Study of Meiosis in the Chimpanzee, 
*Pan troglodytes troglodytes*  
(Blumenbach 1779)

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Received June 23, 1970

In recent years meiosis in man has been extensively studied (Ford and Hamerton 1956, Darlington and Hague 1962, Böök and Kjessler 1964, Kjessler 1966, Sasaki and Makino 1965, McDermott 1966, McIlree *et al.* 1966a, b, Ford *et al.* 1968, Falek and Chiarelli 1968). Crew and Koller (1932) gave accounts of chiasma frequency at diplotene and metaphase in male and female mice, but their diplotene counts were confined to only one completely analyzed nucleus and an additional 85 randomly selected bivalents. Huskins and Hearne (1936, quoted by Slizynski 1955), who were concerned with the chiasma frequency in relation to tumor susceptibility, made their chiasma counts from mid-diakinesis to metaphase in mice of 22 different strains. Slizynski (1955) studied the frequency and behavior of chiasmata in mice and demonstrated that the distribution of chiasmata per bivalent varied with the genetic constitution of the animal.

Later authors have concentrated more on the problem of whether or not chiasma formation occurs between the X and Y chromosomes in mammals. An apparent chiasma between the heteromorphic sex elements in diakinesis of the Chinese hamster was noted by several investigators (Matthey 1957, Husted, Pollock and Smart 1957, Ohno and Weiler 1962, Fredga and Santesson 1964). Benirschke (1967) has studied the meiotic chromosomes of the North American porcupine, *Erethizon dorsatum* and suggested that chiasma formation occurs between the X and the Y in this species as well. There is disagreement in the interpretation with respect to the homologous areas of the sex elements which are involved in meiotic pairing. Husted *et al.* (1957) stated that these may be the long as well as the short arms, although the most frequent association is between the short arms; while Ohno and Weiler (1962) suggested that the distal two-thirds of the long arms of the X and Y are homologous. Fredga and Santesson (1964), on the other hand, believed that the homologous portions are the short arms of the X and Y. Still another investigator (Utakoji 1966) felt that the distal segment of the long arm of the X is homologous to the short arm of the Y.

So far as we know, the meiotic chromosomes of the chimpanzee, *Pan troglodytes troglodytes* have not been studied before. In the present paper, therefore, we wish to present in some detail the morphological features of its meiotic chromosomes,

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particularly with respect to chiasma formation during early meiosis of autosomal bivalents and to describe the behavior of the sex elements.

**Materials and methods**

The testicular tissue of the chimpanzee, *Pan troglodytes troglodytes* (Blumenbach 1779) for this study was collected from the Delta Primate Center, Covington, Louisiana, upon sacrifice of an adult animal for other reasons. Only one animal could be studied as mature chimpanzees are extremely valuable and rarely come to experimental sacrifice which allows the preparation of meiotic material.

Immediately after removal, the testes were prepared as described elsewhere by Benirschke and Brownhill (1963) for marmoset monkeys. In essence, freshly teased tubules were treated with hypotonic saline at 37°C for approximately 45 minutes. Following fixation and centrifugation, air-dried slide preparations were made as with blood cultures and later stained with carbol fuchsin. Small pieces of testis and a blood sample were cultured to study mitotic chromosomes.

**Results**

The mitotic chromosomes of the chimpanzee have been described by Young et al. (1960), Chu and Bender (1961), Chiarelli (1962), Hamerton et al. (1963), Hsu and Benirschke (1967), and Low and Benirschke (1968). Results from blood and testis cell cultures of this animal gave a diploid number of 48 and karyotypes prepared are in agreement with the findings of the previous authors.

The study of meiotic prophase begins with the leptotene nucleus (Fig. 1A), which is about half the size of a pachytene nucleus. It contains poorly defined chromatin and several heteropycnotic areas, some of which may represent sex chromatin.

It was difficult to find a satisfactory zygotene nucleus which perfectly demonstrated the pairing of homologous chromosomes. However, that homologous chromosomes have paired is clearly shown in the pachytene nucleus illustrated in Figure 1B. The sex vesicle is clearly discerned as the darkly stained, heteropycnotic body.

In the diplotene stage, as demonstrated in Figure 1C, each of the bivalents have separated, the sex vesicle has disappeared and the X and Y chromosome are indistinguishable from the autosomal pairs. At a somewhat earlier diplotene stage (Fig. 3) the shape and size of the sex bivalent is quite distinct. Where X and Y make end-to-end contact a thread-like connection is observed. The autosomal bivalents at this stage are found as thickened, thread-like elements forming chiasmata between the homologues. In Figure 3 the 23 autosomal bivalents have been serially aligned in decreasing order of size; diagrammatic representations, constructed on the basis of the much more distinct microscopic examination of the figures, have been drawn next to each bivalent to show the position and number of the chiasmata. The two longest bivalents contain eight chiasmata each, while the smaller bivalents have at least two chiasmata. None of the bivalents found in this stage contained only one chiasma except those labeled #18 and #23; but in these cases also, as seen by
microscopic inspection, there was an indication of terminalization of one chiasma at the free end.

Figure 1D is at late diakinesis and is karyotyped in Figure 4. The number of chiasmata in each autosomal bivalent has become greatly reduced. The largest bivalent contains four and a few others contain three chiasmata, while the third and the eleventh bivalents appear to have two definite chiasmata and one has already terminalized. Number 15, 20 and 23 contain only one chiasma and the remaining ones possess two chiasmata only. The X and Y at this stage are still associated end-to-end.

Fig. 1. Four different stages of prophase of first meiotic division. A, leptotene stage showing heteropycnotic spots. ×1600. B, pachytene nucleus showing prominent sex vesicle at arrow. ×1600. C, diplotene nucleus. ×1600. D, diakinesis stage showing end-to-end association of X and Y at arrow. ×1200.

The distribution of the number of chiasmata in all bivalents of different cells, starting from diplotene to the metaphase stage, is shown in Table 1. From each stage the five most informative karyograms were selected to determine the number of chiasmata. In diplotene the number of chiasmata varied from 59 to 95, the average number per cell having decreased to 68.4. The maximum number found in
the longest bivalent was eight. Bivalents containing one or two chiasmata were very few. At diakinesis the average number of chiasmata per cell had decreased to 48.75 with a range between 45 to 50. A few of the longer bivalents contained four chiasmata, but the most common number at this stage was two. The incidence of figures demonstrating but one chiasma is also greater at this time than at the earlier stage. At metaphase most of the cells contained between 43 and 46 chiasmata, the average being 44.2. The maximum number of chiasmata found in one bivalent was four and very few had three; most of the bivalents had two chiasmata and three to five had only one.

Table 1, therefore, indicates that in the earlier stages of meiosis the longer bivalents contain larger numbers of chiasmata, but as the prophase advances from diplotene via diakinesis to metaphase, the number of chiasmata decreases at successive stages due to terminalization. These data support those of Slizynski (1955) from observations in the mouse.
Figures 2A and B show first division metaphases in which a distinct notch-like structure is found at the junction of the X and Y element. The morphology of each autosomal bivalent is clearly demonstrated, with the largest and several other bivalents showing three distinct chiasmata and thus giving these elements a "figure-eight" configuration. There are also rod-shaped and cross-shaped small bivalents with one chiasma, while the remaining O-shaped bivalents have only two chiasmata. We did not find a figure adequately displaying the first anaphase stage.

Fig. 3. Serial alignments of chromosomes from one early diplotene nucleus showing autosomal bivalents in approximately decreasing order of size, the sex elements being placed last. The visual interpretation of position and number of chiasmata in each bivalent is drawn at the side. ×2400.

Numerous metaphase figures from the second spermatocytic division are found to show the typical structure of the chromosome at that stage (Fig. 2C). Since they are the ultimate result of the first anaphase division in which the X and Y are separated to two opposite poles, some of the complements contain only the Y while others possess only the X. In order to identify the sex-element we have constructed karyograms of numerous second meiotic metaphases, two of which are illustrated in Figures 5A and 5B.

The second telophase stage is represented in Figure 2D and demonstrates the separation of the chromatin material into two parts and concentration into two poles.
### Table 1. Distribution of chiasmata in the bivalents of cells in different stages of meiosis

<table>
<thead>
<tr>
<th>Stages of meiosis</th>
<th>Cell number</th>
<th>Number of chiasmata</th>
<th>Total no. of chiasmata</th>
<th>Average no. of chiasmata per cell</th>
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<tr>
<td>Diplotene</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(See Fig. 3)</td>
<td>1</td>
<td>XY 2 4 6 2 2 3 2</td>
<td>95</td>
<td>68.5</td>
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<tr>
<td></td>
<td>2</td>
<td>XY 2 12 2 3 1</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>XY 2 11 8 1 1</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>XY 2 9 6 1 1</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>XY 4 8 7 2</td>
<td>59</td>
<td></td>
</tr>
<tr>
<td>Diakinesis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(See Fig. 4)</td>
<td>1</td>
<td>XY 3 14 5 1</td>
<td>50</td>
<td>48.75</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>XY 4 15 1 2</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
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<td>XY 5 10 7 1</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>XY 5 11 7</td>
<td>48</td>
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</tr>
<tr>
<td></td>
<td>5</td>
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<td>45</td>
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<td>Metaphase I</td>
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<tr>
<td>(See Fig. 2A)</td>
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<td>46</td>
<td>44.2</td>
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<td></td>
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<tr>
<td></td>
<td>3</td>
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<tr>
<td></td>
<td>4</td>
<td>XY 3 19 1</td>
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<tr>
<td></td>
<td>5</td>
<td>XY 4 18 1</td>
<td>43</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 4. Karyogram of late diakinesis nucleus with the explanation of number and position of chiasmata in each bivalent. ×2400.
Fig. 5. Second metaphase nuclei. Autosomes are arranged in decreasing order of size and sex chromosome at the end: A is of a female complement with X chromosome. B is of a male cell showing the Y element. ×2800.

Discussion

The study of meiosis in the chimpanzee, *Pan troglodytes troglodytes*, indicates that the mechanisms involved in this species are, in general, the same as those described in man and other mammals. Starting from early leptotene to second telophase we could find each stage represented and describe here, step by step, the process of meiotic division. The leptotene nucleus in our preparations demonstrated diffused heteropycnotic bodies, making it impossible to accurately identify the X and Y elements. Sasaki and Makino (1965) demonstrated in human material at leptotene two distinct heteropycnotic bodies, one being larger than the other and interpreted to be the X and Y. Recently Solari and Tres (1967) claimed that in human material at leptotene, recognition of sex chromosomes is difficult because their heteropycnosis is not fully developed, and that at zygotene, two oval heteropycnotic masses of chromatin of different diameters, either separately or in association, can be observed. In the pachytene nucleus, as in human material, the chimpanzee cell forms the so-called “sex-vesicle”, a fused heteropycnotic mass composed of both X and Y.

While the presence of a chiasma between the end-to-end associating X and Y chromosomes has been demonstrated in the meiotic preparations from the Chinese and European hamsters (Matthey, 1961, Ohno and Weiler 1962, Fredga and San-
tesson, 1964, Utakoji, 1966) and by Benirschke (1967) for the porcupine, none of our figures, either from diplotene, diakinesis or metaphase I, shows the configuration of a terminalized chiasma between end-to-end associating X and Y of the chimpanzee. This is similar to the findings of Böök and Kjessler (1964), Sasaki and Makino (1965), and Kjessler (1966) who failed to detect evidence of real chiasma formation between X and Y in human material.

Ohno and Weiler (1962) have suggested that there may be a correlation between the size of the X and Y chromosome and the presence of chiasmata. The demonstration by Benirschke (1967) of a chiasma between the large X and Y chromosomes of the porcupine supports this hypothesis. In this chimpanzee material, the Y chromosome is the smallest element and this small size might contribute to the visual absence of chiasma formation between the X and Y chromosomes. The study of the number of chiasmata in autosomal bivalents prompted us to consider a possible relationship between the length of a chromosome and its average number of chiasma at a particular meiotic stage. Slizynski (1955) remarked that in the male mouse, chromosome length and the number of chiasmata are relatively proportional. In our material, this direct proportionality between the number of chiasmata and the length of the chromosomes seems to be valid only in diplotene nuclei in which long chromosomes contain eight chiasmata and the short ones have but one or two. However, from diakinesis onward most of the longer and shorter chromosomes contain only two chiasmata and it is, therefore, not possible to make generalizations concerning proportionality.

A detailed account of the number of chiasmata in the autosomal bivalents in different stages of prophase has been given by Slizynski (1955) for the mouse and by Kjessler (1966) for man. Ford and Hamerton (1956) counted the number of chiasmata in three human testes from late-diplotene to mid-diakinesis to ascertain the mean number of chiasmata per cell. They found it to be 55.9 and the range of chiasmata per cell was 50 to 63. In contrast, Kjessler (1966) found the average number of chiasmata per cell in 550 primary spermatocytes from 25 men to be 52.7 ranging from 43 to 64; he also suggested that the discrepancy of the two results may be explained by the differences in the stages of first meiotic division at which the two samples of cells were examined. In comparison with the human material, the chimpanzee studied here contained, from diplotene to diakinesis, 68–48 chiasmata per cell, the average number being 58.5. The number of cells from which our figures were derived was probably too small to suggest that a significant difference exists in this respect between the two species.

### Summary

The meiotic chromosomes of the chimpanzee, *Pan troglodytes troglodytes*, were studied in detail and the different stages of division are depicted. Special attention is given to the chiasma formation in the autosomal bivalents and their fate in the successive stages of the first meiotic division. No chiasma was found between the sex elements X and Y which are associated end-to-end during the course of first spermatocytic division. The average number of chiasmata per cell of the chim-
panzee is of the same order as that of man.

Acknowledgement

Financial support from grant GM 10210, USPH, is gratefully acknowledged. Dr. A. Tiopelle, and his colleagues at Delta Primate Center, Covington, La. kindly provided the material. I am grateful to Dr. K. Benirschke in whose laboratories this study was undertaken.

References


