The mechanism of feather pattern development in the chick

II. Control of the sequence of pattern formation

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SUMMARY

During the development of the dorsal feather pattern, a wave of morphogenesis sweeps across the skin forming successive anteroposterior rows of feather primordia. The preceding paper in this series showed that the morphogenetic wave is almost immediately preceded by a wave of determination at which feathers sites are established row by row (Davidson, 1983). The present paper reports an in vitro experimental investigation of the movement of these waves across the skin.

The waves pass undisturbed across a cut made before the pattern forms. Although cultured skin does not grow and consequently forms only a few rows of primordia, the morphogenetic wave takes the same time to cross the prospective feather tissue as in vivo, indicating that the passage of this wave through cultured skin reflects its traverse of the entire pattern in vivo.

These results show that the movement of the waves of determination and morphogenesis does not depend on the propagation of any signal across the skin immediately ahead of primordium formation. Their movement derives from a gradient in the temporal differentiation of the skin, established before stage 29. In this respect, the temporal control of feather development in the chick skin resembles the control of somite development in the amphibian paraxial mesoderm (Pearson & Elsdale, 1979). The present results therefore suggest that a programmed gradient of temporal differentiation across the prospective patterned tissue is a common component of the mechanisms which form regular, repetitious patterns in vertebrate embryos.

INTRODUCTION

During embryogenesis, regular patterns of repeated units generally form at a moving frontier, or 'wave' (Zeeman, 1974), which sweeps across the prospective patterned area, transforming seemingly bland tissue into an array of patterned elements: examples are the patterns of somites (Pearson & Elsdale, 1979), feathers (Holmes, 1935), vibrissae (Hardy, 1951), reptilian teeth (Edmund, 1969), and fish scales (Neave, 1936). It is not known what governs this temporal order of gene expression across the tissue, or, indeed, if the temporal development of each of these diverse patterns is controlled in essentially the same way.

The only indication of the nature of this temporal control comes from studies of amphibian somitogenesis, where the sequence of pattern development is

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governed by an anteroposterior gradient in the time of somite formation. This gradient is programmed across the entire presomitic tissue before the visible pattern begins to form (Deuchar & Burgess, 1967; Cooke, 1975; Pearson & Elsdale, 1979). Both experiments (Elsdale & Pearson, 1979) and theory (Cooke & Zeeman, 1976) suggest that this temporal organisation is crucial for the development of a regular somite pattern. It is, perhaps, to be expected that the development of the prospective somite tissue should be temporally programmed before the pattern forms, for somitogenesis displays a high degree of integration: both the number of somites and the time taken to form the whole pattern are invariant, even in experimentally reduced embryos (Hamilton, 1969; Cooke, 1975).

In this paper, I show that a similar temporal organisation governs the development of a superficially much simpler pattern, that of feather primordia in chick dorsal skin, where equally spaced elements simply continue to form until the available area is filled.

The dorsal feather pattern develops between the 6th and 8th days of incubation (stages 29 to 33+ (Hamburger & Hamilton, 1951)) as successive anteroposterior rows of feather primordia form, in mediolateral sequence, on both sides of the dorsal midline to fill a well-defined region of the skin, the spinal pteryla (see Sengel (1976) for a review). The number of feathers depends on the area of skin available during development (McLachlan, 1980; Davidson, 1983). A wave of feather determination (that is, the commitment of groups of cells to form primordia at particular places) moves across the skin almost immediately ahead of the visible wave of primordium formation (Davidson, 1983).

It has been suggested, on indirect evidence, that each row of developing feather primordia induces the formation of the next by the propagation of a 'wave of morphogenetic activity' from cell to cell across the skin immediately ahead of primordium formation (Sengel, 1976). Such a mechanism contrasts sharply with the development of the somite pattern. It implies that the prospective pteryla is not temporally programmed, but is initially a rather bland tissue in which feather development is initiated at a special locus.

There is, however, evidence against a propagation mechanism. Using chick thigh skin cultured on the chorioallantoic membrane, Linsenmayer (1972) showed that a normal feather pattern develops beyond a cut made 1 day before primordia form, and that feather positions were yet to be determined when the skin was cut. These experiments did not, however, exclude the possibility that development beyond the cut involved the formation of a secondary source of propagation. The present paper takes up the investigation at this point.

**MATERIALS AND METHODS**

**Skin preparation and culture**

White-Leghorn, or Brown-Leghorn eggs were incubated in a humidified atmosphere at 38.5°C. (In the experiment to compare the time course of
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development *in vivo* and *in vitro*, eggs were maintained at 38.5 °C until 6 days 2 h of incubation: thereafter, cultures and eggs were incubated together at 36.3 ± 0.2 °C in order to slow development and thus increase the temporal resolution of the assay.) To avoid differences in the rate of development as a result of temperature differences within the incubator, the positions of eggs were changed several times during the period of incubation. Dorsal skin of the appropriate stage was removed from the embryo and cultured on collagen as described previously (Davidson, 1983).

**Operative treatments**

In the transection experiments, skin was cut using a sterile scalpel. Each scalpel blade was used for only two or three cuts and was dried between use to avoid displacing the skin by surface tension.

**Observation of skin development**

Skin *in vitro* was observed under a Wild dissecting microscope (Davidson, 1983). In order to assay the development of the feather pattern *in vivo*, freshly excised skin was mounted on collagen and observed in exactly the same way, within 2 min of excision.

The numbers of rows of primordia referred to in the Results indicate all the rows from one side of the pteryla to the other.

**RESULTS**

**The development of the feather pattern in transected skin**

In order to test the hypothesis that the waves of feather determination and morphogenesis are propagated, the skin was cut ahead of these waves. On the propagation hypothesis this would disturb the time course of primordium formation. This is so even if a secondary propagation source were set up beyond the cut (Linsenmayer, 1972), since the time course of development would depend on the time taken to set up this new organisation. Such a response could, however, lead, coincidentally, to apparently normal development in skin cut at a particular mediolateral level: pterylae were therefore cut at different distances from the midline.

Skin was excised at stage 29 (before, or as, the initial row formed) and divided into two pieces by an anteroposterior cut made on one side of the pteryla at a distance from the dorsal midline equivalent to between one and three rows of primordia. The complementary pieces were cultured in the same dish, but were juxtapositioned in order to eliminate any directional interactions. Cultures were examined at intervals of about 6 h for the number, and developmental state, of rows formed. The resolution of this assay is limited by the rate of primordium formation: by comparing the developmental state of primordia, the method can
be expected to detect any difference of more than about 7 h in the development of treated and control sides of each specimen.

The operation had no detectable effect on the time course of primordium formation, excepting slight effects associated with spatial restriction at the cut boundary (Table 1).

In the majority of specimens, the time course of development appeared to be identical on the operated and control sides of the pteryla (nos. 1–12, Table 1). The result was the same no matter where the cut was made, even when the lateral part of the prospective pteryla was cut and the first primordia formed beyond the cut more than 48 h after the operation. In four cases (nos. 9–12) the cut was made at an angle to the dorsal midline and passed obliquely through the prospective positions of several rows: no difference was observed in the time of formation of primordia in the same row on either side of the cut.

In five cases, the operation advanced slightly the time course of primordium formation lateral to the cut (nos. 13–17, Table 1). The first row beyond the cut formed a few hours before the equivalent row on the control side of the pteryla. (The time difference was less than the interval between the formation of successive

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>No. of rows formed medial to the cut after the operation</th>
<th>Time (h) after cutting when primordia were first observed beyond the cut</th>
<th>Comparison of operated with control side of the pteryla</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>22</td>
<td>Synchronous</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>23</td>
<td>Synchronous</td>
</tr>
<tr>
<td>3</td>
<td>3*</td>
<td>39</td>
<td>Synchronous</td>
</tr>
<tr>
<td>4</td>
<td>2*</td>
<td>52</td>
<td>Synchronous</td>
</tr>
<tr>
<td>5</td>
<td>1*</td>
<td>49</td>
<td>Synchronous</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>47</td>
<td>Synchronous</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>37</td>
<td>Synchronous</td>
</tr>
<tr>
<td>8</td>
<td>1</td>
<td>23</td>
<td>Synchronous</td>
</tr>
<tr>
<td>9</td>
<td>2</td>
<td>38</td>
<td>Synchronous</td>
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<td>0</td>
<td>25</td>
<td>Synchronous</td>
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<tr>
<td>11</td>
<td>2</td>
<td>38</td>
<td>Synchronous</td>
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<tr>
<td>12</td>
<td>2</td>
<td>41</td>
<td>Synchronous</td>
</tr>
<tr>
<td>13</td>
<td>2*</td>
<td>31</td>
<td>Slightly Adv.</td>
</tr>
<tr>
<td>14</td>
<td>2*</td>
<td>40</td>
<td>Slightly Adv.</td>
</tr>
<tr>
<td>15</td>
<td>2*</td>
<td>30</td>
<td>Slightly Adv.</td>
</tr>
<tr>
<td>16</td>
<td>2*</td>
<td>49</td>
<td>Slightly Adv.</td>
</tr>
<tr>
<td>17</td>
<td>2*</td>
<td>49</td>
<td>Slightly Adv.</td>
</tr>
<tr>
<td>18</td>
<td>2*</td>
<td>–</td>
<td>N.P.</td>
</tr>
</tbody>
</table>

* In these cases, the development of the row of primordia immediately medial to the cut appeared to be spatially restricted by the cut boundary.

See text for an explanation of the terms “synchronous” and “slightly advanced”.

N.P. No primordia developed lateral to the cut.
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In each of these cases, the development of primordia immediately medial to the cut was spatially restricted. This was indicated either by a slight medial shift in the position of this row from an early stage in its development (see, for example, Fig. 1) or by a more gross effect where the size and number of primordia were severely limited. It appears, therefore, that the cut was made closer to the midline than the distance normally occupied by an integral number of rows. Since the first row which developed beyond the cut formed close to the edge, it follows that this row was shifted medially compared with the equivalent row on the control side. Similar spatial restriction of primordium formation was evident in three specimens (nos. 3–5) without any detectable effect on the time course of development.

In a single case (no. 18) no primordia formed beyond the cut. Here, the cut was made close to the edge of the pteryla where there may have been insufficient space for feather development.

The temporal development of the spinal pteryla in culture and in vivo

The results of the preceding experiment suggest that the time when each row of primordia forms in cultured skin is determined before stage 29. There is, however, a difficulty in relating this result to the development of the pattern in vivo. In the embryo, the prospective pteryla expands while the pattern is developing to make space for about eight rows on either side of the mid-dorsal row. Cultured skin does not expand. Thus, skin explanted at stage 29 develops only three or four rows on either side of the pteryla. It is not clear, therefore, if the preceding results reflect on the formation of the first few rows in vivo or on the development of the whole pteryla.

To resolve this difficulty, cultured skin was compared with skin in vivo with respect to the time course of pattern formation. Preliminary observations showed that each row takes about 6 h to form in vivo. Thus, in skin cultured from stage 29, the development of the pattern would take about 1 day (4 × 6 h) if it reflected the formation of only the first few rows in vivo and about 2 days (8 × 6 h) if it reflected the development of the whole pteryla.

The mean time of formation of the last row in the pteryla (t_f) and the mean period between the formation of successive rows (i) were estimated for groups of cultured pteryla and for pteryla in vivo by counting the number of rows formed at suitable time intervals in three replicate experiments. Further information on the number of rows in the completed pteryla in vivo was obtained in a fourth experiment. All times were measured relative to the mean time of formation of the initial, mid-dorsal row in vivo (t_0), estimated as shown in Fig. 2A. (See Table 2 and caption to Fig. 2 for details.) An additional check of t_f was made by noting the proximity of the most recently-formed row of primordia to the edge of the pteryla in each specimen: the pteryla boundary was distinguished from the surrounding tissue by its greater opacity.

The data shown in Fig. 2A suggest that t_f for skin in vivo was estimated to a
Fig. 1. The time course of primordium formation in transected skin. Skin from a single pteryla (no. 16, Table 1) which was cut (along line XY) and explanted before the mid-dorsal row was visible then cultured for 2 days. (A) Control piece, incorporating the initial row (double arrow). (B) Skin lateral to the cut. (C) and (D) tracings from photographs (A) and (B) respectively, showing the positions of developing feather primordia. Note that the first row of primordia (asterisk) lateral to the cut is in the process of forming and is slightly more advanced than the equivalent row (double asterisk) on the control side of the pteryla. The row (arrow) immediately medial to the cut is closer than normal to the preceding row. ×17. Scale bar = 1 mm.
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Table 2. The time course of development of the spinal pteryla in vivo and in vitro

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Time at explantation</th>
<th>No. explants surviving</th>
<th>Mean initial no. rows</th>
<th>Mean final no. rows</th>
<th>( i ) (h/row)*</th>
<th>( t_1 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6 d 2 h</td>
<td>7</td>
<td>1·7 (1·4)</td>
<td>8·4 (1·7)</td>
<td>14.6</td>
<td>8 d 3 h</td>
</tr>
<tr>
<td></td>
<td>6 d 7·5 h</td>
<td>10</td>
<td>3·2 (0·6)</td>
<td>9·8 (1·4)</td>
<td>13.0</td>
<td>8 d 2·5 h</td>
</tr>
<tr>
<td></td>
<td>7 d 3 h</td>
<td>9</td>
<td>8·4 (2·0)</td>
<td>14·7 (1·5)</td>
<td>8·3</td>
<td>8 d 5 h</td>
</tr>
<tr>
<td></td>
<td>in vivo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6 d 7 h</td>
<td>10</td>
<td>3·4 (0·8)</td>
<td>9·8 (1·4)</td>
<td>14·8</td>
<td>8 d 6·5 h</td>
</tr>
<tr>
<td>2</td>
<td>7 d 3 h</td>
<td>10</td>
<td>7·5 (2·5)</td>
<td>14·8 (2·8)</td>
<td>7·4</td>
<td>8 d 6 h</td>
</tr>
<tr>
<td></td>
<td>in vivo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6 d 7 h</td>
<td>9</td>
<td>2·9 (1·4)</td>
<td>10·2 (0·8)</td>
<td>11·8</td>
<td>8 d 2 h</td>
</tr>
<tr>
<td></td>
<td>7 d 3·5 h</td>
<td>10</td>
<td>9·5 (3·0)</td>
<td>15·5 (1·6)</td>
<td>8·7</td>
<td>8 d 5·5 h</td>
</tr>
<tr>
<td></td>
<td>in vivo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>in vivo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figures for skin in vivo in each experiment are based on samples of 10 embryos. In experiments 1 and 3, \( t_1 \) was estimated for skin in vivo as described in the caption to Fig. 2. Standard deviations are shown in parenthesis.

*\( t_1 \), the mean interval between the formation of successive rows on either side of the pteryla, was computed as described in the caption to Fig. 2.

precision between \( \pm 3 \) and \( \pm 5 \) h. \( t_1 \) can be estimated in each specimen of cultured skin to within about half the time taken to form a row of primordia. Since the edge of the pteryla may grow in vivo to accommodate a row of primordia, but remain too small in cultured skin, the present assay may underestimate the time of completion of the pteryla in cultured skin as compared with skin in vivo. Since this underestimate would be greatest where the pteryla is small, skin older than stage 29 was used in most cases. A further error (leading to an overestimate of \( t_1 \) in vitro) is incurred by estimating the mean time of formation of the last row from the time when all the cultures in each group attained the maximum number of rows. The combined effects of these opposing errors is unlikely to be serious.

In the seven groups of cultures examined, the pteryla was completed between 50 and 55 h after \( t_0 \) (Fig. 2 and Table 2). For each group of cultures, the estimated mean value of \( t_1 \) lay within the range \( \pm 2·5 \) h of the mean value of \( t_1 \) in vivo, irrespective of the stage at which the skin was explanted.

Direct observation showed that there was little variation within each group of cultures, despite differences in pteryla size and in the number of rows formed. For example, in the first two groups of cultures in experiment 1 (Table 2), 14 of the 17 surviving specimens completed the full compliment of rows during a period of less than 5 h, after about 2 days in culture.

The interval (\( i \)) between the formation of successive rows in vitro differed greatly in pterylae explanted at different stages of development, indicating that the rate of development was not trivially limited by culture conditions. Analysis
Fig. 2. The time course of pteryla development in vivo and in vitro.

(A) and (B): The rate of formation of successive rows of primordia in vivo (A) and in vitro (B). Ordinates: mean number of rows in the pteryla (per group of cultures). Abscissae: time, in h, after t₀. (A) shows data from experiments 1Δ, 2□, 3○ and 4×. Bars represent ± 1 standard deviation for exp. 1 (n = 10) and for the line parallel to the abscissa which indicates the mean full complement of rows computed from pooled data from experiments 2, 3 and 4 (n = 30). (B) shows the results of a representative experiment (exp. 1). Symbols distinguish groups of pterylae explanted at different stages.

The time of formation of the last row in the pteryla (t₁) (indicated by arrows) was estimated as follows. The full complement of rows in each cultured pteryla is the number of rows which showed no increase over 24 h. The full complement in vivo was assayed when the pattern was clearly completed. For each group of cultured pterylae and for the pooled in vivo data, a line was drawn parallel to the abscissa through the mean full complement of rows. A second line was drawn through the two points on the graph preceding the time of completion of the pteryla, and extrapolated to intersect the mean full complement. The time co-ordinate at the point of intersection was taken as the mean value of t₁. t₀ was estimated by extrapolation of pooled data as shown in (A).

(C) The rate of formation of successive rows as a function of the number of rows in the completed pteryla. Ordinate: 1/i, where i is the mean interval (h) between the formation of successive rows on either side of the pteryla. Abscissa: mean full complement of rows in the pteryla. Open symbols, in vivo; solid symbols, in vitro. Symbol shape denotes experiment number as indicated for (A). For each group of cultured pterylae, i was computed by dividing the mean time between explantation and t₁ by the mean number of rows formed on either side of the pteryla during this period. For skin in vivo, i was computed by dividing the interval between t₀ and t₁ (as estimated in each experiment) by the number of rows on either side of the complete pteryla.
suggests that it varied in constant proportion to the number of rows in the completed pattern, that is, to the size of the pteryla (Fig. 2C). The proportion of the pteryla which had developed at any particular time was approximately the same in skin cultured from stage 30 as \textit{in vivo}.

**DISCUSSION**

The results of the experiments reported here show that the movement of the waves of feather determination and morphogenesis across the back of the chick does not depend on the transmission of any stimulus across the skin after stage 29. That is, the waves are kinematic (Pearson & Elsdale, 1979). Not only the direction of movement of the waves (i.e. the polarity of the tissue), but the time, in development, of feather formation is determined before stage 29.

This conclusion follows from the observation that the formation of successive rows of primordia was neither prevented, nor altered in its time course, by cutting the skin. The only exception to this result is where the development of primordia beyond the cut was advanced slightly relative to the control. Since these primordia were apparently shifted medially by comparison with their counterparts on the control side, this observation is exactly what one would expect on the view that the time of primordium development depends, not on the development of preceding rows, but on position within the prospective pteryla. (So small a temporal displacement is, of course, close to the resolution of the method and this may explain why no temporal effects were detected in other instances where the spatial pattern was restricted.)

Although it is the process of morphogenesis which is observed directly in the transection experiments, the results also reflect on the control of the wave of determination. This is so because the prospective positions of primordia on either side of the midline were not yet established when the skin was cut (Davidson, 1983). It is reasonable to assume that any disturbance of the wave of determination would be reflected as a disturbance in the time course of morphogenesis, for the formation of primordia both depends on, and follows close behind, determination. Since no such disturbance was observed it follows that the wave of determination is also kinematic.

The results show (within the resolution of the present method) that the pattern is completed in cultured skin over the same period as \textit{in vivo}. This strongly suggests that the movement of the morphogenetic wave in skin cultured from stage 29 represents its traverse of the entire pteryla \textit{in vivo}. Hence, the kinematic property of the morphogenetic wave applies over the whole of the prospective pteryla after stage 29.

When we observe a kinematic wave sweeping across the tissue, we are seeing a series of local developmental events whose co-ordination in time and space is a reflection of the way the tissue has become organised earlier in development. The precise nature of this organization remains to be elucidated, although it
presumably resides in the dermis for the orientation of this tissue governs the
direction of the morphogenetic wave (Linsenmayer, 1972). Any hypothesis
regarding its nature must allow that the temporal co-ordination of development
is independent of skin expansion during embryonic growth. One interesting
implication of this fact is that temporal co-ordination is established across an area
much smaller than the final pattern. (The relationship between skin growth and
feather pattern formation will be discussed in a separate publication.)

The periodicity of the spatial pattern raises the question, is the spatiotem-
poral organization of the skin discontinuous? The results suggest that, on the
contrary, the gradient of temporal differentiation is continuous, tissue at every
level of the mediolateral axis developing the potential to form feathers as if a
wave of ‘competence’ moves smoothly across the skin. Two results point to this
conclusion. First, at the present resolution, the period between the formation of
successive rows varies continuously with the size of the pteryla. Second, it ap-
ppears that by effecting a small shift in the prospective position of primordia the
time of their formation was changed by less than the interval between the
development of successive rows.

The present results show that the relative positions of individual feathers are
determined, at least in part, by a local spacing mechanism operating between
incipient feather sites. This conclusion follows from three results relating to the
development of transected skin. First, the exact positions of primordia were
sensitive to spatial constraints at the cut boundary. Only the row immediately
medial to the cut was affected (Fig. 1): this implies that these constraints operate
locally. Second, primordia formed in a well-defined row along the lateral edge
of the cut, rather than at various distances from it. This observation provides
experimental support for the hypothesis that new sites are established as soon as
a sufficient area of skin becomes competent for feather differentiation (Ede,
1972; Novel, 1973). The phenomenon is not a result of any artefactual conditions
pertaining at the cut boundary, for primordia did not form concurrently along-
side a diagonal or mediolateral cut. Third, the row immediately lateral to the cut
comprised normally spaced primordia. Thus, primordium spacing within a row
does not depend on any interaction with established sites in the preceding row.
This result points to the operation of a mutual spacing mechanism acting between
incipient feather sites. It does not, of course, exclude the possibility that inter-
actions between established and incipient sites determine the relative positions
of primordia in successive rows.

Implications for pattern formation in the skin

The present results appear to rule out the hypothesis, inherent in previous
models of feather pattern formation, that feather development depends on the
transmission of a stimulus across the skin immediately ahead of primordium
formation (Ede (1972); Sengel (1976); Stuart, Garber & Moscona (1972)).

The results provide evidence for, (1) an overall temporal co-ordination of
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development and, (2) a local spacing mechanism. These two levels of organisation are sufficient, in principle, to generate a regular array similar to the feather pattern. According to this view, the regularity of the pattern derives from the graded temporal differentiation of the skin: the formation of new feather sites is limited to a narrow band which moves across the tissue, making possible an ordered series of spacing interactions between sites in successive rows. Providing only that the spacing is precise, this mechanism could generate an extensive array in a manner analogous to crystal growth (Ede, 1972).

Crucial to this view is the hypothesis that the temporal organisation of the skin is essential for the geometrical regularity of the pattern. By showing that this organization is inherent in the skin at stage 29, the results suggest how this hypothesis might be tested. By combining dermal tissue, reconstituted from dissociated dermal cells, with intact epidermis it may be possible to obtain a composite ‘skin’ in which feather primordia will develop (Weiss & Taylor, 1960; Moscona & Garber, 1968). These primordia would form all at once or in no particular order and, on the present hypothesis, they would form an irregular pattern with roughly normal spacing.

This hypothesis immediately provides insight into the relation between the various vertebrate skin patterns. Morphological and phylogenetic arguments suggest a close relationship between different integumental patterns (Elias & Bortner, 1957; Spearman, 1964; Maderson, 1972a, b; Regal, 1975), and evidence from heteroclass, dermal–epidermal combination experiments (Dhouailly, 1975; Sengel & Dhouailly, 1977) suggests that a common dermal organization determines the positions of individual epidermal scales and appendages in all amniotes. Our hypothesis therefore implies that the difference between regular and irregular skin patterns lies in the temporal organisation of their respective embryonic fields. It predicts that regular patterns should form sequentially, across a gradient of temporal differentiation, and that irregular patterns will develop where no such gradient exists.

The most detailed information about comparable irregular and regular skin patterns concerns mouse hair formation. This evidence is entirely consistent with our hypothesis. During the formation of the irregular pattern of primary follicles in dorsal skin the first hair primordia develop synchronously, and more primordia are added between existing ones as the skin grows (Hardy, 1951; Davidson, unpublished observations). (A model for the generation of the pelage hair pattern which is consistent with the present hypothesis has been proposed by Claxton (1964).) In contrast to the dorsal pattern, the regular pattern of vibrissae develops sequentially (Hardy, 1951; Kollar, 1966). It will be interesting to see if vibrissa formation is co-ordinated by a temporal programme laid down before the pattern is determined.

Wider implications

It is of particular interest that the temporal organisation of the skin before
feather development bears a striking resemblance to that of the paraxial mesoderm prior to somitogenesis. (Pearson & Elsdale, 1979). Although somitic mesoderm and dermis have a common embryological origin, the patterns they form and their regulative capacity are quite different: moreover, the two tissues are temporally organized along different embryonic axes. The similarity of the graded temporal differentiation across these two tissues therefore strongly suggests that this is a common component of the mechanisms by which regular repetitious patterns are formed in vertebrate embryos.

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REFERENCES


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