subunits in the A-protein and disk states both at equilibrium in the absence of RNA and also during the assembly reaction. Such a microequilibrium implies that the continuity of the disk structure cannot be assumed, and so the arguments for the gliding of a dislocation are not safe in this system.

It seems to us unjustified to make a direct transfer of concepts from the theory of crystal dislocations developed for metals and other strongly bonded crystals, composed of relatively rigid units, to the field of large biological molecules like TMV protein, which deform easily, which associate only weakly into aggregates of limited extent, and which are in rapid association-equilibrium in solution. For this reason we prefer to continue using simple, if somewhat imprecise, notions, of a "ruck" moving, for example, rather than to formulate detailed mechanisms as does Dr Harris.

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## Dislocations in Tobacco Mosaic Virus

I Do not allege that the way Butler and Klug use "dislocation" is incorrect. I merely point out that as crystal dislocations occur in tobacco mosaic virus (TMV) and may perform important functions, "confusion is bound to arise if the term dislocation continues to be used loosely". Confusion is even more likely when the term is used in the same context by the same group in both strict ("screw dislocation"1) and loose (for example on p. 133 of ref. 2, "step dislocation at the end of the single helical rod") senses.

Butler and Klug deny my statement that members of their group refer to helical forms being dislocated or containing a dislocation. The second quotation above is sufficient to show their denial is false. I can supply a corroboratory quotation from every source I cite.

There is nothing wrong with taking the disk as the reference-I find a different reference more convenient. My reference is similar to Klug's radial projection3, which he and his coworkers use elsewhere but not here.

Just as Butler and Klug found it necessary or convenient to present detailed models "to give some general feel for the process", so have I. Without detailed models an explanation would be difficult if not impossible. What may appear to them "differences in detail" are in fact important differences: as I explain, one of their mechanisms converts the disk directly to a portion of a helix with the same number of subunits per turn as in the completed virion whereas the other requires an additional step.

My mechanisms, based on theirs, depend no more on "continuity of the disk" than do theirs. Just because subunits can be gained or lost in no way rules out dislocations. On the contrary, a very important mode of movement of dislocations requires the loss or gain of subunits<sup>4</sup>. It is similar to the mechanism of climb that I describe.

In their final paragraph Butler and Klug express an opinion which I am confident will be proved wrong. What can be stated with certainty is that dislocations are present in many types of biological structures. The bibliography on dislocations in biological structures which I am compiling already contains more than a hundred references.

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- <sup>1</sup> Butler, P. J. G., *Nature*, 233, 25 (1971).
  <sup>2</sup> Durham, A. C. H., thesis, University of Cambridge (1970).
  <sup>3</sup> Klug, A., Crick, F. H. C., and Wyckoff, H. W., *Acta Cryst.*, 11, 199 (1958).
  <sup>4</sup> Harris, W. F., and Scriven, L. E., *Nature*, 228, 827 (1970).

## Low Mating Frequencies in an African Butterfly

DURING mating a male butterfly leaves a spermatophore in the bursa copulatrix of the female. One spermatophore results from each mating and so the number of times a female has mated can be determined by dissection of the bursa. Spermatophores can almost always be recognized even when old and collapsed and they persist throughout the life of the female<sup>1</sup> and in old and dried out museum specimens. In most butterflies the sex ratio is 1 to 1, wild-caught females are hardly ever virgins, most have mated at least once, and some have mated up to ten times.

The African butterfly, Acraea encedon, is exceptional in that in some areas, especially where the environment has been disturbed by man, there are populations which contain very few males. In Uganda there are populations where the males occur at frequencies of less than 4%, while elsewhere in Uganda and in some other parts of Africa the sex ratio is normal<sup>2</sup>. The low sex ratios of some of these populations are known to have persisted for at least forty-five breeding generations. Acraea encedon is not parthenogenetic<sup>2</sup> and to produce fertile eggs a female must mate, a process which lasts several hours. By breeding the butterflies on a large scale we have shown that there are two kinds of female, one producing females only, the other producing males and females in the expected 1 to 1 ratio, but so far we have not been able to find a way of distinguishing between the two kinds of female other than by breeding from them. We have postulated that the inheritance of the all-female broods is through a Y-linked gene (in butterflies the female is XY) causing meiotic drive in the Y chromosome, although we cannot entirely rule out the possibility of a cytoplasmic factor<sup>3.4</sup>.

In populations where there are fewer than six males to every hundred females it is inconceivable that all females can be mated as males can mate only once a day and live for a maximum of two weeks. Females in predominantly female populations frequently lay infertile eggs on plants which are not the larval food and even on each other<sup>2</sup>, and this alone suggests that many females remain unmated. Confirmation that many females do not mate has been obtained by dissecting samples of them for spermatophores from populations with various sex ratios (Table 1). From the spermatophore counts, most of the females in populations with few males are unmated and, of those that are mated, most have done so once only. In the six samples from four Uganda populations, less than a quarter of the females had mated, and in one of these samples all twenty-nine females were unmated. But in a sample from Sierra Leone where the sex ratio is nearly 16%, about 80% were mated, while in a small sample from a normal population in Sierra