

## Regulatory Processes Shown by the Fused Feather Primordia under Grafted Condition<sup>1,2</sup>

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As has been noted by several workers (Willier and Rawles, '31; Rawles, '36), when a whole or a piece of early chick blastoderm is transplanted to the chorio-allantoic membrane of older embryos, the integument usually takes the form of vesicles in the membrane. As these vesicles are inside-out, feather primordia are enclosed within these vesicles when they are developed. This is also true when pieces of older embryos are used for donors, although in these cases the covering walls of vesicles are frequently ruptured and the feather primordia are exposed directly on the surface of the membrane (fig. 1).

When the integument forms a vesicle instead of spreading flatly, feather primordia are often so densely aggregated within a limited area that some adjoining ones are compressed and fused together, and show a tendency to regulate themselves to produce a single primordium. This fact I had already reported shortly ('42). As more materials, however, have been gathered since, further observations and considerations on these matters are dealt with in this paper.

The materials of fusing feather primordia or fused ones were obtained by using pieces of from 2 to 6 day embryos for donors. Their trunk regions were transversely cut two somites wide, and each strip was transplanted to the chorio-allantoic membrane of older embryos. The method of transplantation was as usual and grafts remained on the hosts 8 or 9 days.

### Observations

A total of 75 grafts which contained feather primordia have been examined. These include 22 of the 2 day, 10 of the 3 day, 18 of the 4 day, 8 of the 5 day and 17 of the 6 day embryos. Among these, fusing or fused feather primordia were observed in 40 grafts: 17 out of 22 in the 2 day (77.3%), 6 out of 10 in the 3 day (60.0%), 9 out of 18 in the 4 day (50.0%), 3 out of 8 in the 5 day (37.5%) and 5 out of 17 in the 6 day embryos (29.4%). Results indicate that the frequency

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of occurrence of fusing or fused feather primordia decreases as the age of donors increases.

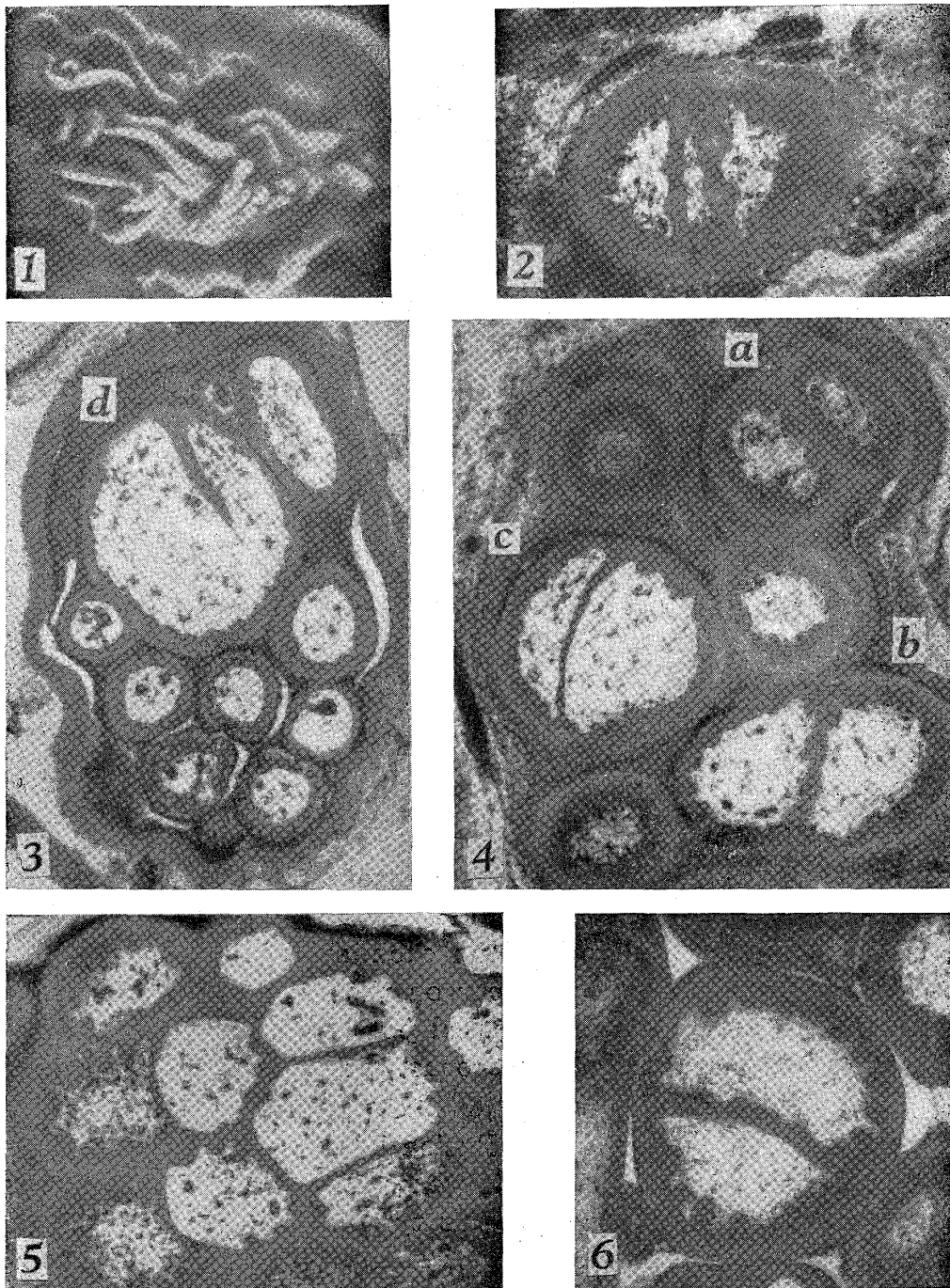


Fig. 1. Feather primordia are exposed directly on the surface of the chorio-allantoic membrane. This example (258-13) was obtained by transplanting a piece of 6 day embryo.  $\times 10$ . 2. Three primordia are fused into one. This example comes from 2 day embryo.  $\times 100$ . 3. Median fused wall is broken through in *d*.  $\times 100$ . 4. Three types of fusion are shown in *a*, *b* and *c*. These are in the same graft with that shown in fig. 3. The graft (251-19) comes from 2 day embryo.  $\times 100$ . 5. Many primordia are fused. The graft (236-25) comes from 4 day embryo.  $\times 100$ . 6. An example of fusion by two primordia. The graft (251-6) comes from 2 day embryo.  $\times 100$ .

Fusion occurs by twos, threes or more of the feather primordia, the first cases being the most abundant (figs. 2, 3, 4 and 5). As the examples of fusion by more than threes are few and pictures shown by them are rather complicated, some representative cases by the twos are selected and presented for an analysis in the following. These can be classified into four types according to their grade of union.

Type I (251-19*a*; fig. 4, *a*). This type seems to represent the cases in which two primordia are in the process of fusing. At the plane of contact, outer stratified sheath layers of both primordia are fused into a common layer, and this layer becomes somewhat thinner. The middle and basal layers of their epidermis are still holding circular forms in cross section, and the primordia of future barbules which are evaginated out of these layers into the inner papilla are well formed around the inner surface of the epidermis. Their number is counted 5 on each side of the medial contact portion, while 10 on each of the remaining portions of both primordia. As these primordia have their own tips and roots, they separate each other at the levels more distal or more proximal than shown in fig. 4, *a*.

Type II (251-19*b*; fig. 4, *b*). In this type, fusion of two primordia is taking place along their whole length. They are flattened against each other taking an elliptical form in cross section. The ratio between longer and shorter axes of this form is about 3:2. The epidermis at the fused portion becomes also thinner, and barbule primordia on both sides of this portion are moreover in a state of degeneration; that is, they become inconspicuous and irregularly shaped, and distances between them are somewhat extended. On the level shown in fig. 4, *b*, where degeneration goes so far, to count their number exactly is difficult; but, this may be assumed to be 4 on each side as the same number of barbule primordia come to appear on the level a few more sections proximally. On the free semi-elliptical portion, 11 of them are observed in one of the pair, while in the other their number is not certain; but, this is approximately 9 or 10.

Type III (251-19*c*; fig. 4, *c*). Fusion of two primordia occurs also along their whole length. Main difference of this type from the former exists in that the cross section of this type shows a circular form instead of an elliptical. The medial fused wall is much thinner and barbule primordia are not noticed anymore on the level shown in fig. 4, *c*. But they appear again a few more sections proximally and 6 of them are on one side and 5 on the other. On the free semi-circular arcs, 10 or 11 are noticed in both primordia.

Type IV (251-19*d*; fig. 3, *d*). Although the paired primordia show a circular form in cross section like the former, their medial fused wall loses not only its barbule primordia completely along its whole

length, but some part of it has been broken through and the papilla of both primordia are united. This is especially true at their proximal part where only a trace of median wall is seen to be attached to the side of the outer wall. The number of barbule primordia is 8 on the one of the semi-circular arcs, while this is more than 9 on the other. At the proximal part where no median wall exists, they are counted 19.

### Considerations

Results of transplanting pieces of embryos ranging in age from 2 to 6 days show that fusion of feather primordia is one of the features of common occurrences under the condition of chorio-allantoic grafting, although some differences in frequency are found according to the donors' ages. Such behavior in the chorio-allantoic membrane may be due to the abnormal condition of the graft. While normal feather primordia grow freely on the surface of the integument, those in the grafts develop within the vesicle where the space to grow is much limited. It is clear that such a situation must have led the primordia to be compressed and united together.

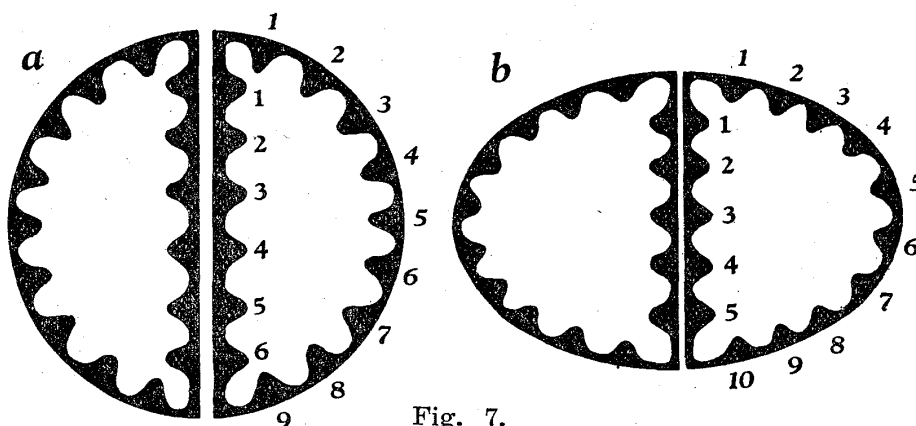


Fig. 7.

The fact that the frequency of occurrence of fusing primordia or fused ones decreases as the age of donors increases means that there are changes of some sort that may be referred to the lack of plasticity taking place in the feather producing tissues as their age progresses, and this also means that the general tendency that the younger organs or tissues are, the more easily they tend to regulate themselves is shown by the feather primordia.

In cases in which the fusion of feather primordia occurs, the regularity of arrangement of the barbule primordia is disturbed in most cases. However, some adequate materials in which it is maintained to a certain degree give some hints to the process of fusion.

If two circles are assumed to be compressed mechanically so as to make one circle as shown in fig. 7a, the ratio between the length of

the medial fused portion and that of the remaining semi-circular arc must be  $2:\pi$ . If these paired circles are made into an elliptical form having ratio of its longer and shorter axes  $3:2$ , the ratio between the length of the medial fused portion and that of the semi-elliptical arc must be about  $2:4$  (fig. 7*b*). Then, if two feather primordia with 15 barbule primordia are fused together and formed a circle or an elliptical form in cross section, distribution of barbule primordia on the median fused portion and on the semi-circular or semi-elliptical arc, should be about 6 and 9 in the case of a circle, and about 5 and 10 in an elliptical form (fig. 7). Although actual results are almost near the above figures, somewhat less number of barbule primordia on the median fused portion and more of them on the semi-circular or semi-elliptical arc than those of the calculated are observed. In example 251-19*c*, where the cross section is a circle, the distribution of barbule primordia is 6 or 5 and 11 or 10, and in example 251-19*b*, which has an elliptical form in cross section, it is 4 and 11 on each. A few examples not presented before also show the similar results: for instances, the distribution of barbule primordia in example 251-6 (fig. 6) is 5 and 11, that in example 264-8 is 4 and 11. Both have nearly a circular form in cross section.

Together with the findings described in the previous observations, these results can be interpreted as follows. When two feather primordia are compressed and put together, their outer epithelial layers at the contact portion are fused into a common layer (stage shown by Type I), and both of the remaining free portions gradually cooperate together to take a form of the least surface: that is, they transform themselves from a cylindroidal into a cylindrical form as a whole (stages shown by Type II and Type III). While these are going on, some cell materials at the contact portion move out so as to be a part of the outer wall, and thus the thinning out of the medial fused portion or its being broken through and a degeneration of barbule primordia result as shown by Type III and Type IV.

Though the phenomena of regulation in general are quite complicated matters, the so-called Roux's simple component such as the law of the least surface is working when the feather primordia are fused and regulated into one.

### Summary

1. When transected pieces of embryos ranging in age from 2 to 6 days are transplanted to the chorio-allantoic membrane of older embryos, fusion of feather primordia is commonly observed. Fusion occurs by twos, threes, and more of them, the first cases being the most abundant.

2. Frequency of occurrence of fused feather primordia decreases as the age of donors increases. This shows that some changes that may be referred to the plasticity are going on in the course of ages.

3. Cases in which the fusion of two feather primordia occurs can be classified into four types according to their grade of union. Some representative examples of these are described.

4. Some adequate examples, in which the regular arrangement of barbule primordia is maintained, give a hint as to the analysis of fusing processes. In the fusion and regulation of feather primordia, the part which is played by the law of the least surface appears to be of prime importance.

#### Literature

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