**'Lampbrush' Phase during Meiosis in
a Species of *Cletus* (Coreidae:
Heteroptera-Hemiptera)**

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What is precisely the nature of the so-called lampbrush processes, especially in the male germ cells, perhaps remains undecided. A substantial quantum of the comparatively recent views devoted to the interpretation of these structures seems to be greatly impelled by the chromomeric or chromonematic hypothesis to which the author individually subscribes. Ris (1945), for instance, considers the lampbrush chromosomes to be merely very long chromonemata and the lateral filaments as the gyres of the laterally separated major coils of the individual chromonema. Hsu (1948), on the other hand, offers an explanation which while linking up three distinct phenomena of spiralization (condensation), heteropycnosis and formation of lampbrush processes is, however, non-committal on the question of the source of origin of these processes. Still more, Srivastava (1954 and 1955), who seemingly differs completely from both Ris and Hsu in his interpretation, regards the lampbrush processes as discrete structures of matrical origin and in association with the chromomeric bodies.

The object of this paper is to describe for the first time the existence of a lampbrush phase during meiosis in a member of Heteroptera and, further, to discuss the relative validity of the views mentioned above in the light of the observations as obtainable from the present study. The work was carried out under the supervision of Prof. M. D. L. Srivastava to whom the author offers his grateful thanks for his criticism, interest and encouragement. The financial support from the Scientific Research Committee, U.P., is also thankfully acknowledged.

Material and method

Adult male specimens of an unidentified species of *Cletus* were collected from the garden of the Botany Department. The testes were fixed in Sanfelice's fluid and the sections were stained with Newton's gentian violet.

The camera lucida sketches reproduced here have been drawn to a magnification of $3000\times$ (approx.).

Observation

The chromosomes on the spermatogonial equatorial plate number 17 (Fig. 1), and of which four are quite large, almost equal in size and nearly kidney-shaped; the third largest pair is rod-shaped so also the odd X-chromosome which is fourth largest element in the complement; a pair of very minute m-chromosomes which mostly remain associated; the rest are round or slightly oval and of nearly equal size. No inter-chromosomal connections are observable.

The course of meiosis can be followed up satisfactorily after the onset of the diplotene stage (Fig. 2), when the nucleus shows ten elements of which the unassociated m-chromosomes as also the X-chromosome are easily discernible. The two largest of the autosomal bivalents usually enclose 3-4 interstitial chiasmata and the smaller bivalents show, on average, 1-3 chiasmata depending on the length of the bivalent. The chromosomes exhibit considerable condensation at the early diakinesis and normally contain 2-4 chiasmata and which, as previously, depend on the length of the bivalent (Fig. 3). The diakinetid bivalents are of particular interest from the point of their morphology, for they appear to possess prominent hair-like structures which recall, of course somewhat remotely, the well known lampbrush processes of the vertebrate oocytes. These structures look like short thick hairs of varying length and project out of the entire body surface of the bivalent. The lampbrush phase persists to the end of diakinesis when the bivalents are further condensed (Fig. 4) and the number of chiasmata further reduced, on an average to 3 in the large and 2 in the small bivalents, but hereafter the processes cease to be observed; whether they are withdrawn or lost is not ascertainable, but the very smooth contours of the metaphase bivalent is suggestive of their being eventually lost.

The behaviour of the m-chromosomes during the prophase of meiosis is rather interesting; for, while all other autosomes undergo regular synapsis, the m-chromosomes mostly remain associated but the association is not chiasmatic. In very rare instances, however, the m-chromosomes remain separate (Figs. 2, 3, 4).

On the first metaphase plate, as observed from the polar configuration of the chromosomes, there are seven autosomal bivalents arranged in a ring with the m-chromosome pair at the centre, and the X-chromosome, which appears bipartite, on the outer border of the ring (Fig. 5). During the first anaphasic movement, the X-chromosome appears to divide synchronously with the separation of the partners of the bivalents, as well as the members of the m-chromosome pair so that at the conclusion of the process each pole shows nine elements (Fig. 6).

The interkinesis is short and is succeeded by a second metaphase in which the chromosomal distribution, as observed from the polar view, con-

forms to a pattern more or less similar to that at the first metaphase (Fig. 7). During the second anaphase, the X-chromosome reaches the pole of its side

Figs. 1-8. Camera lucida sketches of spermatogonial and meiotic chromosomes of *Cletus* sp. ($\times 3000$ approx.). 1, spermatogonial metaphase chromosomes $2n=17$, the rod-shaped X-chromosome being distinguishable by being the fourth largest element in the complement; 2, diplotene with seven autosomal bivalents, the unassociated pair of m-chromosomes and the excentrically situated X-chromosome; 3, early diakinesis with seven autosomal bivalents showing lampbrush processes, the unpaired m-chromosomes and the X-chromosome; 4, late diakinesis with persistent but reduced lampbrush processes; 5, polar view of metaphase I with distinguishable bipartite X-chromosome on the periphery and the m-chromosome pair at the centre; 6, anaphase I showing the synchronous division of the X-chromosome and the separation of the partners of the autosomal bivalents and the members of the m-chromosome pair; 7, metaphase II with the distinguishable bipartite X-chromosome; 8, anaphase II with precocious segregation of the X-chromosome.

somewhat before the daughter chromatids, and hence at the end of the stage, one of the poles, which contains the X-chromosome, shows nine elements and the other pole shows eight elements (Fig. 8).

Discussion

The autosomal bivalents of the *Cletus* sp. become lampbrush during the diakinesis. Lampbrush phase of even more marked degree appears to be associated with the diakinetid chromosomes of certain orthopteroid insects like *Phloebe* sp. (Hsu 1948) and *Catantops* sp. (Hsu 1948), *Chrotogonus* sp. (Srivastava 1954) and *Dissosteira* sp. (Srivastava 1955), and appear to be depicted, if not explicitly mentioned, from the configuration of chromosomes at diakinesis in *Hippiscus* sp. (Ris 1945).

The lampbrush processes, according to Ris, are not structures with any definite entity but are due to the overlapping of the two chromonemata on each side of the diplotene loop and, therefore, resolvable into the gyres of the major coils of the individual chromonema that has become separated laterally. The views of Ris appear to have been unsupported by Srivastava (1954 and 1955) who concludes from his own observation of the meiotic chromosomes in the spermatocytes of *Chrotogonus* and *Dissosteira* that the lampbrush processes are structures with a definite morphology, and even comparable to the lampbrush fibres in the oocyte nuclei of the vertebrates (vide Gall 1954). Hsu's angle of approach to explain the problem is very different as shall be apparent from his ingenious method of linking up three separate features of chromosome morphology, that is, heteropycnosis, condensation and lampbrush formation. Any compromise with Hsu's shall, therefore, imply subscribing to his assertion that heterochromatic heteropycnosis is due to a difference in the capacity to undergo cyclic condensation and not, at least not wholly, to differential nucleic acid synthesis (Darlington and La Cour 1940), so that negative heteropycnosis is, for certain, brought about by the intracellular conditions that permit the growth of lampbrush processes on the sex chromosome (the X-chromosome) and not on the autosomes which now undergo condensation. Conversely, when the intracellular conditions are reverse the result is positive heteropycnosis, that is, the sex chromosome (or chromosomes), by virtue of being positively heteropycnosis undergoes condensation and not the autosomes which now become lampbrush. The nucleoprotein on being polymerised causes the chromosomes either to be coiled or appear lampbrush, only one of the features existing at one time.

Hsu's hypothesis might be considered to have been questioned by Srivastava, as also by my own observations; for, compared to the early diakinetid bivalents in the spermatocytes of the *Cletus*, the bivalents at the late diakinesis remain sufficiently more condensed and yet appear to possess distinct lampbrush processes. This fact in itself strongly suggests the co-existence of condensation and lampbrush formation in any single chromosome and does not, as it would seem, admit the limitations of Hsu's hypothesis. And, then, what seem to have impaired still further the validity of Hsu's claims is the total absence of lampbrush processes in the early spermatogonial

complement in certain grasshoppers, which is nevertheless negatively heteropycnotic (White 1940; Ray-Chaudhuri and Dutt 1947; Ray-Chaudhuri and Bose 1948; Ray-Chaudhuri and Manna 1950 and 1951; etc.). Furthermore, although Hsu believes in the origin of these processes from increased synthesis of nucleoprotein, he nevertheless manages to remain silent over the question of their origin—whether they are derived from the matrix or from the gyres of the chromonemata themselves. These processes appear to have their source of origin in the peripheral matrix of the chromosomes as was originally suggested by Painter (1941) and recently upheld by Srivastava (1954 and 1955). In view of the fact that the staining reaction of the lampbrush processes does not visibly differ from the diakinetid chromosomes (and this fact strongly disputes Serra's (1947) assumption regarding the nature and formation of lampbrush processes), it is logical to ascribe an identical chemical composition to both and which, in turn, implies and rightly so that these processes constitute an integral component of the chromosomes.

Summary

The spermatogonial complement of the *Cletus* sp. is 17, and the mode of sex determination of this insect is XO:XX type. The chromosomes comprise of fourteen autosomes, a pair of m-chromosomes and an odd X-chromosome. The early diakinetid bivalents possess prominent lampbrush processes which persist to the end of diakinesis. These processes originate from the nucleoprotein matrix of the chromosomes and these form an integral part of the latter.

Added in proof. The lampbrush formation in the chromosomes, it is contended (Sharma, G. P. and Ram Parshad, *Nature*, 180, p. 147, 1957), is bound up with depolymerisation of the nucleic acids, but it appears to be a mere speculation unsupported by any factual evidence, whatsoever.

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