SATELLITE DNA

The Mystery Deepens

from our Cell Biology Correspondent

RECENTLY in *Nature New Biology* (240, 102; 1972) Mazrimas and Hatch reported a comparative analysis of the satellite DNA fractions in the genomes of several modern species of kangaroo rats and came up with the interesting speculation that this highly reiterated DNA might have some supragenetic function, for example facilitating recombination and, therefore, genetic diversity. Their basic observation is that highly specialized species of kangaroo rats, which occupy restricted ecological niches, have much less satellite DNA than species which have a broad geographical distribution and their speculation about the function of satellite DNA in recombination is at least as convincing as other suggestions that have been made to account for this portion of a genome, suggestions that include involvement in chromosome pairing or the maintenance of chromosome structure. But the fact remains that one is still at a loss as to the function of satellite DNA, the chief characteristic of which is its comparatively simple and highly reiterated base sequence, and indeed the more that is learnt about the distribution of satellite DNAs the deeper the enigma of its function becomes.

Recently in the *Journal of Molecular Biology* (71, 407 and 419; 1972), for example, Hennig reported the results of an analysis of the satellite DNAs in the chromosomes of *Drosophila hydei* which cannot easily be reconciled with the various functions that have tentatively been ascribed to satellite DNA. Apparently in *D. hydei* several fractions of satellite DNAs, detected by their rapid renaturation, have buoyant densities in the range of that of the bulk DNA and one of these "cryptic" satellite DNAs has a density identical to that of the peak of the bulk DNA. By breeding flies with different genetic and sex chromosome constitutions Hennig has proved that more than 60 per cent of the DNA in the heterochromatic arm of the *X* chromosome is satellite DNA whereas only 15 per cent of the DNA in the heterochromatic arm of the *Y* chromosome is satellite DNA. This finding should be remembered by anybody tempted to jump to the conclusion that heterochromatin can always be equated with satellite DNA. Hennig has also shown that the autosomal chromosomes of *D. hydei* contain 80 per cent of the total DNA of the genome but less than 10 per cent of this DNA is satellite.

Hennig's analysis of the distribution of satellite DNA in the polytene chromosomes of *D. hydei* fat body (each chromosome comprising 128 chroma-

tids) and salivary gland cells (each chromosome comprising 1,024 chromatids) has yielded even more interesting data. Apparently the proportion of satellite DNA in the *X* chromosome decreases with increasing polyteny. On the other hand, some repetitive DNA sequences in other chromosomes have a degree of polyteny as great as that of the non-repetitious sequences. Furthermore, after *D. hydei* DNA is partially digested with exonuclease III some of the fragmented DNA molecules reassociate to form circular structure. This implies, of course, that some highly repetitive DNA sequences are probably interspersed between non-repetitious sequences.

In short, when *D. hydei* chromosomes become polytenic some stretches of satellite DNA are under-replicated whereas others are replicated to the same extent as non-repetitious DNA. How differential replication of satellite DNA sequences is achieved and regulated, why such differential replication is advantageous and how the continuity of chromatids is maintained as this hap-

pens are questions that have to be added to those one has grown used to asking, about satellite DNAs in other organisms.

The origin of satellite DNA during evolution is another riddle, but Sutton and McCallum (*J. Mol. Biol.*, 71, 633; 1972) after comparing satellite DNAs in *Mus musculus* and asiatic species of mice from Thailand have recently proposed a possible mechanism. They have found that satellite DNA from several Thailand species is able to cross-reassociate with satellite DNA of *Mus musculus* to form poorly matched hybrid duplexes. From these and other data, notably analyses of pyrimidine tracts, they suggest some ancestral species possessed a short unstable sequence of perhaps only 8–20 base pairs. If, as different populations diverged, different mutations accumulated in this sequence and then, independently in the different populations, the diverging sequences were massively reiterated coincident with speciation, the result would be what is observed, namely a set of satellite DNAs with related but far from identical sequences.

Press-studs in Chromosomes

Engelhardt and Pusa report in next week's *Nature New Biology* (December 6) that use of the electron microscopy stain, ruthenium red, which preferentially stains for carbohydrates, leads to improved visualization of the elements involved in the attachment of chromosomes to the nuclear envelope. When stained with ruthenium red, nuclear pore complexes seem bipartite with the appearance of a "press-stud". 30–40 Å fibrils connecting condensed chromatin and telomeres with the inner half of the pore complexes are also clearly visible.

Nuclear pore complexes and the lateral elements of synaptonemal complexes of late pachytene are similar in terms of staining properties and structure. The lateral elements appear to be flanked on two sides by a row of ringlets facing the central space, which is probably filled with microfilaments. The authors suggest that the ringlets are the interior halves of the nuclear pore complexes which are deposited on microfilaments in the build-up of the synaptonemal complex, the microfilaments being derived from the inner nuclear membrane.

Another possible example of ringlets derived from nuclear pore complexes is found in the premeiotic *X* chromosome of *Acheta*. Ruthenium red staining reveals structures on the surface of the chromosome which appear to correspond to the inner halves of the bipartite nuclear pore complexes. Engelhardt and Pusa suggest, therefore, that the inner nucleoplasmic half of the pore complex is a permanent chromosomal element — "the cyclo-

mere"—which can be detached from the other half located in the outer nuclear membrane.

Suggested roles for these "press-stud" structures are manifold: synaptic detachment at zygotene, followed by restoration of chromatin-nuclear envelope connexions in pachytene may be implemented by pore complexes; the exterior halves of the complexes might peel off in nuclear envelope-derived annulate lamellae involved in the construction of the envelope at telophase; pairing of homologous chromosomes and/or intertelomeric or intercentromeric fibres may depend on the "press-stud" mechanism; the "press-stud" function in the nuclear envelope may be related to heterochromacy.

Cyclomeres may contain the proteins necessary for DNA replication. They might also be the sites of chromosomal acidic proteins, thus functioning in transcriptional control. There is substructural evidence, for example, that cyclomeres are transcription sites.

Cyclomeres may contribute to chromatin condensation, because hyaluronidase is an uncoiling agent. If cyclomeres characterize condensed chromatin then the bands of polytene chromosomes may turn out to be aggregates of cyclomeres. If these tentative roles are verified, then cyclomeres are alternatively bound to the nuclear envelope and free in different configurations depending on the functional phase they are in. Thus, as controlling and attaching elements, pore complexes and cyclomeres would play an essential part in chromosome organization.