MEIOSIS IN THERMORIA DOMESTICA PACK.

by

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INTRODUCTION

Members of the order Thysanura are a group of insects which might well be termed ubiquitous, for their presence has been documented on almost every major land mass. Indigenous populations exist throughout Europe, Africa, Asia, and Asia Minor. In the western hemisphere their range extends from South America to Canada. Even insular states have not been spared their infestation. Specimens have been collected across Japan, Australia, Great Britain, Borneo, the West Indies, the Azores, the Canary Islands, and Samoa. Natural occurrences of the fire-brat, *Thermobia domestica* Pack., have been confined to the mainland portions in both hemispheres, but Great Britain, because of its extensive shipping industry has, too, fallen prey to these pests.

Under ideal feeding conditions, and in times of low population density, *Thermobia* confines its attentions to mealy substances. But mating is continuous and soon the short interim between generations, the fecundity of these insects, their adaptability to varying conditions of temperature and humidity, and their comparatively sedentary mode of existence can combine to produce large local populations. Once firmly entrenched in a home or warehouse, large infestations assume all of the aspects of invasions of the German cockroach. The insects' appetite then turns to fruits, rolled oats, cornflakes, dried lean meats, animal and vegetable glues, photographs and glazed paper. Under conditions of prolonged starvation, adult fire-brats cause extensive damage to viscose rayon and minor damage to silk crepe and linen (Mallis, et al., 1958).
Despite all this, large infestations are relatively rare and easily controlled. As yet, no species of Thermobia has developed resistance to any known chemical insecticide. Damage is confined to a few localized areas and industries and thus the insect ranks rather low on the list of economically important pests.

Consequently, little money has been allocated for and little effort made toward the study of this insect. Publications concerning it are few and tend to stress morphology and ecological aspects, minimizing cytology and cytogenetics. To date only two papers of any length have dealt with meiosis in Thermobia (Charlton, 1921; Perrot, 1933). These are both of such vintage that no complete photographic records exist. The cytological techniques employed were so drastic, by comparison with modern methods, that either author might well be questioned on artifact.

The objectives of this study have been:

(1) to obtain an accurate photographic record of meiosis in Thermobia domestica Pack. using a minimum of stain and fixative, thereby reducing the probability of artifact.

(2) to obtain an accurate chromosome count.

(3) to determine the fate of the X chromosomes and indicate their significance in the sex determining mechanism.
REVIEW OF LITERATURE

Early papers dealing with *Thermobia domestica* Pack. tended to be more of a descriptive nature and concerned with either problems of morphology or ecology. Sweetman (1934, 1938) established optimum conditions of temperatures and humidity for all developmental stages of the insect. The egg stage was found to have the greatest tolerance for environmental changes, hatching under temperature extremes of $24^\circ - 47^\circ C$ and relative humidities of $12-100\%$. Optimum conditions for all succeeding stages centered around $37^\circ C$ with a humidity of $75-85\%$. Snodgrass (1928, 1931) commented on the evolutionary significance of cephalic and abdominal appendages. He described these insects as morphological intermediates between the simple Crustacea and Chilopoda, and the Pterygota. Spencer (1929, 1930) traced the spread of the fire-brat across Canada; Grensted (1931) did likewise with infestations in Great Britain.

Pertinent to this study are the descriptions of the male reproductive system made by Charlton (1921) and Perrot (1933). The generative tract of the male fire-brat is a symmetrical structure consisting of six paired testicular lobes and their connecting tubules. Three pairs of testicular lobes lay to each side of the median long axis (Fig. 1). These are connected by vasa deferentia to seminal vesicles which empty first into large sperm ducts and finally into a chamber at the base of the penis. The circular accessory glands empty into this chamber also, it being the probable assembly point of the spermatophores. There is no direct copulation between sexes in the
Figure 1. Male genital system, ventral view. p, penis; pr, prostate; sv, seminal vesicle; t, testicular lobe; vd, vas deferens. (After Charlton, 1921, and Perrot, 1933).
fire-brat. Mating consists of females picking up spermatophores deposited on the ground by males (Spencer, 1938).

The blind ends of the testicular lobes contain the earliest stages of gamete development. Here mitotic activity, both body cell (nurse cell, resembling Sertoli cells of mammalian cytology) and germinative (spermatogonial) may be observed. Elsewhere, only progressive germ-cell-development is in evidence.

With the advent of greater degrees of technological sophistication the trend has been away from mere description and toward the study of basic physiological and biochemical problems. Lindsay (1942) studied the distribution of radio-phosphorous labeled compounds in the fire-brat, finding the least accumulation in the fat body, and the most in mid-intestinal epithelium, reproductive accessory glands, and gonads. Kaplanis (1963) investigated the possibilities of cholesterol biosynthesis still existing in Thermobia as it is supposed to have existed in the more primitive forms. No evidence of continuing synthesis has yet been found.

Beament (1964) discovered that the fire-brat's high resistance to desiccation was dependent upon a stiff layer of epicuticular grease. A resistant lamella overlayed this grease. Its capacity for repairing abrasion damage was such that almost no water was lost by Thermobia living in powder-filled habitats. McIver (1966) described the thermal-discrimination mechanism. Thermoception in Thermobia was controlled by trichoid sensilla in the basal antennal segments. Following complete antennectomy thermal discrimination was lost for 1 week after which time it was partially regained as tarsi and maxillary palpi took over the
function. Full function was regained after the next moult when antennal segmentation was completed.

To the present time only two investigators, Charlton (1921) and Perrot (1933) have studied the entire meiotic cycle in the male fire-brat. Their methods, however, consisting mainly of classic differential staining techniques, heavy metal impregnation, and paraffin sectioning, were quite harsh, and vacuolated cellular configurations such as they described have not been encountered under phase contrast by either Bawa (1964) or by this author.

Perrot (1933) also established the XXO sex-determination mechanism of Thermobia, but neglected to comment further. White (1948), a major investigator of this area, theorized on the evolutionary significance of animal sex-determination mechanisms, but his accounts were far too generalized for him to devote much time to fire-brats individually. One thing that White did make extremely clear, though, was that similarity in evolutionary origin did not necessarily conote similarity in sex determination systems nor should similarity of sex mechanisms ever have been used as sole evidence of evolutionary relationships. He illustrated his point by citing the work of McClung (1917) on Hesperotettix viridis, that of Callan (1941) on Forficula auricularia, and Seiler (1925) on three races of Phragmatobia fuliginosa to show that sex mechanisms are independent of evolutionary ties as several may exist simultaneously within a single species.

Recent electron and phase microscope studies of spermatogenesis in Thermobia domestica Pack., by Bawa (1964), have also demonstrated that
in the fire-brat mature spermatozoa are non-motile individually. Rather, two spermatozoa must come into contact, intertwine posteriad along 1/3 of their total length and beat synchronously and rhythmically in order to produce translocatory movements. In this way they move together through the medium in a direction opposite that of the end containing the acrosome, i.e. tail first. Bawa (1964) also demonstrated the "undulating membrane" of Charlton (1921) to be nothing more than an acrosomal flagellum that has come to lie parallel to the long axis of the cell and is adherent to its outer covering.

With respect to cytogenetics, closely related insect groups have not been studied to any greater degree. Until 1956 the chromosome numbers of only 3 species of Collembola were known. Nunez (1962) augmented this list by describing 18 species and cataloguing an additional 20. He also postulated an XX:OX sex-determination mechanism, and showed, by all available results, a decrease in the basic chromosome number parallel to phylogenetic advance. Nunez (1962) demonstrated chromosome bridges, not unlike those in Thermobia, present in all mitotic configurations and in divisions of the second spermatocytes.

Schliwa and Schaller (1963) studied copulatory activities in Collembola, but no other work pertaining to sex or sex-determination was done until Hale (1964) observed instances of parthenogenesis in Onychiurus procampatus.
METHODS AND MATERIALS

All work reported herein was conducted on the fire-brat, *Thermobia domestica* Pack. Specimens were obtained from floors and walls of subterranean steam tunnels. The insects were initially trapped en masse in glass containers baited with dry oatmeal flakes and wheat flour. Subsequent collecting methods involved vacuuming fire-brats individually into tissue-paper-lined flasks attached to electric suction pumps.

Colonies were established in five-gallon glass aquaria. Each aquarium was equipped with 21 upright fibre-board partitions spaced at 1/2 inch intervals. These provided climbing space which greatly increased colonial capacity, but simultaneously prevented overcrowding on the floor. Raising the partitions 1/2 inch almost entirely across the bottoms allowed specimens unrestricted movement through a colony, and ready access to cotton-stoppered water bottles and food. As in the traps, the insects were fed a diet of dry oatmeal flakes and flour. Long cotton stoppers on the water bottles provided the only sources of water and moisture, as no attempts were made to control humidity. An electric slide-warmer placed under the aquaria provided a constant floor temperature of 39°C. The glass walls prevented escapes as these insects are unable to climb polished surfaces, while small-mesh screen covers precluded entrance of contaminants.

Males are easily distinguished from females by absence of the long median ovipositor which forms a fourth posterior projection in the latter (Fig. 2). Male specimens .85 cm. in length, or larger, were
Figure 2. Posterior abdominal segments of male (A) and female (B) fire-brat, *Thermobia domestica* Pack., ventral views. o, ovipositor; p, penis. (After Charlton, 1921).
used in all work. The insects, approximately 300 days old, were asphyxiated in ethyl ether vapors and dissected in physiological saline. Eighty mg. of detergent per liter of saline solution reduced surface tension sufficiently to prevent specimens from floating. Testes were exposed by removing tergites of the third through the seventh abdominal segments with minuten-pin hooks.

Excised testicular tissue was then placed on a microscope slide. Excess adhering fat was washed off with several drops of ethyl ether. A two-minute bath in a drop of 1% sodium citrate, to spread nuclear chromatin, was followed by a five to thirty minute immersion in acetic orcein stain (the time varying with the tissue volume). Subsequently, the tissue was washed and refloated in a drop of 15% acetic acid. Following fixation the preparation was covered with a No. 1 coverslip, squashed, sponged dry with filter paper and sealed air-tight by a ring of clear fingernail enamel.

The technique described by Gassner and Breland (1967) was also employed in examining testicular tissue. This consisted of floating the tissue in a drop of saline solution, coverslipping, but sealing only those edges parallel to the long axis of the slide. After study in saline, acetic acid could be drawn under the coverslip by placing filter paper in contact with the saline at the opposite edge. In like manner liquid stain could be drawn in and the coverslip finally sealed. This method, while not superior to the procedure already described, had the distinct advantage of showing the same field in different stages of fixation and staining. Thus, it served as a check against artifacts produced by the former, less time-consuming technique.
Slide preparations were examined under phase contrast on a Zeiss model WL microscope equipped with an automatic shutter and a Nikon 35 mm. film holder. Photomicrographs were taken under green light on Kodak Plus X-Pan 135-20 black and white film at 1000 diameters employing a Neoflaur 100/1, 30 oil objective. Exposure time was 28 seconds for all photographs.
RESULTS

While studies of mitosis in this insect were not within the scope of this thesis, numerous cells in mitosis were observed. Mitotic figures in spermatogonial metaphase show all of the chromosomes \((32 + X_1X_2)\) connected by thin chromatin bridges, resembling the configurations found in Hemiptera. "Sertoli" cell metaphase (Plate 1) and spermatogonial metaphase (Plate 2) are instances in which the chromosomal configurations of Thysanura resemble those of the Heteroptera (Charlton, 1921; Perrot, 1933; Bowen, 1922).

With the advent of prophase in the primary spermatocyte, the chromatin begins to condense into discrete segments from the heretofore amorphous mass. This progressive chromosomal condensation is most evident in the leptotene series (Plates 3, 4). In the early stages, extremely long, tightly wound, monofilament spireme threads give the nucleus a net-like appearance. Presently these threads become moniliform, remaining, however, much too interlaced to follow from end to end and hence impossible to count (Plate 4B).

By zygotene the chromosomal beading has tended to dissolve (Plate 5). The chromatin threads have come into apposition, although the dualistic nature of the chromosomes in not well defined until pachytene (Plate 6). This duality becomes increasingly apparent throughout pachytene, as does the identity of the sex chromosomes which now exhibit both deeper staining and greater condensation (Plates 6, 7). Up to this point it has been impossible to distinguish sex chromosomes from autosomes morphologically. Had there been a need to do so before this time, identification
could have been accomplished through differential staining (Charlton, 1921; Perrot, 1932) by bringing out the nucleolus and observing any adhering chromatin. There is an intimate association between the sex chromosomes and the nucleolus (Charlton, 1921; this thesis).

In pachytene the sex chromosomes may sometimes be seen as a dark, eyeglass-shaped body, held together by a chromatin strand (Plate 6B). This strand gradually lengthens and thins out, but continues to bind together the two X's throughout the remainder of the first division (Plates 6B-12, 16, 17B). Only the chromosome most closely associated with the nucleolus contributes to the connecting strand, hence the size discrepancy between the two (Charlton, 1921) (Plates 8A and 9-12).

Following pachytene the chromosomes enter a stage analogous to the diplotene-diakinesis of other insects, and undergo maximum condensation (Plates 6-9). Here the first definite chromosome counts may be made in the primary spermatocyte. The counts reveal 18 chromosome bodies; 16 autosomes plus the two tethered X chromosomes.

In metaphase of the first meiotic division all 18 bodies align themselves normally along the equatorial plane (Plates 10-12). Even though tetrads are not visible in the meiosis of *Thermobia domestica*, first and second division chromosomes may easily be distinguished by size and shape (Plate 25), first division chromosomes being much larger and much more varied in shape.

During anaphase the 16 autosomes proceed normally to opposite poles (Plates 13-16), but the X's, still joined by the chromatin bridge, both migrate to the same pole (Plate 15B). Even in those instances in which
they do start in opposite directions (Plate 15B) complete separation is precluded (under normal conditions) and before this stage of maturation is completed both are pulled to the same pole (Plate 17A). In this way cells of 34 chromosomes divide into daughter cells with counts of 16 and 18.

Telophase and progressive cytokinesis ensue (Plates 17, 18), and with the formation of two daughter cells the first maturation division comes to an end (Plate 19).

Chromosome activity subsequent to cytokinesis of the first division and prior to prophase of the second division still remains a mystery. Judging by the comparatively diffuse nature of the chromosomes as they enter second prophase (Plate 20A) it could be postulated that they had totally dispersed and are condensing once again. If this is so, no stage exhibiting this dispersal was recognized. It could very well be that the chromosomes are at maximum distention in Plate 20A and that no further loss of identity occurs. No evidence supporting either statement has as yet been found by this author. As second prophase progresses, however, chromatin begins once more to condense and the unequal chromosome count may again be noted (Plate 20B).

The cells appear to pass through second prophase quickly (based upon rarity of encounter of this stage) and the chromosomes once again align themselves on the equatorial plane (Plate 21). This time, however, only daughter cells containing either 16 or 18 chromosomes will be produced by division of the respective mother cells (Charlton, 1921, Perrot, 1933) (Plates 21B, and 22A).
There follows a normal anaphase (Plates 22 and 23), telophase (Plate 24) and cytokinesis bringing an end to the second maturation division (Plate 24). All chromosomes disperse and dark-staining chromatin fills the nucleus of the ensuing spermatid, nuclear volume accounting for almost its total mass (Plate 26A). Sperm formation begins by a progressive lengthening of this nucleus (Plates 26-29) which extends throughout the greatest portion of the mature (650 μ long) spermatozoan.

Mature spermatozoa exhibit an acrosome-derived "undulating membrane" (Plates 30 and 31) (actually a flagellum lying along side of the main body of the cell and pulling up the outer membrane in a soap-bubble-like effect) extending better than 2/3 of the total cell length (Bawa, 1964; this thesis). As previously mentioned, this had long been suspected of being a motility factor, analogous to the undulating membrane of Trypanosomes (Charlton, 1921), until Bawa (1964) showed that motility is dependent upon rhythmic undulations of two intertwined spermatozoa, and that singularly they were non-motile (Fig. 3).
Figure 3. Motility configuration of mature spermatozoa of Thermobia domestica Pack. Arrow indicates direction of movement. a, acrosome.
DISCUSSION

Spermatogenesis in *Thermobia* appears, in most respects, to be of the normal type. From this, and the works of earlier investigators, it is evident that the most interesting aspect of the entire process lies in the complex XXO sex-determination system. While such a mechanism is not peculiar to the Thysanura, a discussion of its place in the animal kingdom seems in order to afford a better understanding of its significance.

Most Metazoons possess genetic sex-determination mechanisms of one sort or another. Notable exceptions are many hermaphrodite individuals belonging to such groups of invertebrates as the Mollusca, Plathyhelminthes, Aschelminthes, Nemertina, and those belonging to groups in which chemical stimuli from the environment play a major role in determining the sex of the offspring. The genetic sex-determination mechanisms usually consists of a pair of chromosomes which may be regarded as having become specialized in the course of evolution in accordance with their particular function (White, 1948). Having made the above statement, White goes on to ask -- "What is the general biological significance of the evolution of the sex chromosomes? Do new kinds of sex determination mechanisms become established in phylogeny because they are more effective as sex-determining agencies - or is their survival more or less accidental?" We can begin to answer these questions by taking a glance at basic determining-mechanisms.

-17-
Many groups of organisms still subscribe to the ancient XY sex-determining mechanism, and in these groups it seems extremely stable. The only difference between the X's and Y's of these species being in the length of the differential segments. However, care must be exercised in making such statements because the XY mechanism employed by some could be a neo-XY', a reversion to the ancient system after having exhibited other determining mechanisms. Just as the rest of the organism is being continually subjected to selection pressures and evolutionary changes on the macroscopic level, micro-selection pressures are at work constantly altering genetic environments. It is, of course, quite uncertain as to what degree these changes are adaptive, but since the rest of the genetic system is continually evolving, the apparatus which produces an XY or XA balance (A = autosome) must evolve "pari passu" (White, 1948).

If the X and Y have truly arisen from autosomes by evolutionary divergence and translocation, as is suspected by White (1948), then we should be able to postulate two theories about them - 1) that they can, by translocation, form a different sex-determining mechanism and 2) that in the more primitive species we should expect less sex-determination mechanism differentiation, and adherence to the older mechanism, whereas more advanced species should exhibit new mechanisms, and ones much more differentiated.

This latter supposition we may discount almost immediately, for special sex-chromosome mechanisms have been evolved in the Arachnida, Dermaptera, Thysanura, Odonata, and Heteroptera - groups that have existed since at least Paleozoic times, while the Diptera, not known
before the Jurassic exhibit apparently much more primitive sex-determining mechanisms (White, 1948; Nowlin, 1906; Katayama, 1939; Nakahara, 1919; Perrot, 1933; Charlton, 1921; Painter, 1914; Stevens, 1911; Whiting, 1917; and Moffett, 1936). The former postulate, however, may well be a plausible explanation for the occurrence of various modifications of the basic mechanism. Formation of the XO sex-determinant could easily occur by permanent fusion of the pairing segment of the Y to the homologous segment of the X chromosome (Fig. 4). The Y would in effect be "lost" since the differential segment would become sexually inert.

Reversion to the XY (or neo-XY) condition might occur in like manner if centric fusion takes place between an acrocentric autosome and an acrocentric X. The homologous "unfused" autosome would in effect become a Y (White, 1948). That this does occur is demonstrated by two genera of Acrididae - Hesperottetix and Mermiria. Individuals of H. viridis may be either XO of XY indicating that the new translocation has not yet spread through the whole species (White, 1948; McClung, 1917).

Chromosome arm transfers between sex chromosomes and autosomes, although apparently much more rare than transfers between two sex chromosomes or two autosomes, serve as the best possible explanation for the more elaborate sex-determination mechanisms. Figure 5 shows the possibility of such an occurrence forming both XXO and XXY determinants.

The major difficulty now is to try to imagine why several X's should travel to the same pole in the absence of a Y chromosome. This phenomenon could be achieved by several means - 1) by the X chromosomes
Figure 4. XY mechanism going to X0 by fusion of the pairing segments (p) of the sex chromosomes, with a loss of the Y differential (d).
Figure 5. (a) XY forming XO by fusion of pairing segments, then forming XXO mechanism by translocation with an autosome (A).

(b) XY mechanism forming XXY by translocation with an autosome (A), then forming XXO by fusion of X and Y pairing segments.
forming a compact mass and thereby all traveling to one pole, as in the tenebrionid *Blaps lusitanica* (Nonidez, 1915, 1920) and in the ostracod *Heterocypris incongruens* (Bauer, 1940) or 2) by the formation of chromatin bridges between the X's and thereby being pulled mechanically to the same pole as in the thysanuran *Thermobia domestica* (Perrot, 1933; Charlton, 1921; this thesis). A third possibility still exists in that, although the discarded differential segments of the Y's are now sexually inert, they may still serve as mechanical deterents to any X's going to the same pole.

The latter possibility seems normally to be one of the major functions of the Y chromosome. Except for the axolotl (Humphrey, 1942) no other animal is known in which the Y is of significance in sex-determination. White (1948) stated that sex is determined either by (1) the absolute number of X differential segments in a zygote, (2) a ratio between the number of X's and the number of autosomes, or (3) an algebraic difference between the number of X's and the number of autosomes. Bridges (1925, 1932) has shown that in *Drosophila* the autosomes are Σ determining, while X's are Ψ determining and that the sex of the zygote depends on a ratio between the two. Possibly this is the mechanism in *Thermobia*, since no evidence thus far has indicated otherwise.

As stated above, organisms are being constantly subjected to evolutionary pressures from all sides. Internal pressures come from chromosomal variations, external pressures come from the environment acting on the animal throughout life. Creatures which live in different
environments and in different modes as larvae and adults are subjected to two of these selection forces --- one along larval paths and one along adult paths. It is interesting, then, to note, (based on the facts available at present) that in those invertebrate organisms in which environmental evolution has produced its greatest effects sex-chromosome-mechanism-differentiation has lagged. Conversely, those creatures in which ontogeny is the least varied exhibit the most involved sex-determinants. Species which ontogenically lay between these extremes show a corresponding increase or decrease in sex-determinant complexity, based on their relative position on the scale (Fig. 6).
Figure 6. Sex-determinant complexity vs ontogenic complexity.
CONCLUSIONS

From the data obtained in the course of these studies of *Thermobia domestica* Pack. the following conclusions may be drawn:

1. The chromosome number in this species is 32 autosomes plus $X_1X_2$ in males. Females are $32A + X_1X_2$.

2. Sex chromosomes remain linked by a chromatin strand throughout the first meiotic division in males.

3. All diads divide equally during the second meiotic division forming spermatids with either 16 or 18 chromosomes, supporting the postulate of Perrot (1933), and do not form spermatids of a third type containing 17 chromosomes as supposed by Charlton (1921). Both types are apparently viable.

4. All diads must by necessity divide equally in the ova in order to attain constant counts of 34 chromosomes in the males and 36 in the females.

5. Sex of the offspring is totally dependent upon the complement of X chromosomes and not upon the presence or absence of a Y or Y-like chromosome in the zygote. $X_1X_2 + 0$ individuals are male and produce $X_1X_2$ and 0 gametes. $X_1X_1X_2X_2$ individuals are female and only produce gametes containing $X_1X_2$ chromosomes.

6. It is probable that sex is determined by the ratio of sex chromosomes to autosomes and that all individuals possessing a ratio of 2:32 or a value of .063 ($2/32 = .0625$), or any
multiple of that value, will be male while all individuals possessing a ratio of 4:32 or a value of .125 (4/32 = .125) or any multiple of that value, will be female.

7. Individual mature spermatozoa gyrate and undulate in the medium but exhibit almost no change in geographical position.

8. Paired spermatozoa (i.e. those intertwined throughout a section of the posterior, roughly equal to 1/3 their total length) undulate synchronously and are capable of smooth translocatory movements tail first.

9. It is impossible at this time, to deduce if this pairing is at random or whether there is a definite preference of one spermatozoon type for another (i.e. spermatozoa with chromosome counts of 16 + others with 16, or 18+18, or 16+18; or whether only 16+16, 18+18, or 16+18 pairs are formed).
REFERENCES CITED


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Nurse cell metaphase (nurse cells being analogous to the "Sertoli" cells of earlier writers and to the true sertoli cells of mammalian cytology).
PLATE II

A. Spermatogonial metaphase

B. Spermatogonial metaphase showing chromatin bridges
A. Chromosomal condensation, leptotene

B. Continuing condensation, leptotene
PLATE IV

A. Leptotene series

B. Late leptotene
A. Zygotene

B. Zygotene
PLATE VI

A. Early pachytene

B. Pachytene with dense staining sex chromosomes (arrow)
Beginnings of post-pachytene condensation
A. Interim stage, analogous to diplotene-diakinesis in other insects

B. Condensation and tetrad formation, interim stage
Tetrads approaching metaphase plate
PLATE X

A. Chromosomes on equatorial plane, 1st metaphase, polar view

B. 1st metaphase, polar view
A. Metaphase plate, side view

B. Metaphase plate, side view
PLATE XII

A. Metaphase plate, oblique view

B. Metaphase plate, oblique view

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A. Early anaphase, 1st division

B. Anaphase series, 1st division
A. Anaphase series, 1st division

B. Anaphase series, 1st division
PLATE XV

A. Mid-anaphase, 1st division

B. 1st anaphase, sex chromosomes being drawn to opposite poles, both are still joined by chromatin bridge
A. Late 1st anaphase

B. 1st anaphase completed
A. Telophase, 1st division, with X chromosomes being pulled across cleavage plane by chromatin bridge

B. 1st telophase, inception of cytokinesis
PLATE XVIII

A. Cytokinesis, 1st division

B. Cytokinesis nearing completion
End of 1st meiotic division; daughter cells contain unequal chromosome counts, the upper cell with 16 chromosomes and the lower cell with 18; a network of chromatin bridges now connects all of the chromosomes in each cell
A. Beginning of second division; prophase

B. Late prophase; second division
PLATE XXI

A. Chromosomes approaching equatorial plane, second division

B. Second metaphase depicting cells with 16 and 18 chromosomes
A. Early anaphase, second division

B. Mid-anaphase, second division
A. Anaphase series, second division

B. Late anaphase, second division, with equal numbers of chromosomes in daughter cells
Telophase, second division
Comparison of first and second division chromosomes, those of the first division being much larger and much more varied in shape.
A. Dark-staining nuclei of early spermatids beginning to lengthen; in the mature spermatozoan the nucleus will occupy the greatest portion of the total length

B. Progressive nuclear elongation
A. Progressive nuclear elongation

B. Progressive nuclear elongation
PLATE XXVIII

A. Nuclear elongation

B. Nuclear elongation
Nuclear elongation nearing maximum state
A. Mature spermatozoa exhibiting "undulating membranes"

B. Mature spermatozoa
Mature spermatozoa
Meiosis in **THERMOBIA DOMESTICA** Pack.

by

Jan Kankrlik

**ABSTRACT**

Testicular tissue removed from 10 month old fire-brats, **Thermobia domestica** Pack., was prepared for cytogenetic examination by the squash technique. Chromatin staining with acetic orcein and the use of phase contrast microscopy simplified preparatory procedures and preserved the greatest amount of cell integrity.

Photomicrographs taken of the complete meiotic cycle in the male indicated 34 chromosomes in reduction division -- 32 autosomes + \(X_1X_2\). While all autosomes followed normal division patterns, the X chromosomes remained united by a chromatin strand and moved as a unit to one pole. Resultant products of this uneven division were daughter cells containing either 16 or 18 chromosomes.

All diads divided normally during the second phase. Thus, cells with 16 chromosomes produced daughter cells with 16, and cells with 18 chromosomes produced daughter cells with 18, respectively.

Spermatozoa produced by this maturation division were of two types -- those with heterochromatin and those without. Both are apparently viable, and no evidence of degeneration of either type was found.

All studies, thus far, indicate that in **Thermobia** individual spermatozoa are non-motile. Two must intertwine for approximately 1/3 their total length in order to produce translocatory movements.