SUPPLEMENT TO TOBIAS, P.V. Cytological and cytogenetical studies on the testis of the gerbil.

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CYTOLOGICAL AND CYTOGENETICAL STUDIES ON THE TESTIS OF THE GERBIL, TATERA BRANTSII DRACO.

- - S U M M A R Y - -

of a thesis presented for the degree of Doctor of Philosophy.

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This thesis presents an integrated account of the morphology and behaviour of the chromosomes and the cells in the seminiferous tubules of the gerbil's testis.

As a preliminary to the main study, the spermatogonial chromosomes of the albino rat, a mammal with many small chromosomes, are investigated. The diploid chromosomal number of 42 is confirmed and the complement is analysed by group characterisation and graphical representation.

The gerbil is found to possess 34 chromosomes in dividing spermatogonia and the complement is characterised in the same way as in the albino rat. The relative constancies of the chromosomes are considered first as the end-result of an evolutionary line of descent. By a comparative study of the karyotypic constancies of the gerbil and of other mammals, especially the Rodents, it is concluded that chromosomal evolution in the mammals does follow specific trends, the most important of which to emerge from this study are the tendencies to uniformity and to multiformity displayed by various mammalian families. A

further part of the 'cyto-phylogenetic' and 'cyto-taxonomic' study discusses the evolution of the sex-chromosomes, the peculiar internal differentiation of which makes these chromosomes valuable indicators of directions in mammalian chromosomal evolution.

The modifications of mitotic chromosomal morphology have made it necessary to examine the determinants and the mechanisms of variation of the chromosomes. Valid chromosomal characterisation, it is concluded, requires the determination of a set of relative constancies at the more stable phases of the chromosomes. These stable phases should be explicitly defined in any cytogenetical study.

All the stages in spermatogenesis, from spermatogonial mitoses, through meiosis to spermioteleosis, are described in detail, attention being given to both cytoplasmic and nuclear behaviour. The cytoplasmic changes are analysed and correlated with the sequence of nuclear events. It is shown that the appearance of specific cytoplasmic inclusions is a cytoplasmic manifestation of particular stages of the spermatogenetic wave-cycle. In a study of the mosaic of cytoplasmic inclusions which appear in primary spermatocytes, the behaviour of the centrioles and spindle-fibres is shown to be peculiar to the first meiotic division and to be correlatable with nuclear events, namely the length of prophase and the nature of the meiotic tetrads. The significance of the chromatoid body in spermiogenesis is shown, for the first time, to be similar to that of other formed

elements of the spermatocytes, namely to play a definite rôle in spermiogenesis.

The relations between the chromosomes and the chromatic nuclear membrane are discussed and a cytogenetical interpretation is given of the long-known cytological fact that the chromatic membrane consists of peripherally-aligned chromatin.

Characteristic premeiotic mitoses are described and it is shown that the excessive contraction of the chromosomes in these figures arises from the fact that the nuclei undergo a lengthy prophase, consisting of three stages, the metamorphosis from the dust-like to the crust-like nucleus, the crust-like pause and the final rapid charging and spiralisation. These stages correspond to the lepto-pachytene charging of the chromosomes, the pachy-diplotene pause and reversal and the final rapid diakinetic charging and spiralisation, in the lengthy prophase of the first meiotic division. It is suggested therefore that the premeiotic mitoses are intermediate in their properties between premitotic mitoses and meiosis.

Plasmosomal behaviour in the gerbil receives detailed analysis and the conception of homologous and non-homologous synergism of plasmosomal organisers is elaborated to explain a variety of species of plasmosomal behaviour. Differences in plasmosomal behaviour are shown to reflect subtle differences between cells, which it would be impossible to detect by any other indicator.

The genetical and mechanical properties of

the sex-chromosomes are analysed. It is found that the sex-chromosomes of the gerbil have an interstitial differential segment and two terminal pairing segments - an arrangement so far found in only one other mammal, the cat. The possible lines of evolution of such a sex-chromosome are discussed.

The sequence of events in the nucleic acid cycle is analysed from Feulgen-light green and methyl green-pyronin preparations. The structure and the properties of heterochromatin in the gerbil is examined. It is shown that the biochemical differences between cells, at different stages in the spermatogenetic wave-cycle offer a fresh yardstick, supplementing the morphological indicators, of cell-differentiation in the adult testis and provide evidence for the influence of general environmental factors on cell chemistry and morphology.

The series of changes on the basement membrane of the seminiferous tubule is established: it is demonstrated that the compact mitoses are those of cells undergoing the last two premeiotic mitoses, namely the cells with 'crust-like' nuclei. The dust-like spermatogonia are confronted at a certain stage with two possible lines of development - they may change into premeiotic spermatogonia, divide twice and move on to preleptotene, or they may remain as a reservoir of premitotic spermatogonia giving rise to the next generation of spermatogonia.

Finally, from a study of the various cell-combinations in the four generations of cells in each tubule, various conclusions are drawn about the nature of the spermato-

genetic wave: it is not a self-sufficient wave of regularly-occurring events, propagated within the tubule as a closed system, but is subject to external influences which may come into operation as boosting stimuli at certain stages. At least one element in these later stimuli is associated with pituitary secretion.

The conclusion is drawn that the seminiferous tubule is a reacting-system within which cyclical changes occur in response to stimuli, as yet not fully known. These cyclical changes impress themselves on the individual cells in the tubule in devious ways, according to the type of the cell, its position in the tubule and its biological age. In this way, emphasis has been diverted back from the chromosomes as isolates towards the milieu in which the nuclear changes occur.

The final conception of intra-tubular events throws light on the relation between the environment and the morphology of the chromosomes. There seems to be a direct influence at the chromosomal level, while, at the same time, the chromosomes, by manifesting a special differentiative stage of the cell, indirectly reflect the environmental impact on cell-differentiation.

A combined study of the chromosomes and their context is presented here in the hope that it may illuminate the dynamics of both the chromosomes and spermatogenesis.