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Rhythmic pigmentation in Porcupine quills

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Receipt of Ms. 5. 7. 1976

Introduction

Porcupines show a striking alternation between black and white regions down the length of their quills. Such quills, which represent modified hairs, are far easier to examine than similarly banded hair from other mammalian sources, and they invite a study of pigment patterning which could be relevant for pigment function generally.

The purpose of this investigation was to establish the main features in the pattern of quill pigmentation, and hence the steps required in generating patterns of this type. Sets of loose quills from 3 porcupines and quill-covered skins from 5 other specimens were available, all belonging to *Hystrix africaeaustralis*.

Z. Säugetierkunde 42 (1977) 231—239

ISSN 0044—3468/ASTM-Coden ZSAEA 7

Observations

Transition and growth phenomena

Quills are carried on the hinder portion of the porcupine body. At the border of this site the hairs could be traced through intermediate steps to small sized quills (Fig. 1). In this transition, the flattened hair shaft becomes fuller and more thickened, the thread-like portion at the tip becomes taken up in the enlargement, while the pigment withdraws from the hair base to from a miniature black-and-white defence quill. With increasing length, the series extends up to the proper defence quill, while still displaying the same simple black-and-white colour pattern.

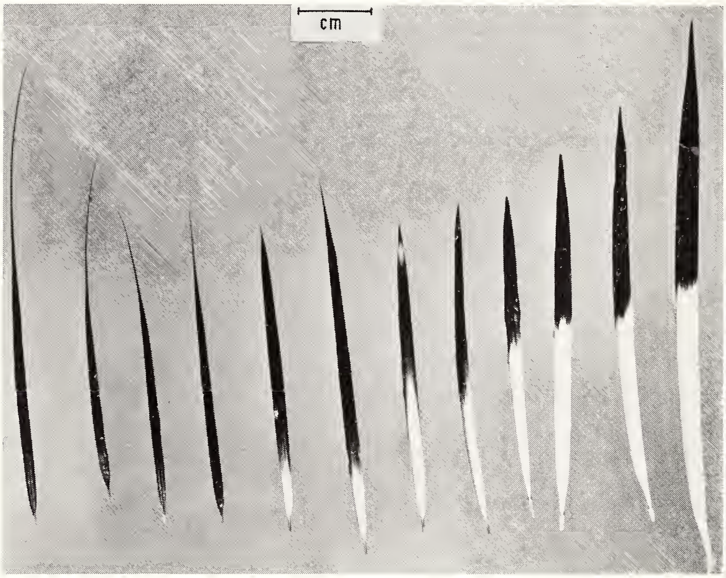


Fig. 1 (left). Hair-to-quill transition. The shaft broadens, up to the tip, absorbing the bristle, and replacing it with a sharp spike. Colour becomes confined to the distal half of the shaft. Series collected from the edge of the quill-bearing area. — *Fig. 2 (right).* A = Defence quills. These two have a simple black-and-white pattern. They are fully grown, having tapering colourless roots; B = Needle quills. These two are not fully grown. The roots are abruptly narrower, pinched off, and often pigmented

The common type of defence quill was short and rigid, with a gradually tapering, glossy distal spike and a dangerously sharp tip (Fig. 2A). The stabbing end of these quills was often bayonet-like, with sharp lateral ridges and a keel-like third edge. The root of the fully developed quill was smoothly tapering, with a dull conical cap and a blunter point. In studying quill length, incompletely grown quills were necessarily excluded. The important differences in root structure which distinguish fully grown quills and growing quills are illustrated by comparing figs. 2A with 2B. The growing quill root (Fig. 2B) shows an abrupt, pinched-off appearance, compared with the smoothly tapering point of one whose growth is complete (Fig. 2A).

Colour arrangement in the simple defence quill

Among 195 defence quills with a mean length of 134,96 mm (SD 26,51), the distal black portion was 61,33 mm mean length (SD 14,72). The black section therefore comprised almost half the total quill length on the average. To decide if the black region owed its colour to same „quantum" of pigment per quill regardless of the individual quill length, the length of the black section was plotted against total quill length grouped according to a series of size ranges (Fig. 3). Here it is seen that the black length is a function of quill length, the bigger quills generally having a rather longer pigment portion than the smaller ones. Some supplementary measurements on perfect quill specimens showed that the colour change occurred near the widest part of the quill. These findings showed that the amount and change of colour was related to the growth of the individual quill, both in length and breadth, and was not a feature imposed on all quills from some source outside the growing quill roots.

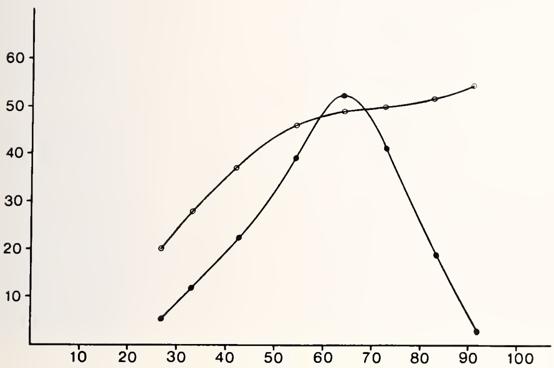


Fig. 3. Graphs to show that the shorter defence quills have relatively less pigments than the longer. 192 black-and-white defence quills were grouped in 10 mm lengths of the black portion (horizontal axis) against numbers in the group (vertical axis), giving a bellshaped curve. The same lengths plotted against percentage of the total length (vertical axis) gives a sigmoid curve, with a 50:50 relationship near the mean

Banding and quill length in the defence quill

298 defence-type quills were grouped according to numbers of white sections compared with total length. Table 1 shows that the bands increase in number with quill length, but that the relationship is not linear.

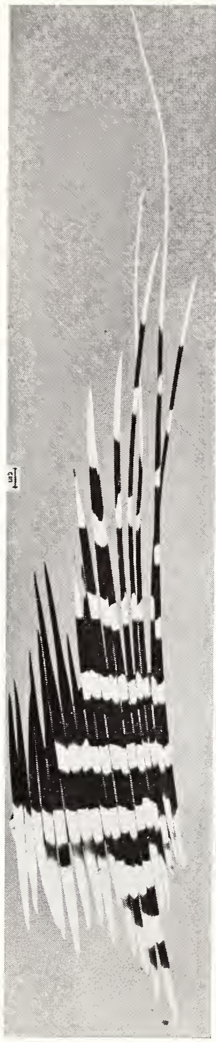
Table 1

To show that length of quill is related to numbers of white bands

No. of white sections	1	2	3	4	5	6
Average quill length (mm) range	90—180	193	230	257	(insufficient)	280

Other quill types

In the quill-bearing area one may identify 3 principal types of long quill, each of increasing final length. Existing terminology (Mohr 1965) refers to the quill types according to their stiffness or wobbliness on the stem and the presence of a brush-like tip. Here we amplify the distinctions, but note the correspondence between defence or bayonet-type quills which Mohr (1965) calls „quills", needle-like pliable quills called "spines" and whiplike quills called "bristles" in her text. Besides the



From left to right:

Fig. 4. Quill series. A sample of defence, needle and whip types. Congruence of the white bands, and terminal white portions can be seen. — *Fig. 5.* A follicle group. All the roots originally lay at the same level. The 4 quills are displaced to show band congruence. In this position the roots do not lie together. — *Fig. 6.* Colour variation in the Terminal portion of hairs. — *Fig. 7.* Congruent rhythmic pigmentation: Systematic shortening of black and lengthening of white towards the root. Pigment lightens to the root. Note also the conformity of fine detail in the switch-off and switch-on zones respectively down the same quill

shorter defence type, there were the needle and the whip types. The needle type (Fig. 2B, Fig. 4, Fig. 5) is less dangerous, resembling more a knitting-needle than a bayonet. Its distal end comprises only a short conical segment, which soon passes into a longer, thin, cylindrical, body portion which is pliable, in contrast with the more fusiform, stumpy, rigid body with long distal spike in the defence quill. The whip type (Fig. 4) realises, on the largest possible scale, certain features also seen in the soft hairs elsewhere on the skin (Fig. 6). There is an extended distal whiplike portion, expanding slightly on to a thin body, making in the longest of the 3 quill types. Occasional transitional quills could be fitted in between these 3 groups, in respect of length and morphology, but otherwise the typing was quite distinctive.

The smaller quills, secondary hairs, white quills and rattle quills, not being able to contribute to the pigment study, do not figure here.

Rhythmic interrelationships between banding phenomena in quills

Arising from the preliminary observations just described, a number of remarkably consistent "rules" of pigment patterning came to be recognised in the quills. These will first be briefly enunciated and then elaborated.

1. Black bands shorten and white bands lengthen along the shaft towards the quill root.
2. The distal spiny part of the hair or quill behaves as if under separate pigmentary control from the shaft.
3. There is a fairly close correspondence in length of the successive black and white segments of the quill bodies independently of the length or morphological type of the quill concerned.
4. The "switching-off" of pigmentation (the black-to-white transition) is an abrupt and precise event in the earlier part of quill growth, but loses is sharpness eventually. "Switching-on" (white-to-black transition) is of another character, being relatively damped, dissociated from the above, and not a mere reversal of the switching-off process.
5. The stages of pattern formation in quills from the same follicle groups are independent of each other.
6. Pigment production declines before the quill is fully grown out.
7. Radial dislocation occurs with pigment switching.

1. Systematic changes in band length

In figs. 2, 4, 5 and 7 one can easily notice the declining lengths of the black bands towards the base of the quill. This is the rule throughout the shaft of the quill, i. e. that portion lying proximal to the conical spike (see 2 below). Several zoologists who had worked with porcupines expressed surprise when this feature, so obvious when once noted, was first pointed out. Associated with the shortening of the black sections is a far less obvious lengthening of the white sections, best demonstrated by measurements (Figs. 4, 5, 7 and 8).

2. Pigmentary independence of the tip region

The dominant colour of the porcupine pelage is black, and the quills and hair are generally pigmented at the free end (Fig. 1). It became obvious however, that in certain regions of the skin, regardless of the type and length of hair or quill, the distal part showed, as a variation, a white portion (Figs. 2, 5, 6 and 7), sometimes with a dash of pigment at the tip. Where these pigmentary differences occurred on quills long enough also to show rhythmic banding down the shaft, there was no congruence between the pigmentary rhythm of the shaft (see below) and that of the tip. This phenomenon of terminal and subterminal banding of the hair, traditionally known as "agouti" type banding, was therefore distinctly separable from the rhythmic banding of the shaft. The latter type of banding was only seen in the shaft of longer quills, while the "agouti" colour change could affect all sizes and shapes of hair or quill.

3. Inter-quill congruence of banding

By the simple procedure of aligning loose quills beside one another, certain properties of the banding phenomena became evident. In the simplest case, a series of 55 quills having only one white band, the average length of the band was 16 mm (S. D. 2,2) — a degree of conformity between them which was far closer than that of total length for instance. The next step was to take sets of quills with equal numbers of black and white bands and do the same. Again, within each quill set (e. g. Fig. 7), the black and white bands of separate quills could be brought into close alignment with one another. This finding was surprising in view of the systematic changes in band length which were always to be seen. In such sets a similar trend was evident as had been noted earlier, viz. the longer quills had relatively longer, and the shorter quills relatively shorter black bands, but insufficient to disrupt the mutual conformity. Following from congruence of band length in quill sets with the same number of bands, a similar type of cross-classification was attempted between the sets with differing numbers of bands.

For the last-named purpose, 120 quills from one source were visually aligned, and it was found that, from the short bayonet-type through the longer needle up to the longest whip type of quill, a degree of correspondence of black and white pattern length could be obtained in the series which lent itself to mathematical presentation. Fig. 4 illustrates an abridged series of this type, the full details of wich appear in Table 2. The procedure commenced with the identification of a white band flanked by

Table 2

Congruent band lengths in 120 quills

White Series		Black Series	
11,48	(1,67)	36,75	(8,38)
12,22	(1,54)	33,11	(5,84)
12,57	(1,26)	29,02	(3,87)
12,30	(1,4)	24,38	(2,61)
12,65	(1,36)	19,38	(4,22)
14,95	(1,96)	12,97	(3,71)
15,33	(2,29)	11,22	(2,85)
16,00	(1,54)	10,78	(2,32)
16,48			

From top to bottom reads tip to root; mean lengths in mm; standard deviations in brackets.

two black sections of congruent sizes in a defence quill. One step downward led to the plain black and white quill which was identical except that it lacked the proximal black band. With the increase in length of quills, the longer segments of black-plus-white were added above and the shorter black-plus-white segments below this initially established unit. It was by applying this method of congruent addition that the principle, indicated in section (2) above, became evident. In other words, a stepwise addition to the conforming rhythmic band patterns were to be found only in the roughly cylindrical "body" portion of the quill and not in the tapering spike portion. As the quills lengthened, most of the band additions were distal, and a few proximal, as seen in Fig. 4, without there being any obvious regularity by which this occurred.

4. Pigment "switching"

As one moves towards the quill root along the alternating black and white bands, the black-to-white "switch off" of pigmentation usually shows a sharp jagged transition (Figs. 7 and 8), and this line of transition moves around the quill with a rather wide up-and-down excursion as one traces it round the circumference. Where the

Fig. 8. Comparison of white bands down same quill. The quill is sawn up and the differences between switch-off (distal) and switch-on (proximal) pigment zones can be seen. There is some rotatory displacement of the fine structure

"switch-on" occurs, the transition is more gradual and fluffy, and the up-and-down excursion of the junction zone as one turns the quill round is conspicuously smaller. "Switch-off" zones (see Figs. 5, 7 and 8) sometimes showed a repetition of the jagged excursion pattern at two or more homologous zones down the quill. Similarly, the "switch-on" zones tended to have a similar family resemblance as regards their up and down fluctation at successive points down the same quill.

5. *Pattern production within the same follicle group*

Several sets of banded quills belonging to the same follicle group, but differing among each other in age and stage of development, were removed and compared in order to determine the relationships between their rhythmic banding patterns. Fig. 5 shows four such quills from a single follicle group, ensuring thereby that the roots stood at the same level and in a closely united environment. From the illustration it can be seen that the banding patterns were shiftet into congruence without difficulty, but in doing so the four roots were displaced so as to lie at differing positions. From this simple observation it could be concluded that the quill patterning was not governed by a shared rhythm in the follicle group, nor by a communal rhythmic signal given out from some remoter source in the animal body. Pigment band production was therefore a regular phenomenon whose behaviour was linked to the stage of growth of the individual quill in question only.

6. *Final lack of switching and pigment decline*

Approaching the root of a quill, two phenomena, both suggesting an exhaustion process, could frequently be seen to occur. Firstly the pigment becomes lighter (brown to grey) and secondly the final switching off is incomplete or ineffective. As a result of the switch failure the pigment trails away in a faint "smoke" down towards the root.

7. *Radial displacements in the pigment-forming process*

A quill grows without any apparent torsion, as can be demonstrated by the parallel arrangement of the radially placed longitudinal laminae of the inner cortex, which impart an obvious striated appearance to the smooth surface (Figs. 7 and 8). The pigmentation of these laminae, seen end-on, produces the thin dark streaks seen in the photographs. Since these laminae can be followed continously down the quill shafts, it can be readily verified in suitable specimens that the fine nuances in vertical fluctuation of the pigmentary switching lines as described in (4) above, may be slightly displaced radially, in a clockwise or anti-clockwise direction, round the shaft, as judged by their fluctuations measured on the longitudinal laminae. A radial displacement of the curve by the breadth of one or two such columns was not unusual. No certain conclusions could be drawn from this phenomenon, but one could suggest that the set of melanocytes supplying the growing quill became completely detached from the keratinocytes during the switch-off period and re-attached themselves with some slight radial displacement of the set as a whole.

Conclusions

The shafts of banded porcupine quills studied here showed a series of rhythmic alternations in coulour which possessed some hitherto undescribed properties. There were obviously two quite distinct colour phases along the quill and the changes from one to the other were sharp. These changes exhibited the phenomenon of hysteresis: there was an increasing delay in the return from the unpigmented to the pigmented area and an even more marked shortening of the period of pigmentproduction in the course of time. In the main range of the dual colour, no intermediate state was seen between black and white. And finally, disturbances in the tip region or exhaustion phenomena towards the root region were responsible for local departures from these findings which were valid throughout the shaft area of the quills.

These pigmentary phenomena followed a consistent course which was independent of the length or type of quill, its position on the body surface or its stage of growth. Thus one may conclude that the rhythmicity must reside entirely in the pigment producing process itself, i. e. in the intrinsic behaviour of the set of melanocytes supplying the individually growing quill. To some extent the melanocyte function is regulated by the type and scope of growth in the individual quill, but any such modification of the intrinsic rhythm never dominates the process.

Quite predictably, these considerations must bear upon phenomena taking place at a celluar level. A process of progressive melanocyte "fatigue" is perhaps the most obvious conclusion to be drawn: this is seen in the gradual failure of pigment production by the colour becoming paler, the duration of pigment production becoming shorter with its final collapse before the quill has fully grown out. Conversely, the "resting" phase of the melanoctes, i. e. the white bands, between the episodes of pigment production becomes longer, and the pigment switching from "on" to "off" sometimes becomes conspicuously inefficient.

From the shapes produced at the zones of colour junction, it appeared that the "switch off" and "switch on" processes were, as might be anticipated, different in type. The fine detail of the "swich off" junction line was sometimes clearly replicated at corresponding points down the same quill shaft. Such features might mean that the propagation of the "switch off" signal occurring between the cells of the melanocyte population at the quill root showed minor though regular imperfections in synchronisation. The „switch on“ was different in pattern and clearly less subject to such regular imperfections.

It follows that the set of melanocytes which supplies a quill root acts as a functionally autonomous rhythmic unit with its conspicuously bimodal behaviour (activity in producing pigment; inactivity in producing none). The details of such discontinuous patterns fall into the mathematical class of "cusp catastrophes", as may be seen in many biological rhythms, for example the heart beat, nerve impulses, and in shifts between other mutually incompatible patterns of behaviour which possess "all-or none" features (Zeeman, 1972, 1976).

It may be relevant to note that in the sphere of pathology of the human skin surface a parallel situation may arise. These features have been described as 1. a breakdown in synergism between melanocytes in the epidermis, 2. a stepwise gradation of pigmentary increase or decline 3. the development of melanocyte races with differing capacities for supply and spread in epidermal pigmentation (FINDLAY 1962; FINDLAY and WHITING 1971).

Summary

The quills of the South African porcupines. *Hystrix africaeaustralis,* were studied to elucidate the control of the banded colour pattern seen on the quill shafts. The banding evidently resided in the autonomous rhythmic behaviour of the set of melanocytes belonging to each individual quill. Evidence for group control or central control of pigment production was entirely lacking. Pigment supply was influenced by the presumptive length of the quill, but tended to show fatigue before the quills were fully grown. Behaviour of the pigment forming process conforms to the pattern of a "cusp catastrophe", in which a function with two sharply separated phases are connected by switching points that vary in their relationships according to the growth stage reached.

Zusammenfassung

Rhythmische Pigmentierung der Stacheln von Stachelschweinen

Es wurden die Stacheln des südafrikanischen Stachelschweines, *Hystrix africaeaustralis,* untersucht, um zu klären wie die ringförmige Farberscheinung im Schaft des Stachels entsteht. Offenbar wird die Streifung durch ein autonomes rhythmisches Verhalten einer Reihe von Melanozyten im einzelnen Stachel erzeugt. Es gab keinerlei Hinweise für eine gruppierte oder zentrale Kontrolle der Pigmenterzeugung. Die Versorgung mit Pigment wurde durch die Länge des Stachels beeinflußt, aber sie hatte die Tendenz erschöpft zu sein, bevor der Stachel ausgewachsen war. Die Verhaltensweise bei der Pigmenterzeugung ist gleich dem Modell der „Scheitelpunktkatastrophe“. Zwei scharf getrennte Phasen werden verbunden durch Schaltpunkte, die in ihrem Verhältnis variieren je nach der Wachstumsphase, die erreicht ist.

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