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Cytological characteristics of chromosome behaviour during female meiosis in *Sphinx ligustri* L. (Sphingidae, Lepidoptera)

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The behaviour of chromosomes was studied in female meiosis of *Sphinx ligustri* L. (Sphingidae, Lepidoptera) by using improved cytological methods. The haploid chromosome number is n = 28. Throughout prophase from pachytene until metaphase I, bivalents consist of two chromosomes aligned in parallel, i.e., meiosis is achiasmatic. All bivalents appear to be homomorphic, thus the ZW bivalent could not be identified. In early vitellogenesis, bivalents begin to associate nonhomologously via telomeres, forming a simple chain consisting of all 28 bivalents. After secondary modifications, a more complex, branched chain is produced. The branched chain configuration of bivalents is retained throughout the time when yolk is produced, and it breaks down during prometaphase. At metaphase I, only short chains are remaining. Based on present knowledge on chromosome behaviour in female meioses in different ovary types, it is suggested that the formation of the nonhomologous associations of bivalents is a prerequisite for karyosome or karyosphere formation, the karyosome being meiotically a resting stage. The effects of nonhomologous associations of bivalents on segregation are discussed.

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Based on the type of ovary, female meioses in insects fall into two groups, each possessing characteristic cytological features (BAUER 1933; BONHAG 1958; MAHOWALD 1972). In females with panoistic ovaries, meiotic prophase is characterized by a long lasting diffuse stage or lamp brush stage, during which the RNA needed for yolk production is synthesized (BIER et al. 1967, 1969). In meroistic ovaries, the RNA needed for yolk production is synthesized in nurse cells, while chromosomes in the oocyte are metabolically relatively inactive (BIER et al. 1967, 1969; TRAUT 1975). In addition, the prophase of meiosis is characterized by the packing of chromosomes into a karyosome (BAUER 1933) or a karyosphere (BAUER 1933; BIER 1965). Within the karyosome, the chromosomes are metabolically inactive.

The meroistic ovary type can be still subdivided. In the polytrophic type, the nurse cells follow the developing oocyte within the ovariole, whereas in the acrotrophic type, all nurse cells are situated in the germarial part of the ovarioles.

The karyosomal organization of chromosomal material during female meiosis of the meroistic ovary type has made it quite difficult to understand chromosome behaviour in these meioses in detail. In 1973, DÄVRING and SUNNER succeeded in describing early meiotic stages before the formation of the karyosome in *Drosophila melanogaster*. They observed that the centromeric regions of pachytene bivalents form a common chromocenter. This observation has been confirmed later by NOKKALA and PURO (1976). In addition, it has been established that in *Drosophila melanogaster*, the chromocenter does not disintegrate until prometaphase I (PURO and NOKKALA 1977). The observation that bivalents are nonhomologously associated during most part of prophase shows that clear differences exist in chromosome behaviour during prophase between male and female meiosis.

In the present study, an attempt is made to elucidate the significance of nonhomologous associations of bivalents for chromosome behaviour in more detail in female meiosis. Methods have been developed, with the aid of which the behaviour of chromosomes can be followed throughout the meiotic prophase in female Lepidoptera. The observations made by TRAUT (1975, 1977) of the presence of nonhomologous associations in lepidopteran female meiosis are confirmed. Based on the beha-

viour of nonhomologous associations during prophase, a suggestion is made for their function, and their effects on segregation are discussed. Present knowledge concerning bivalent structure in Lepidoptera is briefly summarized.

Material and methods.

Larvae of *Sphinx ligustri* L. (Sphingidae, Lepidoptera) were collected from their food plants in late July and early August. The larvae were allowed to pupate outdoors into a mixture of turf and coarse sand. At the beginning of January, the pupae were transferred to + 4°C after being exposed to frost during several weeks. After two weeks' time at + 4°C, the pupae were transferred to room temperature. In these conditions, male meiosis was found after one week, and in female, all stages of prophase I and metaphase I were found in ovaries prepared from individuals at late pupal stage just before eclosion. Adult males and females were eclosed in two weeks.

Both testes and ovaries were prepared in Ringer's solution and fixed in Carnoy 6:3:1 fixative. For male meiosis, slides were made according to the technique described by MURAKAMI and IMAI (1974). For early stages of female meiosis (late pachytene and the formation of bivalent chains), the following method was used. After fixation, the ovaries were transferred into distilled water through a decreasing alcoholic series. Preparation of slides in 45% acetic acid was preceded by softening the material in 0.5% pyronin solution for 10-15 min. The cover slip was removed by carbon dioxide ice method. After a brief rinse in absolute alcohol, the slides were immersed in glacial acetic acid for 25-30 seconds, and were air dried with a hair dryer. Air dried slides were stored in 40°C incubator for at least overnight. For staining, slides were rinsed in Sørensen's phosphate buffer (pH 6.8) for at least 5 min, and subsequently treated with trypsin (2000 E/g, Merck) solution containing 200 mg of trypsin in 100 ml of Sørensen's buffer (pH 6.8). This step is essential for the prevention of cytoplasmic staining. The trypsin solution was rinsed off with Sørensen's buffer (pH 6.8) for 2 x 5 min. Slides were eventually stained in 10% Giemsa in Sørensen's buffer (pH 6.8) for 10 min, followed by a rinse in distilled water and air drying with a hair dryer. The air dried slides were embedded in Entellan.

For late prophase and metaphase I stages in female meiosis, the method developed for studying female meiosis in *Drosophila melanogaster* described by PURO and NOKKALA (1977) was used with the following modification. Before Giemsa staining, the trypsin treatment described above was performed to prevent cytoplasmic staining.

Results

The ovary of *Sphinx ligustri* consists of four ovarioles, and one developing egg follicle contains seven nurse cells in addition to the oocyte. At pachytene, the oocytes and nurse cells can be distinguished in oocyte – nurse cells clusters. Oocyte nuclei at this stage reveal twenty-eight bivalents which are evenly scattered within the nucleus (Fig. 1). All bivalents are homomorphic, and hence the ZW bivalent can not be recognized. Only the bivalent carrying nucleolar organizing region can be identified. During the subsequent stage when yolk production in developing egg chambers has just begun, short chains of bivalents appear in the nuclei (Fig. 2). The chains may include branching points (Fig. 3). The lengthening of chains then follows (Fig. 3-4), resulting in all bivalents being included in one branched chain (Fig. 5). All connections within the chain are found between nonhomologous telomeres. The connections are so firm that even if the nucleus is broken by squashing, all bivalents remain in the chain. The bivalents appear in the branched chain during the time when yolk is produced (Fig. 6 and 7). Typical of the chain is that telomeres do not touch each other but an unstained gap remains between two telomeres. Apparently, the branched chain configuration of bivalents obtained during late vitellogenesis (e.g., Fig. 6-7) is a modification product of a more simple chain configuration (e.g., Fig 4). Concurrently with yolk production, the size of the oocyte nucleus is increased enormously, reaching its maximum at the time when nurse cells are degenerating (Fig 8 and 9). Within the nucleus, the branched chain of twenty-eight bivalents can be observed forming a so-called karyosphere, and the giant sized nucleolus is also apparent. Subsequently, the nucleolus breaks down, resulting in the appearance of numerous spherical bodies within the oocyte nucleus (Fig. 10 and 11). The chain of twenty-eight bivalents is still intact during this stage and will not break down until prometaphase. At early prometaphase (Fig. 12 and 13), only few separate bivalents can be observed near poles, while most bivalents are still associated in the chain. The nuclear material stands out from the yolk still at

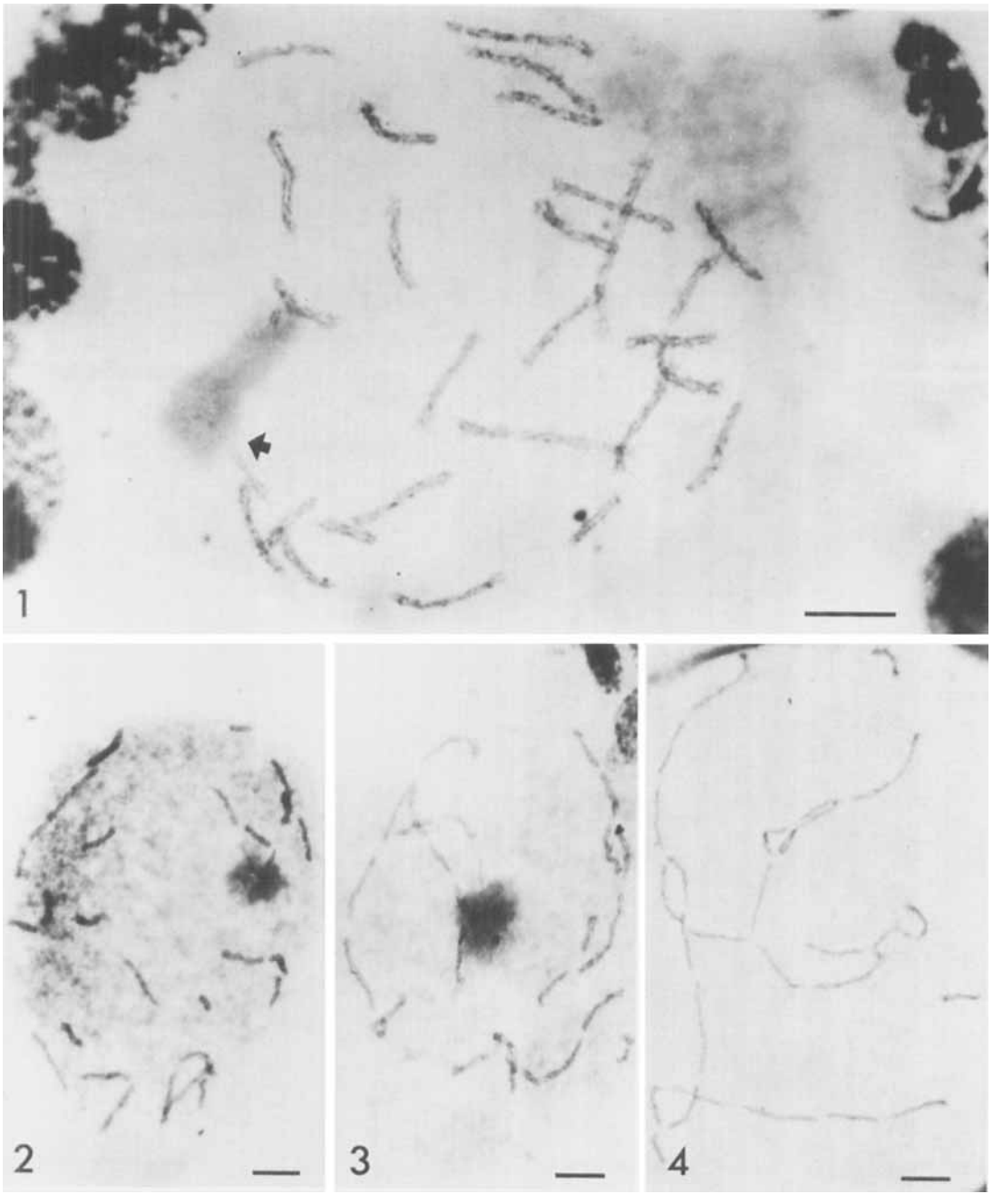


Fig. 1–4. Chromosomes at pachytene in female *Sphinx ligustri*. Pyronin method. **Fig. 1.** A pachytene nucleus showing 28 homomorphic bivalents. Only the bivalent carrying NOR is identifiable (arrow). **Fig. 2.** An oocyte nucleus at early vitellogenesis, showing short chains of bivalents. **Fig. 3.** An oocyte nucleus at early vitellogenesis. The chain is lengthening. **Fig. 4.** An oocyte nucleus at early vitellogenesis. Almost all bivalents are now included in the same, branched chain. (Bar=10μm).

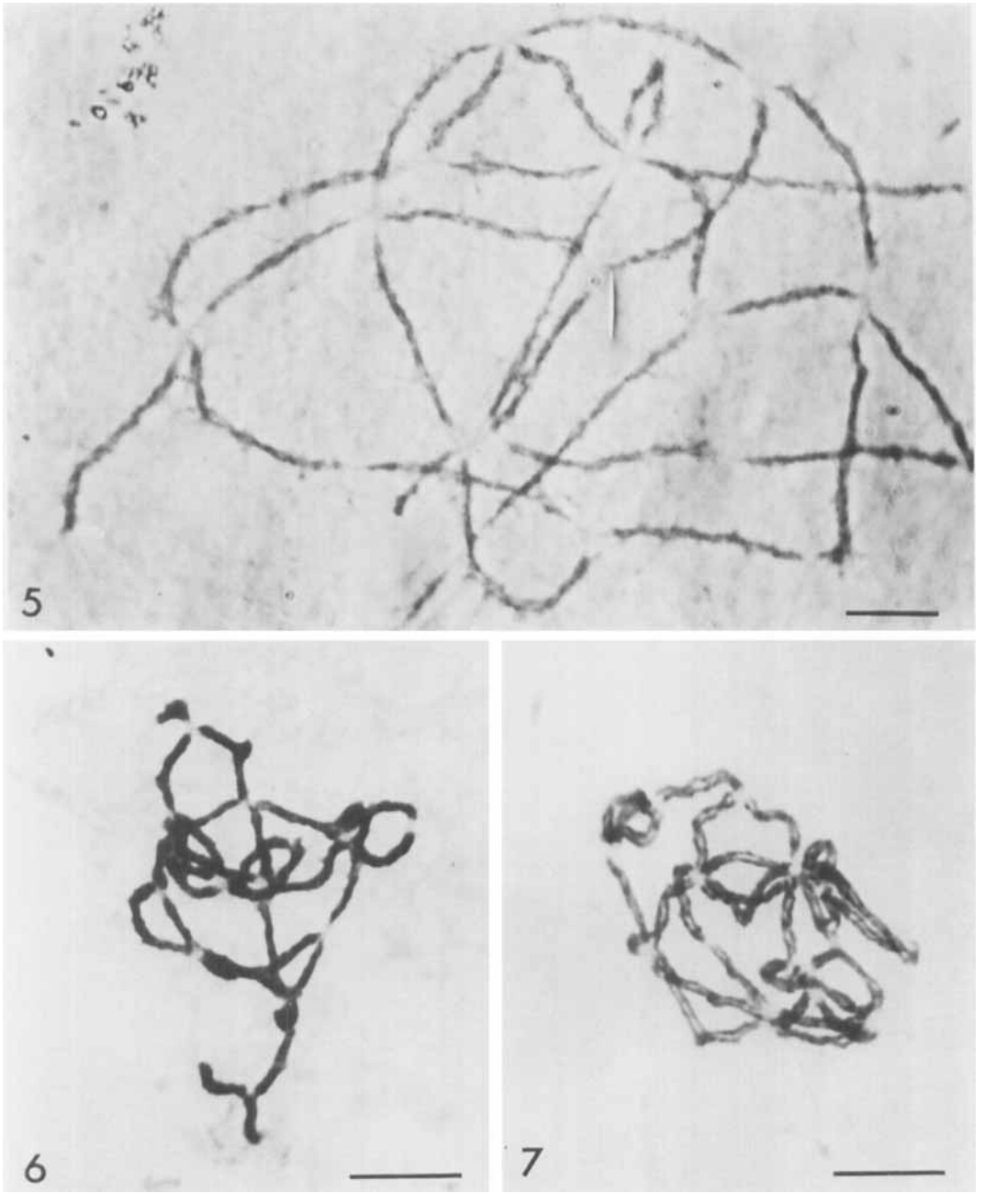


Fig. 5-7. Chromosomes in vitellogenetic nuclei in female *Sphinx ligustri*. **Fig. 5.** An oocyte nucleus at early vitellogenesis. All bivalents are included in one branched chain. Pyronin method. **Fig. 6.** The branched chain in a mid-vitellogenetic nucleus. Feulgen-Giemsa method. **Fig. 7.** The branched chain in a mid- vitellogenetic nucleus. Feulgen-Giemsa method. (Bar=10μm).

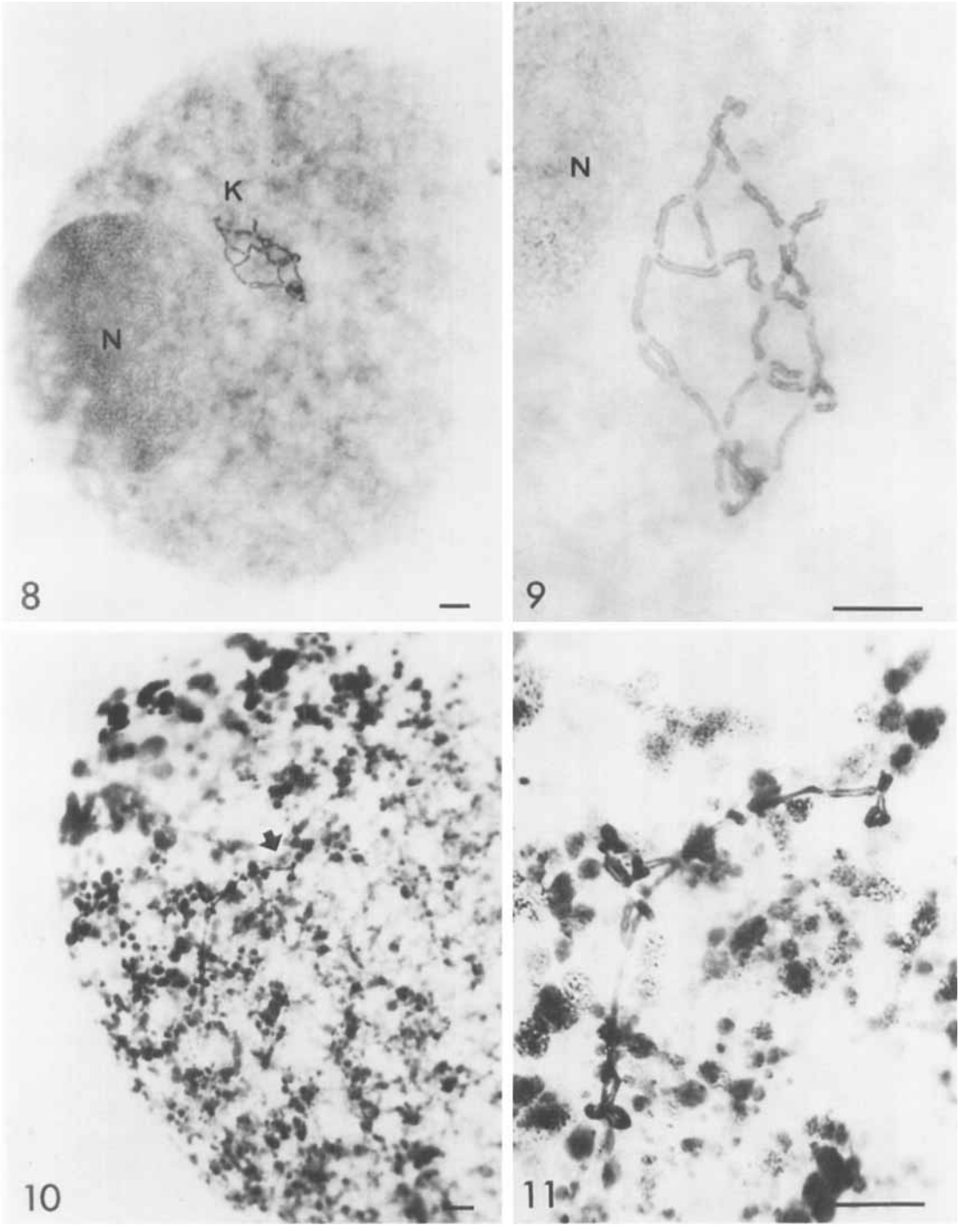
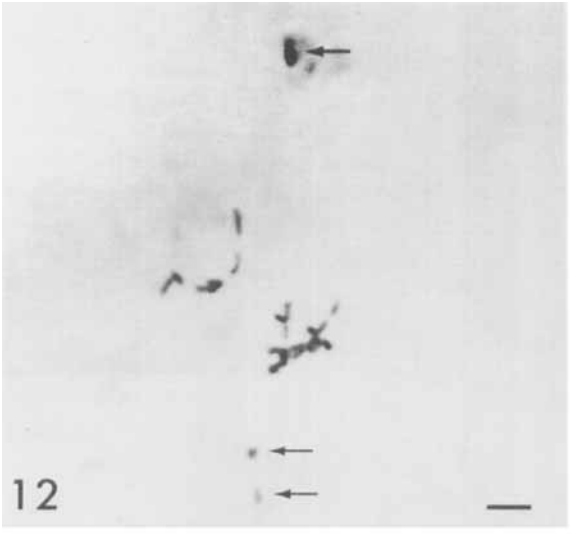


Fig. 8-11. Chromosomes in late vitellogenetic nuclei in female *Sphinx ligustri*. Feulgen-Giemsa method. **Fig. 8.** Oocyte nucleus, showing karyosphere (K) and a giant nucleolus (N). **Fig. 9.** Enlarged karyosphere, revealing the branched chain configuration of bivalents. N=nucleolus. **Fig. 10.** Part of an oocyte nucleus after the breakdown of the nucleolus. Bivalent chain is arrowed. **Fig. 11.** Enlarged bivalent chain. (Bar=10μm).



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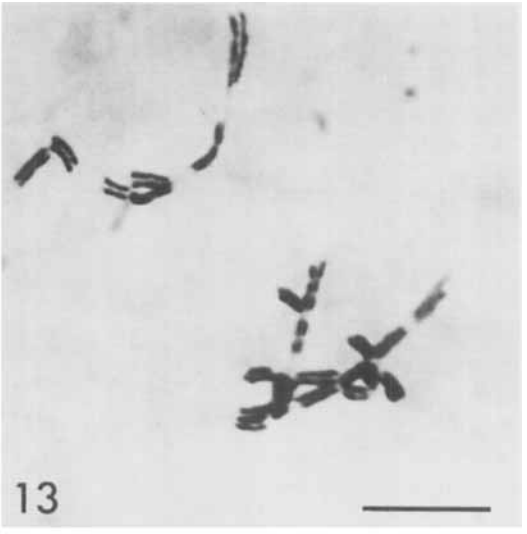

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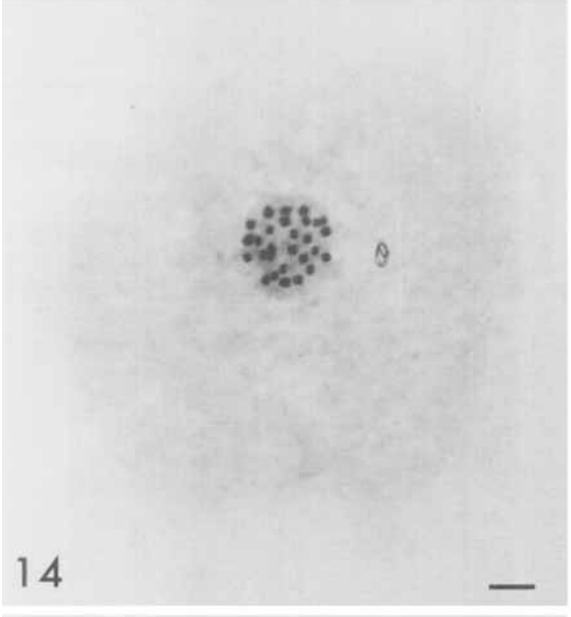

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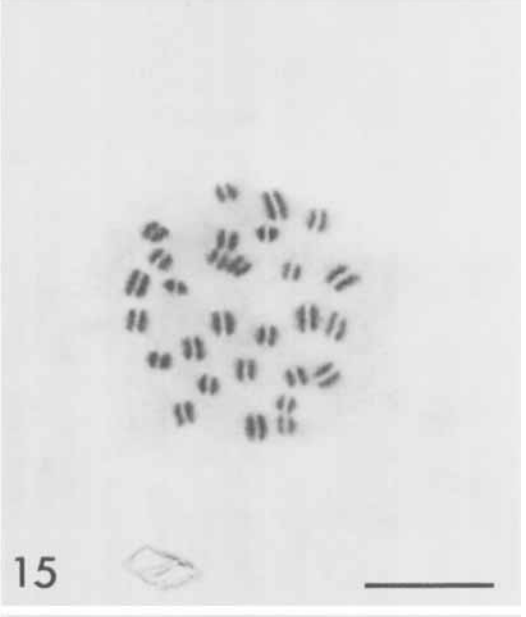

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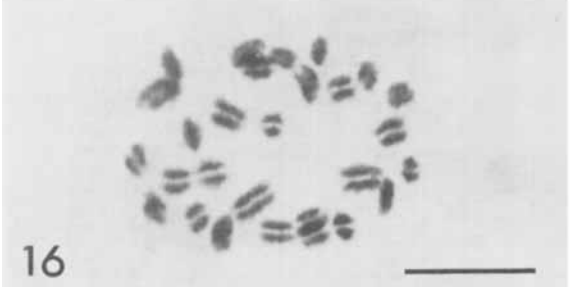

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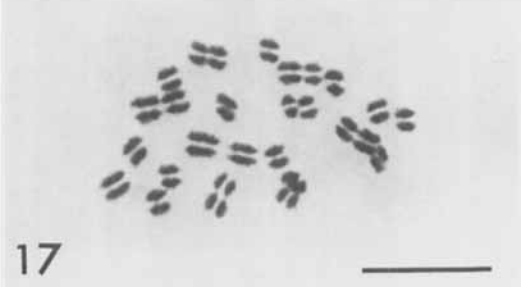

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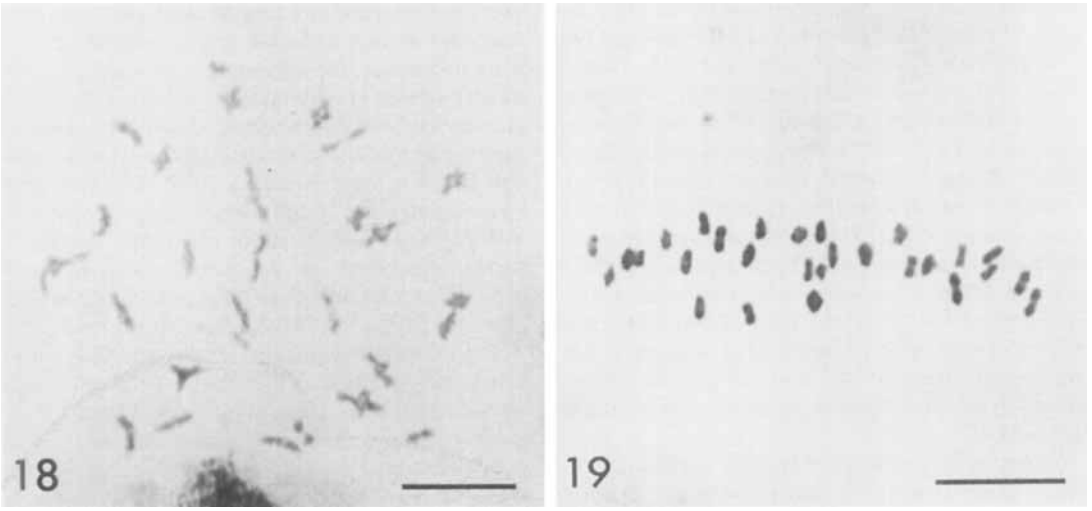

Fig. 18-19. Meiotic chromosomes in male *Sphinx ligustri.* **Fig. 18.** A nucleus at diakinesis, showing 28 chiasmatic bivalents. **Fig. 19.** Metaphase I in side view, showing 28 bivalents. (Bar=10μm).

early metaphase I (Fig. 14). As shown in Fig. 14, the spindle is formed in an area considerably smaller than the size of the nucleus. During metaphase I, only short chains consisting of two or three bivalents are remaining (Fig. 15-17).

In male meiosis, diakinesis and metaphase I stages revealed twenty-eight chiasmatic bivalents without any tendency to adhere with each other (Fig. 18 and 19).

Discussion

The present results show the haploid chromosome number in *Sphinx ligustri* to be n = 28, which seems to be common in Sphingidae. This chromosome number is somewhat lower than the most common lepidopteran haploid chromosome number n = 31 (see ROBINSON 1971).

Throughout prophase, from pachytene until metaphase I in *Sphinx ligustri* female meiosis, the bivalents consist of two chromosomes aligned in parallel and condensation proceeds without intervening diplotene and diakinesis stages. Hence apparently, meiosis in female *Sphinx ligustri* is achiasmatic.

Achiasmatic meiosis in female Lepidoptera has been earlier observed in Bombycidae (MURAKAMI and IMAI 1974), Geometridae (SUOMALAINEN 1965), Pyralidae (SUOMALAINEN 1969a; TRAUT 1977), Tortricidae (SUOMALAINEN 1969a, 1971), Micropterygidae, Eriocraniidae, Hepialidae, Incurvariidae (SUOMALAINEN 1969b), Heliconiidae (SUOMALAINEN et al. 1973), Satyridae (*Erebia:* FEDERLEY 1938, according to the interpretation by BAUER 1939), and Noctuidae (FONTANA 1976). The families include both primitive and advanced taxa, indicating that achiasmatic female meiosis is a common feature to all Lepidoptera, especially so, since achiasmatic female meiosis has also been observed in the closely allied insect order Trichoptera (SUOMALAINEN 1966). Hence, it is conceivable, as postulated by SUOMALAINEN (1966), that achiasmatic female meiosis has arisen in the common ancestor of Lepidoptera and Trichoptera.

The lack of chiasmata in female Lepidoptera is

Fig. 12-17. Bivalents at prometaphase I and metaphase I in female *Sphinx ligustri.* **Fig. 12.** Early prometaphase I. Few separate bivalents (arrowed) are seen near the poles. Most bivalents are still associated in chains near the equator. Feulgen-Giemsa method. **Fig. 13.** Bivalent chains near the equator at early prometaphase I. Feulgen-Giemsa method. **Fig. 14.** Metaphase I nucleus at a low magnification. The nucleus is differentiated from the yolk. The spindle is formed in a small area within the nucleus. Feulgen-Giemsa method. **Fig. 15-17.** Metaphase I plates, showing short bivalent chains. **Fig. 15 and 17.** Feulgen-Giemsa method. **Fig. 16.** Pyronin method. (Bar=10μm).

accompanied by the lack of crossing-over. The absence of recombination of linked loci has been observed in *Bombyx mori* (STURTEVANT 1915; TAZIMA 1964), *Galleria mellonella* (SMITH 1938), *Heliconus* species (TURNER and SHEPPARD 1975), and *Ephestia kuehniella* (TRAUT 1977). However, KÜHN and BERG (1955) interpreted their F_2 data of crosses between *b* and *bch* with linkage and recombination in both sexes. Among 457 offspring, they obtained 12 *b bch* animals which ought not to have appeared without recombination in female meiosis. However, the results obtained by KÜHN and BERG (1955) do not necessarily suggest the presence of crossingover, but can be explained on the basis of pseudo-linkage caused by nonhomologous associations of bivalents (see below).

In most achiasmatic meioses so far studied, the bivalent structure attained early in meiosis is retained as such until anaphase I. The most simple mechanism by which this is achieved is described in *Bolbe nigra* spermatocytes by GASSNER (1969), who found that synaptonemal complex remains as such between the homologous chromosomes until early anaphase I. In lepidopteran female meiosis, the synaptonemal complex is gradually transformed into elimination chromatin, which ties homologous chromosomes intimately together and ensures the regular disjunction of chromosomes at anaphase I (RASMUSSEN 1976, 1977).

A slightly different mechanism for keeping homologous chromosomes intimately paired during meiotic prophase and metaphase I has been found in male meiosis of *Panorpa communis*. WELSCH (1973) found that although the synaptonemal complex disintegrates during meiotic prophase, connections between homologous chromosomes are left to keep the chromosomes together. It seems plausible that in the case of *Panorpa communis*, the role of the synaptonemal complex is confined to being the mechanism of synapsis, allowing connections to be formed between homologous chromosomes, after which disintegration of the synaptonemal complex can occur without any disturbances in segregation. According to this line of thinking, the connections formed between homologous chromosomes are to be homologized to collochores, which are responsible for the regular segregation of homologous chromosomes in the achiasmatic male meiosis of *Drosophila melanogaster* (COOPER 1964). If several collochores are formed along the chromosomes, the homologues remain closely aligned throughout their length until anaphase I. This type of meiosis has been referred to as the alignment type of achiasmatic meiosis (NOKKALA and NOKKALA 1986). However, in the collochore type of achiasmatic meiosis, only one or two collochores per bivalent are formed, and hence, the appearance of bivalents is very much like that of chiasmatic bivalents. This kind of meiosis has been described aside *Drosphila melanogaster*, recently also in the heteropteran family Miridae (NOKKALA and NOKKALA 1986). In *Drosophila melanogaster*, the synaptonemal complex is not formed (MEYER 1960). It seems likely that mitotic synapsis described in *Drosophila* somatic cells (HALFER and BARIGOZZI 1972) is intimate enough to allow the formation of collochores in meiotic cells.

The examples mentioned above show that within achiasmatic meiosis, two evolutionary levels can be identified; a more primitive type in which the regular segregation of homologues is ensured by synapsis, and a more evolved type in which the regular segregation is ensured independently of synapsis. In other words, in the former type, already the achievement of synapsis between homologous chromosomes guarantees their regular segregation, but in the latter type, in addition to synapsis, at least one collochore per bivalent has to be formed to ensure regular segregation. If a chromosome pair fails in collochore formation, the pair will appear as two univalents during later stages of prophase, resulting in disturbances in their segregation (see NOKKALA 1986).

It is apparent that lepidopteran female meiosis belongs to the group of achiasmatic meioses, in which the synapsis of two chromosomes ensures their segregation. Accordingly, an opportunity emerges to give explanation of differences in bivalent formation in males and females of lepidopteran interspecific hybrids. For example, FEDERLEY (1931) established that in meiosis of interspecific hybrids, the maximum number of bivalents was formed in females, whereas in males, univalents were abundant. The observation can be explained on the basis of our present knowledge on events occurring during synapsis (for a review, see RASMUSSEN and HOLM 1980). It has been established that there are two phases in the formation of the synaptonemal complex. During the first phase, the synaptonemal complex is formed between homologous chromosomes, followed by a phase where synaptonemal complex formation between nonhomologous chromosomes occurs. In addition, if multivalents are formed, they will break down yielding the maximum number of bivalents, if chiasmata do not stabilize the multivalent configuration. Accordingly, in hybrid females, in which chiasmata are absent, synapsis gives rise to the maximum number of bivalents, and on the other hand, since synaptonemal complex is

transformed into elimination chromatin, the bivalent condition is retained until metaphase I. However, male meiosis in Lepidoptera is chiasmatic (this study; for further references, see TRAUT 1977), i.e., in addition to synapsis, chiasma formation is necessary for bivalent formation. Thus, in hybrid males, although synapsis might be similar to that in females, chiasma formation usually fails, resulting in the abundant occurrence of univalents at metaphase I. The most likely reason for the failure of chiasma formation in hybrid males is that synapsis in hybrids occurs most probably between nonhomologous chromosomes.

In *Sphinx ligustri* female, all pachytene bivalents are morphologically similar, and the sex chromosome bivalent can not be identified. A similar situation is described also in *Bombyx mori* females, where the ZW bivalent could not be identified at pachytene either at the light microscopic level (TRAUT 1976) or at the electron microscopic level (RASMUSSEN 1976). However, both genetic (cf. ROBINSON 1971) and cytological (SEILER 1921; FEDERLEY 1938; TRAUT and MOSCHBACHER 1968; SUOMALAINEN 1969a, 1971; TRAUT and RATHJENS 1973) observations unambiguously show female heterogametia in Lepidoptera. The presence of the W chromosome in species which lack morphologically differentiated sex chromosomes, can be deduced by the fact that, in their somatic interphase nuclei, females carry positively heteropycnotic sex chromatin, proved to be the inactivated W chromosome (TRAUT and MOSCHBACHER 1968; SUOMALAINEN 1969a). In *Sphinx ligustri,* sex chromatin was present in the polyploid interphase nuclei of follicle cells, but was absent in the polyploid interphase nuclei in males. Hence, the occurrence of achiasmatic meiosis in female Lepidoptera is in accordance with the suggestion of BEERMANN (1954) that achiasmatic meiosis is confined to the heterogametic sex.

The behaviour of bivalents during meiotic prophase in female *Sphinx ligustri* differs from that found in male. During late pachytene, telomere to telomere connections between bivalents are formed, resulting in all bivalents being nonhomologously attached to each other. Bivalents are nonhomologously associated in a branched chain during all the time of yolk production, and the chain will not break down until prometaphase I. Thus, the nonhomologous associations of bivalents in female Lepidoptera behave essentially similarly as the chromocenter in female *Drosophila,* where the centromeric regions of bivalents form a chromocenter at pachytene (DÄVRING and SUNNER 1973; NOKKALA and PURO 1976), and the chromocenter breaks down at prometaphase (PURO and NOKKALA 1977).

It is apparent that the nonhomologous association of bivalents, via telomeres as in Lepidoptera or centromeric regions as in *Drosophila,* is a peculiarity of female meiosis of the meroistic ovary type. In insects with the panoistic ovary type, bivalents are not nonhomologously associated during meiotic prophase (NOKKALA, unpublished). Typical of the meiotic prophase in the meroistic ovary type is the formation of karyosome (BAUER 1933; BIER et al. 1967, 1969). Evidently, the occurrence of the nonhomologous association of bivalents is a prerequisite for karyosome formation. The branched chain configuration in Lepidoptera is clearly equivalent to the karyosome, e.g., in *Drosophila*, but due to the fact that synaptonemal complex is transformed into elimination chromatin, the structure of bivalents is different, leading to a different appearance. During the karyosome stage, the meiotic chromosomes are metabolically inactive (BIER et al. 1967, 1969; TRAUT 1975), suggesting that the karyosome is meiotically a resting stage comparable to the dictyotene stage in mammals. As a consequence of the nonhomologous association of bivalents, the bivalents occupy a relatively small volume within the enormous oocyte nucleus at the time when spindle is formed. Evidently, the association facilitates the formation of a relatively small spindle in spite of the huge size of the nucleus.

Since in the meroistic ovary type, bivalents are nonhomologously associated throughout prophase until prometaphase, it is expected that the associations have an effect on the segregation of chromosomes. The effect is quite clearly observable in *Drosophila* female, where the peculiar phenomenon of preferential segregation of achiasmatic chromosomes (for references, see GRELL 1976; NOVITSKI and PURO 1978) is attributable to the existence of a chromocenter (PURO and NOKKALA 1977). In Lepidoptera, associations are formed only between telomeres (see also TRAUT 1977). This difference as compared to *Drosophila* is probably due to the fact that lepidopteran chromosomes are holokinetic (BAUER 1967; MURAKAMI and IMAI 1974). In addition, the associations are formed sequentially so that, firstly, short chains are formed, followed by the lengthening of the chains, and finally a branched chain is formed after secondary modifications in a long, structurally simple chain. At metaphase I, short chains are remaining. If it is assumed on one hand, that short chains formed early in meiosis have a tendency to occur as short

chains at meaphase I, and on the other hand, that in the associations, there exists maternal-paternal specificity, pseudolinkage of markers in nonhomologous chromosomes will be expected.

If the observations made by KÜHN and BERG (1955) are explained by assuming pseudo-linkage in female, the results obtained suggest that the order of bivalents within the chain would be quite strictly determined and that maternal telomere should face maternal, and paternal telomere, paternal. Apparently, the existence of some kind of connective structures between nonhomologous telomeres and the shortening of the structures provides the most simple mechanism for the formation of nonhomologous associations of bivalents in lepidopteran oocytes. Cytological evidence for the existence of specific telomere connections between nonhomologous chromosomes in mitotic cells has been presented by ASHLEY (1979). However, it remains to be elucidated as to what extent the nonhomologous associations of bivalents in meiotic cells represent connections described in mitotic cells, and if the order of bivalents in the associations in nonrandom.

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