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Mapping Chromosome Centromeres by the Analysis of Unordered Tetrads

IN many fungi, such as most of the Ascomycetes and Ustilaginales, the products of meiosis are arranged regularly in a linear order, and by examining them or by isolating them in order, it is possible to distinguish between segregation of a pair of allelomorphs at the first and at the second division of meiosis. The relative frequencies of first- and second-division segregation for a given locus are dependent on the frequency of crossing-over between that locus and the centromere of the chromosome. Hence, the centromere can be plotted on the cross-over map of the chromosome.

In an unordered tetrad, in which the products of meiosis are not linearly arranged, direct observation of the relative frequencies of first- and second-division segregation for particular loci is not possible. When segregation occurs for two pairs of allelomorphs (A/a and B/b), a proportion of meioses will result in all four products differing from one another (1 AB, 1 ab, 1 Ab and 1 aB), the remainder having two types of products (either 2 AB and 2 ab, or 2 Ab and 2 aB). If the loci are linked, the proportion of four-type tetrads is dependent on the frequency of crossing-over in the segment of chromosome lying between them. On the other hand, if the loci are not linked, the relative frequencies of two- and four-type tetrads are dependent on the frequencies of crossing-over between the loci and the centromeres of their respective chromosomes. The relationship in the latter case has been shown[1,2] to be :

$$p = x + y - \frac{3xy}{2},$$

where p is the proportion of four-type tetrads and x and y are the proportions of second-division segregation at the A and B loci, respectively. From this expression it is not possible to determine the precise frequencies of first- and second-division segregation for either locus. However, by introducing a third independent locus, the required proportions of first- and second-division segregation can be determined for all three loci. Lindegren[3] indirectly made use of this fact in mapping the centromeres of chromosomes in yeast, employing a graph of the proportion of two-type tetrads for various frequencies of second-division segregation at two loci. However, this method is awkward, as it would require a three-dimensional graph for a straightforward solution. Perkins[2] has pointed out that an algebraic solution is possible, but has not obtained the actual expressions for the proportions of first- and second-division segregation for the three loci, such as would be needed in applying the method to experimental data. The algebraic solution is as follows.

With a third pair of allelomorphs (C/c), such that the locus of C shows no linkage to either the A or B loci,

$$q = y + z - \frac{3yz}{2} \quad \text{and} \quad r = x + z - \frac{3xz}{2},$$

where q and r are the proportions of four-type tetrads for loci B and C and for loci A and C, respectively, and z is the proportion of second-division segregation at the C locus. The solution of the three simultaneous equations gives :

$$x = \frac{2}{3}\left[1 \pm \sqrt{\frac{4 - 6p - 6r + 9pr}{4 - 6q}}\right]$$

$$y = \frac{2}{3}\left[1 \pm \sqrt{\frac{4 - 6p - 6q + 9pq}{4 - 6r}}\right]$$

$$z = \frac{2}{3}\left[1 \pm \sqrt{\frac{4 - 6q - 6r + 9qr}{4 - 6p}}\right].$$

When there are two real solutions to any of these formulæ, one is necessarily greater than 2/3 and the other less than 2/3. Since proportions of second-division segregation greater than 2/3 are likely to be rare[4], the smaller value is more likely to be the true one.

These expressions could be usefully applied in many analyses of unordered tetrads. Thus, Quintanilha and Balle[5] analysed more than two hundred tetrads of spores from the tetrapolar Hymenomycete *Coprinus fimetarius* (L.) Fr. showing segregation, not only for the two loci for heterothallism, but also for a gene causing dwarfness ('nanism'). They found no linkage between the loci, and so their unpublished tetrad data should enable the three loci to be mapped in relation to the centromeres of their respective chromosomes. Lindegren[3] has published extensive results from tetrad analysis in yeast. The formulæ above provide a simpler and more accurate means of mapping centromeres than does his graphical method. The following example from his data shows the use of the formulæ. Three unlinked loci a (mating-type), ad (adenine-less) and g (galactose-nonfermenter) gave the following fractions of four-type tetrads : a ad 91/169, a g 167/327 and ad g 45/147. From the above formulæ, the proportions of second-division segregation for the three loci are a 0·474 (or 0·859), ad 0·222 and g 0·128, and hence the distances in cross-over units of the three loci from their respective centromeres are a 23·7 (or 42·9), ad 11·1 and g 6·4. Lindegren's corresponding figures, obtained graphically, are a 23·6, ad 11·25 and g 6·25.

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South African Fossil Hominoids

PROF. S. ZUCKERMAN'S remarks concerning the teeth of the fossil Australopithecinæ of South Africa[1] call for certain comments.

In the first place, it is open to serious question whether the major dimensions and indices of individual teeth can by themselves provide adequate