

However, this is not gynodioecism (where all plants in a population are seed fertile), but functional true dioecism.

In the case of *Mussaenda* the heterostylous and dioecious species occur in the same genus and there is no difficulty in tracing the evolutionary connection. This is a very different matter from a gynodioecious species in a family where heterostyly and self-incompatibility are both unknown—as in *Silene maritima* and the Caryophyllaceæ. The evolutionary story in the *Silene* case remains to be worked out and no generalisations can be made from it at this moment.

4. REFERENCES

- BAKER, H. G. 1948. Corolla size in gynodioecious and gynomonocious species of flowering plants. *Proc. Leeds Phil. Soc. (sci. sect.)*, 5, 136-139.
- BAKER, H. G. 1953. Race-formation and reproductive method in flowering plants. *Symp. Soc. Exp. Biol.*, 7, 114-143.
- BAKER, H. G. 1958. Studies in the reproductive biology of West African Rubiaceæ. *Journ. West African Sci. Assn.*, 4, 9-24.
- BAKER, H. G. 1959. Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harb. Symp. Quant. Biol.*, 24, 177-191.
- BAKER, H. G. 1966. The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceæ. *Evolution*, 20, 349-368.
- CROWE, L. K. 1964. The evolution of outbreeding in plants. I. The angiosperms. *Heredity*, 19, 435-457.
- EAST, E. M. 1940. The distribution of self-sterility in the flowering plants. *Proc. Amer. Phil. Soc.*, 82, 449-518.
- FRYXELL, P. A. 1957. Mode of reproduction of higher plants. *Bot. Rev.*, 23, 135-233.
- MARSDEN-JONES, E. M., AND TURRILL, W. B. 1957. *The Bladder Campions*. Ray Society, London.

THE CO-ORIENTATION OF NON-HOMOLOGOUS CENTROMERES

K. R. LEWIS

Botany School, Oxford

and

B. JOHN

Department of Genetics, Birmingham

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MULTIPLE and multivalent associations can orient in various ways though the possibilities are limited somewhat by the form of the association as determined by chromosome morphology and the frequency and distribution of chiasmata. The factors influencing the orientation of structurally similar associations have been discussed frequently and generally in relation to simple rings of four chromosomes.

The discordant arrangement depends on the co-orientation of only two centromeres which are at opposite sides of the ring. In multiple associations these are non-homologous and neither in them nor in multivalent associations is this orientation expected to give numerically equal separation. This can be achieved, however, when only two pairs of centromeres co-orient. In

the case of quadrivalents this behaviour is chromosomally disjunctional because all four chromosomes are homologous and their order in the association is variable. Hence high fertility in autotetraploids is often associated with high quadrivalent frequency irrespective of the frequency of zig-zag orientation. For these same reasons there is no need or basis for distinguishing between adjacent homologous (adjacent-2) and adjacent non-homologous (adjacent-1) orientation.

This distinction, however, can and must be made for multiple associations where the chromosomes are not completely homologous and, consequently, their order in the multiple is fixed. Both give genic non-disjunction but the former depends on the co-orientation of non-homologous centromeres while the latter follows the co-orientation of homologous ones.

The disjunctional (alternate) orientation of multiples requires more co-orientations (see below) than other arrangements. On the basis of random co-orientation (see Burnham, 1956; Rickards, 1964; John and Lewis, 1965; and contra La Chance *et al.*, 1964) the frequency of alternate orientation in rings-of-four should equal the joint frequency of the two types of adjacent orientation which should equal each other.

If, however, homologous centromeres, which alone lie alongside each other at pachytene, are preferred in co-orientation, the adjacent non-homologous arrangement would preponderate over the other type of adjacent orientation. Such a preponderance has been inferred on the basis of breeding results the implication being that the homology or otherwise of associated centromeres has a bearing on their orientation (La Chance *et al.*, 1964). This we deny.

It must be admitted that only the homologous centromeres of non-interchanged arms are consecutive in the opened-out ring. The others (in the differential segments of unbranched pachytene crosses) while aligned with their homologous centromeres at zygo-pachytene, are separated at diakinesis by chromosomes the numbers of which depend on the size of the association and the position in it of the centromere-pairs under consideration.

Thus, only in rings-of-four can there exist a comparable mechanical relationship between homologous centromeres on the one hand, and non-homologous centromeres on the other. And only in this special case, therefore, could any preference based on homology be entertained. The situation can be compared with the competitive conditions of pairing which exist in allopolyploids like *Primula kewensis* and where the degree of preferential autosyndesis is considerable despite the high frequency of allosyndesis which obtains under the non-competitive conditions of pairing in the diploid (contra Dawson, 1962).

Even so, in closed multiple associations with regular alternate orientation, each centromere is co-oriented with respect to both its neighbours which means that there are as many co-oriented pairs as there are chromosomes in the ring. Thus, even in a ring-of-four, disjunctional separation depends as much on the co-orientation of non-homologous centromeres as on that of homologous ones while in the largest ring of *Oenothera* non-homologous co-orientations exceed homologous ones by a factor of six ($2n-2$ versus $2 = 12:2$). In view of the regularity shown by this multiple one can hardly conclude that non-homologous centromeres are at a disadvantage in co-orientation. A comparable argument could be developed in relation to the behaviour of multiple sex-chromosome associations.

It is true that, under certain conditions, homologous centromeres segregate from multiple associations more often than expected and may do so invariably (Burnham, 1956). But this preferential orientation does not depend on homology *per se* but on position as the exclusive occurrence of the opposite behaviour shows (Lewis and John, 1963). And preferential position, in turn, may depend on relative arm lengths, crossing-over in interstitial segments or the prolongation of parallel pairing in achiasmatic meiotic systems (fig. 1, a, b and c, respectively).

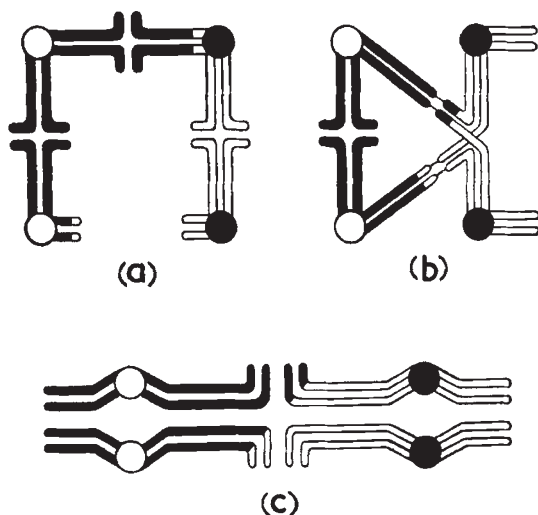


FIG. 1.

REFERENCES

- BURNHAM, C. R. 1956. Chromosome interchange in plants. *Bot. Rev.* 22, 419-552.
 DAWSON, G. W. P. 1962. *An introduction to the cytogenetics of polyploids*. Blackwell, Oxford.
 JOHN, B., AND LEWIS, K. R. 1965. *The Meiotic System, 1-335*. Springer-Verlag (Vienna, New York).
 LA CHANCE, L. E., RIEMANN, J. G., AND HOPKINS, D. E. 1964. A reciprocal translocation in *Colchyomyia hominivorax* (Diptera: Calliphoridae). Genetic and cytological evidence for preferential segregation in males. *Genetics*, 49, 959-972.
 LEWIS, K. R., AND JOHN B. 1963. Spontaneous interchange in *Chorthippus brunneus*. *Chromosoma (Berlin)*, 14, 618-637.
 RICKARDS, G. K. 1964. Some theoretical aspects of selective segregation in interchange complexes. *Chromosoma (Berlin)*, 15, 140-155.