconstructed germaria.

As already suggested, synapsis in *M.e. ehrenbergii* may be through multiple initiation sites as in *Lilium longiflorum* (Moens, 1968; Holm, 1977) and in *Pales ferruginea* (Fuge, 1979). Each stretch of SC found at pachytene may represent the extent of pairing from one initiation site and the longer stretches of SC in the reconstruction may show areas where SCs from two or more initiation sites have joined up.

A comparison has been made with the total amount of SC found in pachytene nuclei of other species known to have fully paired bivalents (see

Table 3. Amount of SC present at pachytene in species with fully paired bivalents

Species and sex	Amount of SC in μm	Reference
Schizophyllum commune	29	Carmi et al., 1978
Neurospora crassa	45	Gillies, 1972
Gricetulus griseus ♂	153	Moses et al., 1977
Bombyx mori ♀	212	Rasmussen, 1976
Homo sapiens ♂	231	Holm and Rasmussen, 1977
Locusta migratoria ♂	314	Moens, 1973
Zea mays PMCs	353.2	Gillies, 1973
Stethophyma grossum ♀	377.7	Wallace, 1980

Table 3). The amount of SC found in pachytene nuclei of *M.e. ehrenbergii* is greater than that found in most of the fully paired species, and is similar to the amount present in *S. grossum* oocytes which are also fully paired and have a large genome size (Wallace, 1980). This suggests that the bivalents are substantially paired in *M.e. ehrenbergii* oocytes and that any gaps or discontinuities in pairing are relatively short.

In the reconstructed nuclei, polycomplex is found only in the pachytene nuclei when the bivalents are maximally paired. Stacks of polycomplex have occasionally been found in survey sections of elongate oocytes. The presence of polycomplex at the pachytene stage of pairing rather than at diplotene when SC is being discarded from the bivalents, may be due to crystallisation of excess SC subunits which are not required for pairing. Polycomplex found in the elongate oocytes is more likely to be the result of discarded SC subunits associating together, as proposed for its appearance in diplotene nuclei of other organisms (Roth, 1966; Dudley, 1973). SC is lost very quickly from the bivalents after pachytene in *M.e. ehrenbergii* oocytes as shown by the absence of many nuclei with intermediate amounts of SC in the post pachytene part of the germarium. The nuclei may be very efficient in breaking down the SC as it is released and not have to store it as polycomplex, or it may be held in a form not visible in EM sections and only occasionally associating to produce polycomplex, otherwise it might be expected that the immediate postpachytene nuclei would contain large quantities of polycomplex.

Oocyte Maturation in the Winter Eggs

This study of the later meiotic stages in the winter eggs shows conclusively that oogenesis is achiasmate. Drawings made by von Voss (1914) from sectioned summer eggs show that he found very similar stages to those described here. Thus the division stages of both summer and winter eggs of *M.e. ehrenbergii* appear to be the same.

As stated in the Introduction some achiasmate systems retain the SC until metaphase I, and in these cases it is proposed that the SC takes over the function of bivalent maintenance normally carried out by the chiasmata.

However, SC does not seem to be retained in the bivalents of *M.e. ehrenbergii* oogenesis. No trace of SC could be found in post-pachytene oocytes in EM sections. It is possible that the SC may be retained in a modified form, which is unrecognisable as SC in EM sections, but this seems unlikely as no organised structure was visible in the chromatin of the post pachytene oocytes which could conceivably perform this role. It is also possible that the SC could be reassembled from its molecular components just prior to metaphase I but this is considered unlikely. The wide separation of homologous chromosomes without visible connections for much of their length during the condensation of the chromosomes in the winter egg also suggests that no synaptic structure of the type found in *Bolbe nigra* (Gassner, 1969) or *Bombyx mori* (Rasmussen, 1976) is present between homologues after pachytene.

It is noticeable that homologous chromosomes lie parallel to and twist around one another in the diplotene stages. The twisting is more pronounced than that found in chiasmate systems at equivalent stages. The number of twists decreases as meiosis proceeds until at metaphase I only a remnant of twisting remains distally. In addition, some metaphase I bivalents have configurations consistent with the homologues being physically joined in one or two very short, localised regions in the distal parts of the bivalents. These localised physical connections between the homologues may be established while they are joined by SC or at a later stage possibly at points where the homologues are brought into contact by twisting. Ultrasturcutral studies on maturing oocyte nuclei are required in order to confirm the existence of physical connections between homologues and to clarify their nature. Because the homologues are only joined at a few points, separation begins as soon as the bivalents become orientated onto poleward pulling spindle fibres. As the homologous chromosomes are pulled apart during the segregation phase, any physical connections between them are broken and the twists are resolved distally.

A similar twisting of homologous chromosomes during late prophase and prometaphase has been observed in the achiasmate spermatogenesis of *Sphaerium corneum* (Keyl, 1956) and *Callimantis antillarum* (White, 1938). In the latter species a precocious separation of homologues similar to that described here also occurred. No EM studies have been carried out on either of these organisms so the extent of SC formation and whether or not it is retained in post pachytene nuclei is not known.

In normal chiasmate systems, sister chromatids spread apart after metaphase I and are joined only at the centromere (John and Lewis, 1965; White, 1973). In *M.e. ehrenbergii* the sister chromatids in both male and female meiosis remain closely associated until anaphase II. Maguire (1974) proposed that the sister chromatid cohesiveness displayed until metaphase I in chiasmate systems is necessary for chiasma maintenance which in turn is required for the correct disjunction of homologues at anaphase I. When normal disjunction occurs at anaphase I the sister chromatid cohesiveness breaks down, releasing the chiasmate association between the homologues. Maguire (1978) has proposed that sister chromatid cohesiveness may be a function of the SC, and EM studies on metaphase I chromosomes of

Locusta and *Chloealtis* have revealed the presence of SC-like material lying between sister chromatids (Moens and Church, 1979).

The phenomenon of sister chromatid cohesiveness remaining through anaphase I and metaphase II has been reported from other achiasmate systems e.g. *Drosophila pseudo-obscura* spermatogenesis (Darlington, 1934), *Phryne fenestralis* spermatogenesis (Wolf, 1950) and oogenesis of three species of *Tigrinopus* (Ar-Rushdi, 1963). However, in the achiasmate spermatogenesis of two species of *Hydrachnellae* the sister chromatids are separated as in chiasmate systems (Keyl, 1957). There have been no EM studies on these species so the role of SC in these achiasmate meioses is not known. However, in *M.e. ehrenbergii* oogenesis the continuation of sister chromatid association until anaphase II cannot be explained as a function of SC as no trace of SC was found in post-pachytene oocytes. In this case it may be a modified form of mitotic association of sister chromatids operating during meiosis as suggested by Darlington (1934).

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