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Introductory Remarks

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IV. FUNCTIONAL UNITS

Introductory remarks

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During this session we will be considering the question of what constitute the functional units of eukaryotic genomes. In 1928 the plant cytologist Belling proposed that the chromomeres evident in the chromosomes at leptotene of meiosis represent genes, each being a unit of mutation and recombination as well as of function. The beads-on-a-string notion of genomic organization endured for some 20 years. It received powerful support from the great body of cytogenetic work on the cross-banded polytene chromosomes of *Drosophila*, following their rediscovery in 1933, which soon led Painter (1934) to declare that by studying these objects we would be led to the 'lair of the gene'. The beads-on-a-string concept was challenged by Goldschmidt in 1938, it was swept under the carpet during the great postwar surge of microbial and biochemical genetics, and appeared to suffer the *coup de grâce* when the string as well as the beads were shown to contain one continuous duplex of DNA; in other words, all the genomic material is string.

It is something of an irony that despite falling into disrepute, chromomeres won't go away, and when nowadays we discuss the functional genetic units of eukaryotes we cannot help but return to consider the significance of chromomeric organization. Beermann was the cytologist primarily responsible for re-establishing the reputation of chromomeres. At first, few shoulders were shrugged when Kosswig & Sengün (1947) made their claim that the patterns of compaction of chromosomal material were quite different in the polytene chromosomes of diverse tissues of *Chironomus*, for it was widely assumed that such diversity of compaction merely reflected the diversity of genes active in different tissues. However, Beermann (1952) destroyed this simplistic concept by showing that there is a standard pattern of crossbands along polytene chromosomes which is common to four different tissues of an individual *Chironomus* larva (salivary glands, Malpighian tubules, mid-gut and rectum), a pattern which is, however, overlaid in tissue-specific manner by the decompaction or 'puffing' of those bands within which, or alongside which, transcription happens to be in progress in a particular cell.

Whether or not the individual crossbands of polytene chromosomes, or crossbands and their adjacent interbands, should be accepted as units of function, will be discussed in this session. However, lest they be overlooked, the Y-chromosome loops of *Drosophila* spermatocytes, which are altogether absent from somatic polytene nuclei, almost certainly should be considered as units of function, for at least they behave as units of transcription.

This leads me on to consider for a moment the lampbrush chromosomes of amphibian and other oocytes. Twenty years ago it seemed logical to equate the chromomeres of lampbrush chromosomes and their attendant lateral loops with the chromomeres which constitute the crossbands of polytene chromosomes, and likewise the interchromomeric fibrils of lampbrush chromosomes with the interbands of polytene chromosomes. Today, however, we may reasonably doubt whether this claim for comparability is valid.

Those lateral loops whose heredity has been studied behave as units of inheritance, and this is likely to be true of all. Some lateral loops are units of transcription, but this is certainly not true of all. Some lateral loops consist of several units of transcription, and for at least one example of this kind, the giant loops on chromosome II of *Notophthalmus viridescens*, there is strong circumstantial evidence that successive units are transcribing identical sequences. There are yet other lateral loops consisting of more than one unit of transcription where successive units may be transcribing different sequences. I should be inclined to regard a unit of transcription as equivalent to a unit of function, though the immense lengths of most transcriptional units along the lampbrush chromosomes of organisms with large *C* values poses a considerable problem, one which underlines the as yet unresolved *C* value paradox.

Be all this as it may, what about the chromomeres on the axes of lampbrush chromosomes? Some pairs of lateral loops are unquestionably associated with single chromomeres, and this relation led me to suppose that the single chromomere plus its attendant pair of sister loops constitutes a functional unit. However, there are many 'complex' chromomeres, in the sense that they carry several pairs of lateral loops, with considerable variation from oocyte to oocyte; furthermore, chromomere complexes build up by the lateral amalgamation of previously single chromomeres as transcription shuts off towards the end of oogenesis, or when transcription is artificially blocked by actinomycin D. This leads me to the conclusion that the chromomeres of lampbrush chromosomes, far from being themselves functional units, are passively generated by the transcriptional activity of interspersed functional units; as RNA is transcribed and acid proteins associate with the transcript to form lateral loop matrix, the erstwhile uniformly compacted chromosome is constrained to split up into chromomeres which only remain connected to one another by intervening stretches of non-transcribing chromonema. This view, if correct, sets the chromomeres of lampbrush chromosomes apart from those of polytene chromosomes, for the latter retain their individuality even in the absence of transcription, and perhaps precisely because of the special restraints imposed by polyteny.

So chromomeres remain enigmatic, whether they be transitory features of germ-line chromosomes, or so-to-say 'permanent', differentiated features of somatic polytene chromosomes. It is to the resolution of this problem that we must address ourselves now.

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