SYNAPTINEMAL COMPLEXES IN PRIMARY SPERMATOCYTES OF THE MOUSE: THE EFFECT OF ELEVATED TEMPERATURE AND SOME OBSERVATIONS ON THE STRUCTURE OF THESE COMPLEXES IN CONTROL MATERIAL*

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With 4 Figures in the Text

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Synaptinemal complexes were first seen by Moses (1956) in crayfish and grasshopper and almost simultaneously reported by Fawcett (1956) in pigeon, cat and man. The subject has recently been well reviewed by Kaufmann, Gay and McDonald (1959). According to Moses (1958) the synaptinemal complex, which appears during meiotic prophases in higher animals and plants, consists of "three filamentous elements, parallel, uniformly spaced and arranged in a single plane to form a ribbon. The lateral elements which are symmetrical are usually denser and larger than the central one which is often evanescent... the complex (or 'core') lies embedded in the axis of the chromosome (actually a bivalent ...) and is integral with the surrounding Feulgen-positive material ...". A little later Nebel (1959b) found that the synaptinemal complexes of the mouse are not seriously affected by acute exposures to X-rays (1000 r). In this, the first statistical study, it was shown that in random electron microscope photographs the length of the complexes decreases by 39 per cent between early zygotene and pachytene. A complete tripartite complex was called a "double core". Single cores represent a single lateral component of the complex, obviously corresponding to a univalent chromosome. It was found that the proportion of "singles" decreased from leptotene to pachytene, when pairing reaches a maximum. In agreement with this are the observations of Charard (1959) of single cores in orchids. These he interprets as being the dense osmiophilic regions of univalent chromosomes which later in synapsis form the complete synaptinemal complexes.

In the following year Sotelo and Trujillo-Cenóz (1960) published an extensive study of the morphogenesis of chromosomes in the meiosis of Grillus, Laplatracris and Blaptica. Several new terms were introduced: S.E.T., single elementary thread, corresponds to the single core of Nebel or the single lateral component of the complex of Moses. P.T.G., or primary tripartite group, corresponds to the double core or the synaptinemal complex proper. Sotelo and Trujillo-Cenóz (1960) also showed the medial component of tripartite groups in Blaptica dubia to be double and occasionally multi-stranded in certain regions which are called puffy. These authors observed spermatid nuclei of Blaptica and

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*Grillus* to contain synaptinemal complexes which occurred sometimes singly and sometimes in groups side by side. In the latter case a group of 2 complexes arranged side by side showed only 5 individual tracks due to the apparent fusion of adjacent lateral elements; a group of 3 complexes thus showed only 7 tracks. In contrast to all other authors SOTELO and TRUJILLO-CENÓZ (1960) suggest that a P.T.G., that is, a synaptinemal complex, represents a univalent not a bivalent chromosome.

The present study was undertaken to investigate the occurrence and structure of synaptinemal complexes and the relationship of single and double cores to the pairing of chromosomes. We have traced their origin and disappearance relative to the meiotic stage. Also we have observed the action of elevated temperature on the synaptinemal complexes and by observing the prolonged aftereffect of elevated temperature we were led to appreciate at least one feature of chromosome pairing of which we were not previously aware.

In addition, the findings of WILSON (1959) with the light microscope concerning the effect of heat on chiasma frequency suggested to us the combination of heat treatment and electron microscopic examination of synaptinemal complexes. If after heat treatment the frequency of "singles" should be found greater than in corresponding stages of non-treated material the assumption that the cores are the essential organelles of pairing would be further strengthened.

**A. Materials and Methods**

Twenty C57B1 male mice at least 100 days old were exposed to an environment of 34.5°C and 60 per cent humidity for 761/2 hours. Four control mice were maintained in the usual controlled environment in the animal quarters (22°C, 60% humidity). Sacrifices were made during exposure and at 11, 14, and 19 days after termination of the exposure. The testes were fixed in Dalton's modification of Altman's fixative, embedded in methacrylate (40% ethyl and 60% butyl methacrylate) and sectioned with a Porter-Blum microtome set at 3/40 μ. The sections were stained for 1 hour with 2% uranyl acetate to increase contrast.

In the electron microscope we ascertained the tubular stage of a section by inspecting the spermatids according to the scheme of OAKBERG (1956). For the convenience of the reader a brief chart of the spermatogenic stages as they refer to meiosis in the male mouse is given. Roman numerals indicate stages. Arabic numerals refer to the spermiogenic stage.

<table>
<thead>
<tr>
<th>Roman</th>
<th>Arabic</th>
<th>Pachytene</th>
<th>“Resting” leptotene</th>
<th>Dipl diak</th>
<th>MI, MII</th>
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<tr>
<td>I</td>
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Thus, if the electron microscope section contains stage 8 and 16 spermatids, it is labeled stage VIII and the spermatocytes of the younger generation are by definition in early leptotene.

**B. Observations**

1. **Synopsis**

The findings of this study are summarized in the Table. The figures in this table are of two kinds. Cores/cell is the result of counting all available cores from all sections of meiotic cells cut equatorially or nearly so and dividing the sum by the number of cells used. Values for single cores are expressed as percentages of the total number of cores. One finds the stage VIII-X spermatocytes to contain few thin cores with a ratio of 24% single to 76% double. There is thus a slight