Winter plumage of the Rock Ptarmigan: Structure of the air-filled barbules and function of the white colour

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(Med et dansk resumé: Fjeldrypens vinterdragt:
De luftholdige bistrålers struktur og funktionen af den hvide farve)

INTRODUCTION

Finn Salomonsen wrote in his doctoral thesis on the moult and plumage sequence in the Rock Ptarmigan *Lagopus mutus* (Salomonsen 1939), »The ptarmigan may, or may not, derive some benefit from the whiteness of the W-plumage, which possibly is of some selective value, but this is a secondary phenomenon not to be discussed here. However, the white plumage in the northern countries is worn in the polar winter in which the daylight is so inconsiderable that the protective value of the white plumage appears to be almost illusory.«

More than thirty years later, in his presidential address to the XVth International Ornithological Congress, he said: »It cannot be denied that at present we are unable to prove whether this similarity with snow or its capability of reducing heat loss is the main advantage of polar whiteness. A very vivid discussion has been carried out about this subject, which I have summarized previously (Salomonsen 1939, 1958 (Freuchen & Salomonsen 1958)), and not much news have appeared since then in spite of various experiments« (Salomonsen 1972).

Chandler (1916, p. 276) drew attention to the fact that the white feathers of the ptarmigan differ from those found in most other species in that the barbules contain air bubbles.

The purpose of this paper is to study in some detail the building of these air-filled feather parts and their ability to reflect light in the hope that such a study may contribute to an understanding of the function of white colour.

MATERIAL AND METHODS

White back and belly feathers were taken from an adult male Rock Ptarmigan shot on April 6, 1978, at Tuopait, Disko Island, West Greenland. Presumably the bird belonged to the race *L. m. saturatus* Salomonsen. In order to compare the ptarmigan feathers with white feathers of other gallinaceous birds with presumably compact barbules, feathers were plucked of an albinistic Pheasant *Phasianus colchicus* in the collections of the Zoological Museum in Copenhagen and white feathers originating from the Domestic Hen *Gallus domesticus* were taken from the ground at a chicken run.

Intact feather parts were observed and photographed in reflected light with the Zeiss camera microscope »Ultraphot« equipped with objectives for vertical and oblique illumination.

For observations with the transmission electron microscope (TEM) (Zeiss EM 9 S-2) 1 μm and ultrathin sections were prepared from rami embedded in hard *epon 812*. Prior to embedding in *epon*, the feathers were immersed in a 0.5 M NaOH solution for 30 minutes at room temperature followed by immersion in a formic acid: absolute alcohol = 2:3 (v/v) mixture for two hours, also at room temperature. This permitted the air of the feather parts to be replaced by *epon*.

The ability of the feathers to reflect light was measured with a Zeiss microspectrophotometer 01. Measurements were made on single barbule cells using a ×40 objective and a diameter of the field of measurement = 8μm

as well as on feather samples using a ×4 objective and a diameter of the field measurement = 80 µm. For the former measurements a silicon carbide standard and for the latter a magnesium oxide standard were used. For further details, see Dyck (1978). The barbules were cut off a cleaned feather with a scalpel and placed dry on an object slide. Feather samples were prepared in order to simulate the intact plumage: 2 × 5 feathers were placed close behind each other in two neighbouring, partly overlapping, rows in a piece of plasticine placed on a glass plate. An eleventh feather was placed behind the ten feathers and between the rows. Measurements were made on the pennaceous part of this feather.

For nomenclature of feather parts, see Lucas & Stettenheim (1972) and Dyck (1971).

RESULTS

Microscopy

Only the pennaceous, distal part of the body feathers is considered.

Transverse sections of a ramus and its attached barbules are very similar in the three species (Figs. 1, 2). The pear-shaped ramus section contains an air-filled medulla in its reverse part (obverse and reverse refer to the planes of the feather away from respectively towards the body of the bird). The barbules (which have been cut somewhat obliquely) are lamella-shaped with the lamella oriented at right angles to the feather plane; terminally the plane of the barbule approaches somewhat the feather plane. A larger number of barbule sections on the ptarmigan section indicates that this species has longer barbules than the other two.

A barbule consists of a single row of cells and is usually divided into a base and a pennulum. The latter bears the various outgrowths of which the hooklets of the distal barbules are the best known. The barbules of the three species resemble each other closely (except that no hooklets were observed on the distal pheasant barbules) and conform to the general galliform structure described by Chandler (1916) and Lucas & Stettenheim (1972), and are therefore not described here.

Viewed in reflected light, however, the barbules of the three species differ. The ptarmigan barbules appear much whiter than

Key to Labelling:
Figurforkortelser:
ACa: Air-filled Cavity. *Luftfyldt hulrum.*
B: Barbule. *Bistråle.*
C: Cortex. *Bark (i fjerstråle).*
CB: Cell Boundary. *Cellegrænse.*
CS: Column-like structure. *Søjlelignende struktur.*
E: Epicuticle. *Epicuticula.*
K: Keratin.
KF: Keratin Fibril.
M: Melanin granule. *Melaninkorn.*
MC: Medullary Cell. *Marvcelle (i fjerstråle).*
Mdl: Medulla. *Marv.*
N: Nuclear remnant. *Kernerest.*
Rm: Ramus. *Fjerstråle.*

Fig. 1. Transverse section of barb (= ramus + barbules) of white Rock Ptarmigan belly feather. In the ramus the air-filled medulla is seen. Stain: toluidine blue. Lightmicroscopical photograph. Key to labelling: see above. Scale: 20 µm.
Tværsnit af stråle med tilhørende bistråler fra en hvid Fjeldrypebugfjer. I stråletværsnittet ses den luftfyldte marv. Farvet med toluidinblåt. Lysmikroskopisk fotooptagelse. Figurforklaring: se herover. Målestok: 20 µm.

Fig. 2. From a white feather of a Domestic Hen. Otherwise as Fig. 1.
Fra en fjer af en hvid Tamhøne. Iøvrigt som Fig. 1.

Fig. 3. Barbule of white Rock Ptarmigan belly feather in reflected light. Numerous bright spots are seen in the cells. Scale: 20 µm.
*Bistråle fra Fjeldrypebugfjer fotograferet i reflekteret lys. I cellerne ses mange små lyse pletter. Målestok: 20 µm.*

Fig. 4. Barbule of white feather of a Domestic Hen in reflected light. Note lack of bright spots. Scale: 20 µm.
Bistråle fra fjer af en hvid Tamhøne, fotograferet i reflekteret lys. Bemærk fraværet af små, lysende pletter. Målestok: 20 µm.

Fig. 5. Air-filled medulla in ramus of white ptarmigan feather. Longitudinal section. TEM. Scale: 5 µm.
Den luftfyldte marv i en fjerstråle af en hvid rypefjer. Længdesnit. TEM. Målestok: 5 µm.
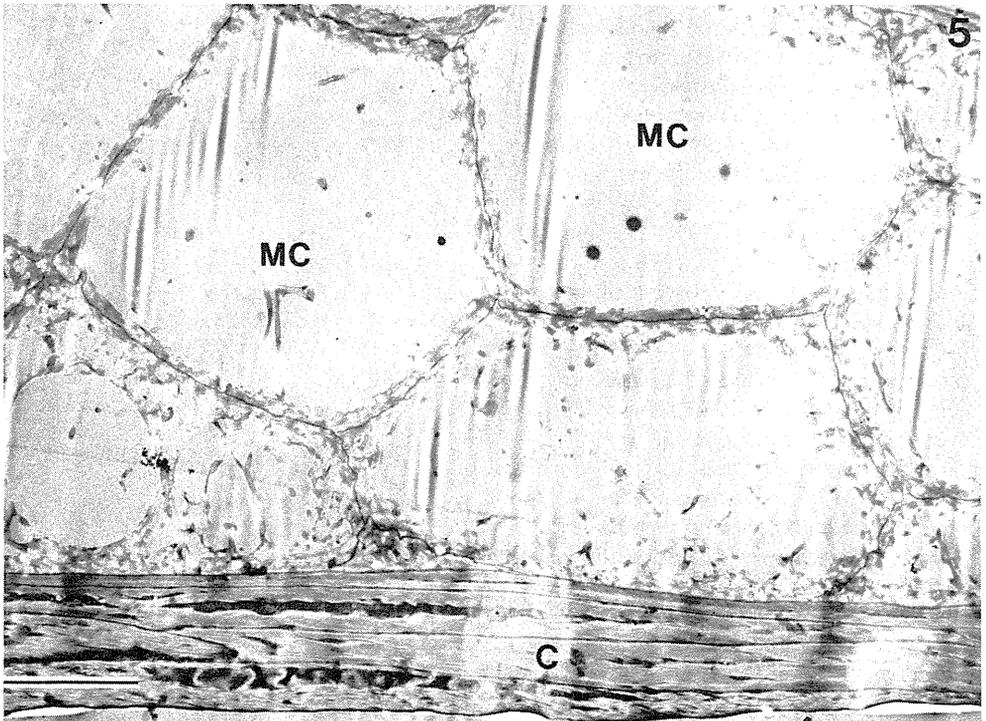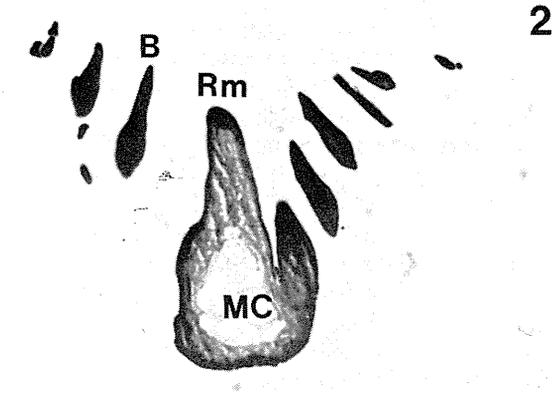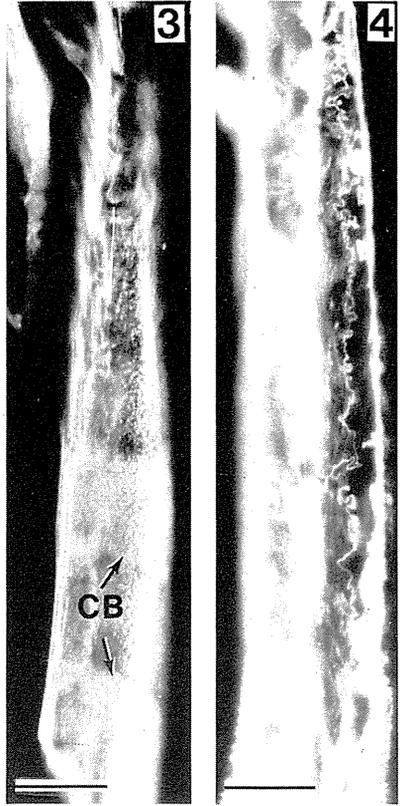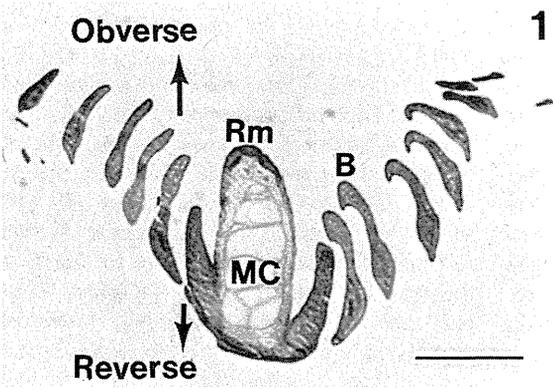
the hen and pheasant barbules. In the ptarmigan barbules numerous white spots, partly interconnected, are seen at a high magnification (Fig. 3). The white spotting is best seen in the base, but appears to be present in the pennulum as well, although not in the outgrowths. Hen and pheasant barbules lack this white spotting. They appear white also, but this white reflection appears rather as stripes (probably corresponding to longitudinal furrows and ridges on the surface) and compact areas and in some areas the barbules look transparent (dark) (Fig. 4).

The ultrastructure of the cells was studied on sections like those shown as Figs. 1 & 2. Since a distinction between keratin (the substance making up the feather parts) and air-filled cavities is of importance, the air-filled medullary cells of the rami are described shortly first. The medulla consists of large, polygonal cells (Fig. 5). Most of the medullary cell is air-filled, but at its periphery is found an irregular keratin rod − network (Figs. 6, 7). The keratin appears as a faintly dotted substance with scattered aggregations of denser material. In contrast the air-filled cell parts, which have been filled in with *epon,* appear homogenously light grey. The boundary line between keratin and air is denser than the keratin. Here and there lighter areas appear on the photographs; presumably these are due to uneven sectioning.

Fig. 8 is a total view of a hen barbule section and Fig. 9 a portion of a corresponding section enlarged. The latter figure shows a rather homogenously dotted appearance. Some cell membrane profiles are present, and the surface of the barbule is covered by a dense epicuticle. The ultrastructure gives no evidence that air-filled cavities are present, in agreement with the observations in reflected light. Fig. 10 is a corresponding picture of a pheasant barbule; neither is there evidence of air-filled cavities here, but the structure of the keratin differs in several aspects from that of the hen. A ptarmigan barbule section corresponding to Figs. 9 & 10 is shown as Fig. 12. By comparison with the medulla pictures (Figs. 6, 7) it is clearly seen to consist of keratin as well as air. The air-filled cavities are irregularly shaped, fissure-like, and rather evenly distributed among the keratin. Fig. 11 shows the most extreme air-filling observed; the air-filled cavities are to a large extent connected and impinge

in some areas directly on the epicuticle (compare Chandler's (1916) observation, that the horny outer sheath of the barbules can be broken to let balsam penetrate the air-filled cavities). Direct connection between air in- and outside a barbule where the epicuticle is defect is seen at the reverse end (Fig. 13) of the same section, as also Fig. 11 illustrates. Fig. 14 shows the relations of the cavities to the remnant of a nucleus; the cavities are found at the periphery of the remnant, not within it. In one case it was observed that structures resembling the air-filled cavities with respect both to shape, size and position obviously had not been air-filled before embedding, but instead appear electron-dense (Fig. 15). There are a few small air-filled cavities in the same cell and some more in a neighbouring cell, so some rare outcome of the staining process cannot be held responsible. The dense structures may represent some intermediate stage in the formation of the air-filled cavities.

It is apparent from the above description that the proportion of a barbule section which appears air-filled varies considerably. There is probably some pattern in this, but it has not been attempted to elucidate this.

Longitudinal sections (Figs. 16, 17) show

Fig. 6. Ptarmigan ramus. Detail of region where four medullary cells meet. Longitudinal section. TEM. Scale: 1 µm.
Fjeldrype fjerstråle. Detalje af område, hvor fire marvceller mødes. Længdesnit. TEM. Målestok: 1 µm.

Fig. 7. Hen ramus. Peripheral part of medullary cell. Transverse section. TEM. Scale: 0.2 µm.
Tamhøne fjerstråle. Den perifere del af en marvcelle. Tværsnit. TEM. Målestok: 0,2 µm.

Fig. 8. Transverse section of hen barbule. TEM. Scale: 1 µm.
Tværsnit af Tamhønebistråle. TEM. Målestok: 1 µm.

Fig. 9. Detail of transverse section of hen barbule. TEM. Scale: 0.2 µm.
Forstørret udsnit af tværsnit af Tamhønebistråle. TEM. Målestok: 0,2 µm.
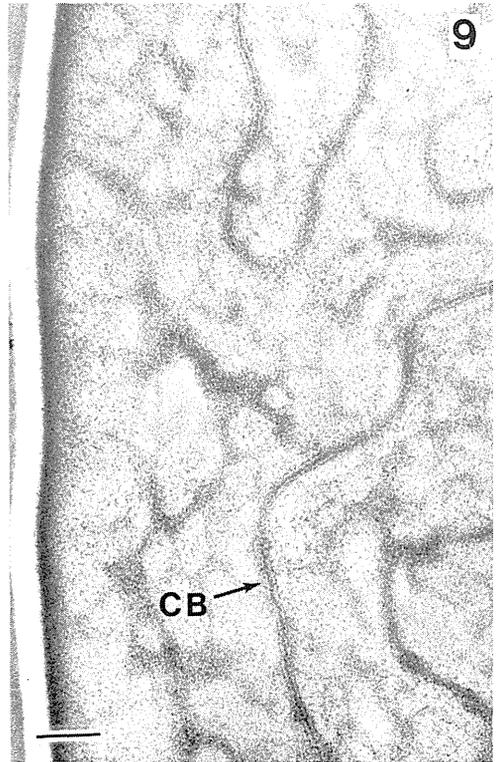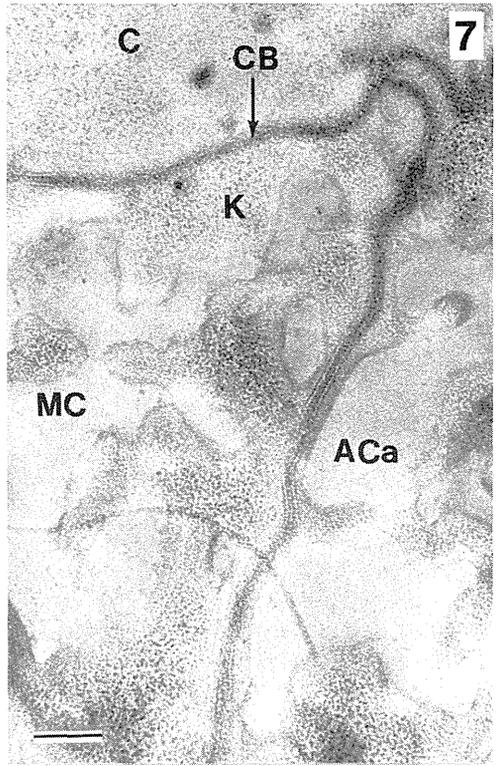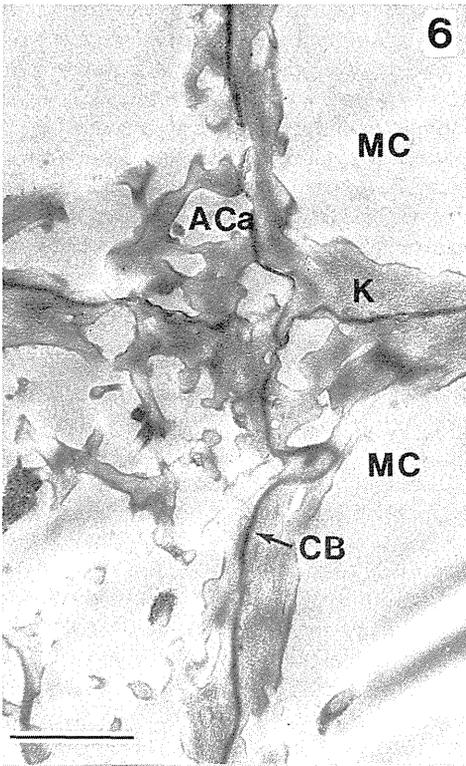
that the air-filled cavities are in fact oblong, oriented with their long axis in the main direction of the barbules. The cavities are found between the length-oriented interwoven keratin fibrils. Across the cavities, at right angles to the main direction of the barbule, are found dense, column-like structures with a granular appearance (Fig. 16). They appear to connect two neighbouring fibrils and so may have a function in supporting the fibril network. It has to be borne in mind, however, that the feathers before embedding were treated with both sodium hydroxide and formic acid; both these agents may have caused changes in the ultrastructure. Fig. 18, finally, shows what is probably the remnant of a nucleus, suspended between keratin fibrils. Most of the surface of the remnant is in contact with air, but with a single exception, the air-filled cavities do not seem to have diverticles within the remnant.

The smallest dimensions of the cavities on a transverse section is about 80 mm. The cavities appearing as fissures typically have a width of 100–120 nm. The largest cavity on a transverse section measures about 400×400 nm. The length of the cavities probably exceeds that which can be seen on the longitudinal sections considerably. It is not unlikely that they in some cases span from one end of a cell to the other; possibly most or all cavities in a cell are interconnected.

No qualitative differences between the ultrastructure of back and belly barbules were noted. No air-filled cavities were observed in the ramus cortex.

Reflectance measurements

The percentage of incident light reflected as a function of wavelength in the visible region (400 to 700 nm) is the reflectance spectrum. The spectrum of an air-filled ptarmigan barbule differs in two respects from the corresponding spectra of compact hen and pheasant barbules:

(1) The reflectance values are higher throughout the visible region which means that the ptarmigan barbules are lighter than the barbules of the other species, confirming the microscopical observations and (2) its shape is different (Fig. 20). The ptarmigan spectrum shows a gradually increasing reflectance from 540 nm to 400 nm and relatively constant reflectance in the remainder of the visible

spectrum. This means that the reflected light is bluish and corresponds well with the fact that in transmitted light the barbules appear pale yellowish-brown, as noted by Chandler (1916). The spectra of the two other species show very constant reflectance throughout the visible spectrum region (except for slight increases at the extreme ends of the visible region), as is to be expected for reflectance from a relatively horizontal surface of a solid substance with a refractive index which varies little throughout the visible region. Four spectra of air-filled and four of compact barbules were obtained (Table 1) and it will be seen that all spectra show the same features as shown by the spectra of Fig. 20.

The differences in reflectance at 540 nm and in the ratio of reflectance at 420 nm to the reflectance at 540 nm (Table 1) are statistically significant (Mann-Whitney U test: p = .03 (one-tailed), respectively p = .03 (two-tailed)).

The above measurements were performed with light impinging vertically on an approximately horizontally placed barbule surface. Under these conditions the difference between the two types of barbules is probably underestimated, since light not reflected at the surface of the partly transparent, compact barbules will transverse the barbules to be reflected from the surface of the object slide on which the barbules are placed. This glass-reflected light adds to the barbule-reflected light, while probably rather little light transverses the air-filled barbules. Under these conditions the ratio in reflectance at 540 nm between air-filled and

Fig. 10. Detail of transverse section of barbule of albinistic pheasant feather. TEM. Scale: 0.2 μm.
Forstørret udsnit af bistråle fra en fjer af en albinistisk fasan. TEM. Målestok: 0,2 μm.

Fig. 11. As fig. 12, except for larger air-filled cavities. TEM. Scale: 0.2 μm.
Som fig. 12, men de luftfyldte hulrum er større. TEM. Målestok: 0,2 μm.

Fig. 12. Detail of transverse section of ptarmigan barbule. Air-filled cavities are present. TEM. Scale: 0.2 μm.
Forstørret udsnit af tværsnit af rypebistråle. Der er luftfyldte hulrum til stede. TEM. Målestok: 0,2 μm.
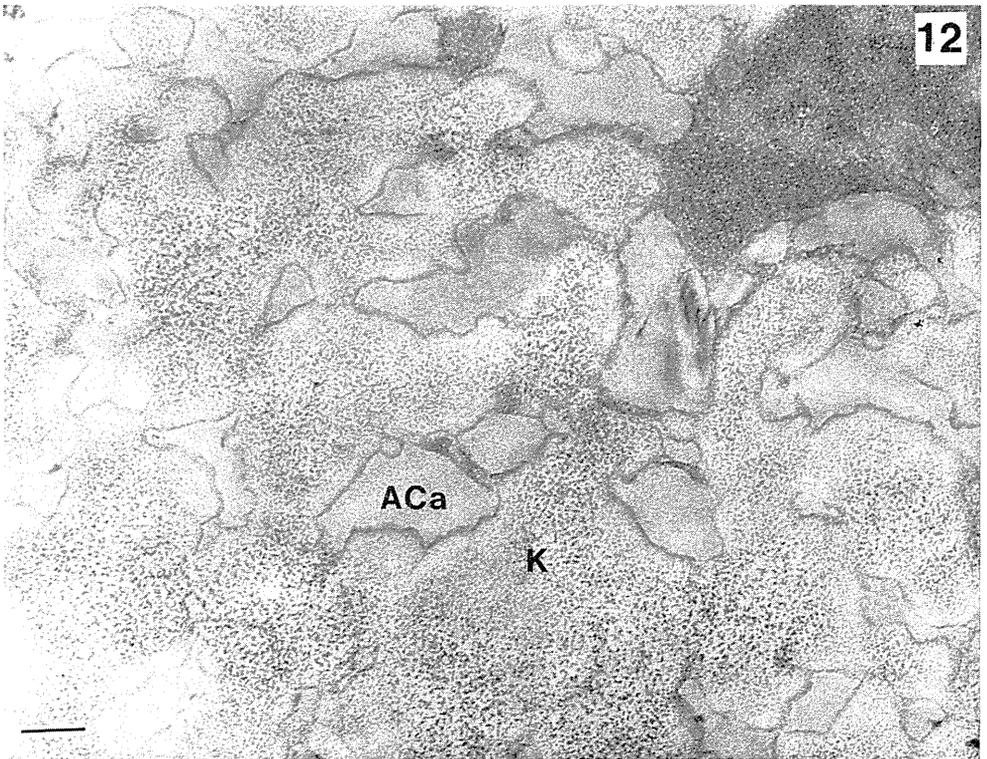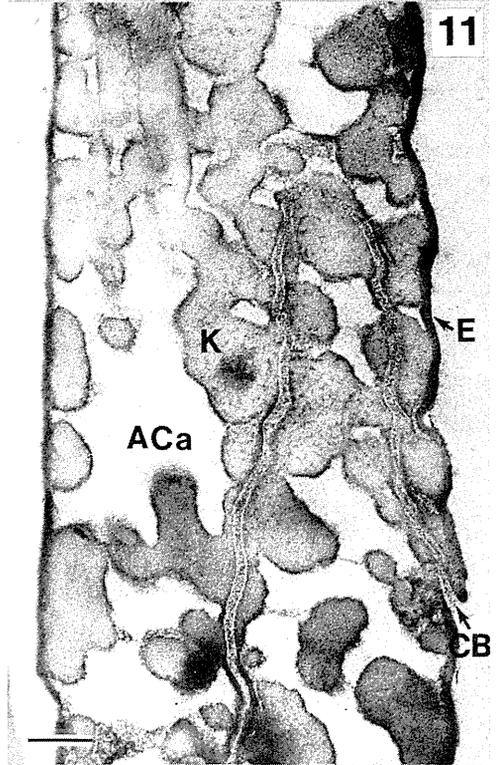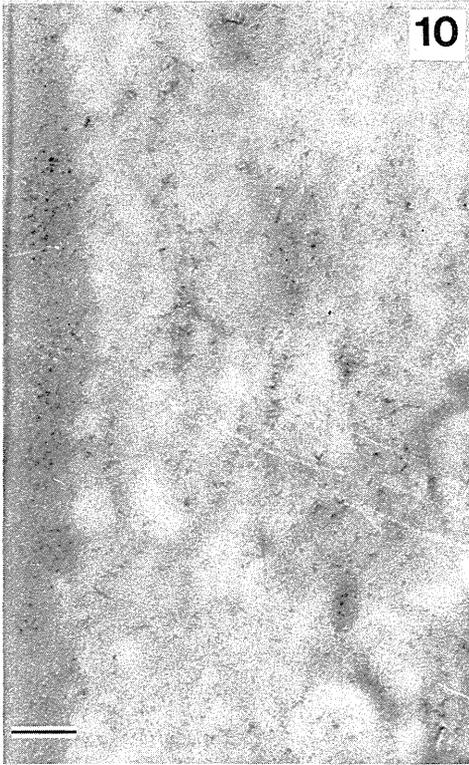
Table 1. Reflectance values (in %) of barbule surfaces of some white galliform feathers. For method of measurement: see text.
Refleksionsværdier (i %) af bistråleoverflader fra hvide hønsefuglefjer. Målemetode: se tekst.

Species and plumage region Art og fjerparti	Reflectance at wavelength (nm) Refleksion ved bølgelængden				$\dfrac{R_{420}}{R_{540}}$	$\dfrac{R_{620}}{R_{540}}$
	420	540	620	680		
Lagopus Back *Ryg* 1	18.6	14.5	15.1	15.2	1.28	1.04
Lagopus Back *Ryg* 2	19.1	16.0	14.7	15.8	1.19	0.92
Lagopus Belly *Bug* 1	19.4	15.2	15.0	14.8	1.28	0.99
Lagopus Belly *Bug* 2	15.4	12.5	12.3	12.4	1.23	0.98
mean *middel*					*1.25*	*0.98*
Gallus 1	9.2	8.8	8.8	9.9	1.05	1.00
Gallus 2	15.3	13.3	13.4	16.3	1.15	1.01
Phasianus 1	10.4	9.7	9.8	10.3	1.07	1.01
Phasianus 2	14.2	12.4	12.2	12.5	1.15	0.98
mean *middel*					*1.11*	*1.00*

compact barbules is 1.38 (Table 1). If instead reflectance is measured with obliquely incident light (»Epiplan HD« × 40 objective) the ratio in reflectance at 540 nm becomes 2.09 (p = .014, one-tailed Mann-Whitney U test). This is probably a more realistic estimate of the difference in reflection properties between air-filled and compact barbules.

The lack of a suitable standard reference for measuring with obliquely incident light is the reason that only spectra obtained with vertically incident light are presented.

Reflectance spectra of feather samples at low magnification (»semi-micro« conditions) were measured in an attempt to determine the colour as it looks in the natural situation. Four reflectance spectra were measured on a ptarmigan and four on a hen feather sample. Fig. 21 shows the calculated mean spectra. The ptarmigan feather sample reflects three to four times as much as does the hen feather sample (p = .014, Mann-Whitney U test, one-tailed). The ptarmigan spectrum shows a minimum at 570 nm, the hen spectrum at 510 nm (p = .014, Mann-Whitney U test, one-tailed). This difference in the position of the reflectance minimum corresponds to a slightly bluish colour of the ptarmigan feathers and a slightly yellow colour of the hen feathers. The difference between the two spectra is very slight, however, much less than would be expected from the measurements on single barbules, and the difference in hue between the two feather samples is difficult to see.

Fig. 13. As figs. 11 & 12. The epicuticle on the surface of the barbule is defect at one point (arrow), and here there is connection between air in- and outside the barbule. TEM. Scale: 0.2 μm.
Som figs. 11 & 12. Epicuticulaen på bistrålens overflade er gået i stykker et sted (pil), og her er der forbindelse mellem luften inden- og uden for bistrålen. TEM. Målestok: 0,2 μm.

Fig. 14. Ptarmigan barbule, transverse section. A dense nuclear remnant is surrounded by air-filled cavities and keratin fibrils. TEM. Scale: 0.5 μm.
*Rypebistråle, tværsnit. En elektrontæt kærnerest er omgivet af luftfyldte hulrum og keratinfibriller. TEM. Målestok: 0,5 μm.*

Fig. 15. Ptarmigan barbule, transverse section. Dense areas (arrows) with size and shape corresponding to those of the air-filled cavities are present. TEM. Scale: 0.5 μm.
Rypebistråle, tværsnit. Der ses elektrontætte områder (pile), der i størrelse og form svarer til tværsnittene af de luftfyldte hulrum. TEM. Målestok: 0,5 μm.

Fig. 16. Ptarmigan barbule, longitudinal section. Dense column-like structures stretch across the air-filled cavities. TEM. Scale: 0.5 μm.
Rypebistråle, længdesnit. Elektrontætte søjleformede strukturer strækker sig tværs over de luftfyldte hulrum. TEM. Målestok: 0,5 μm.
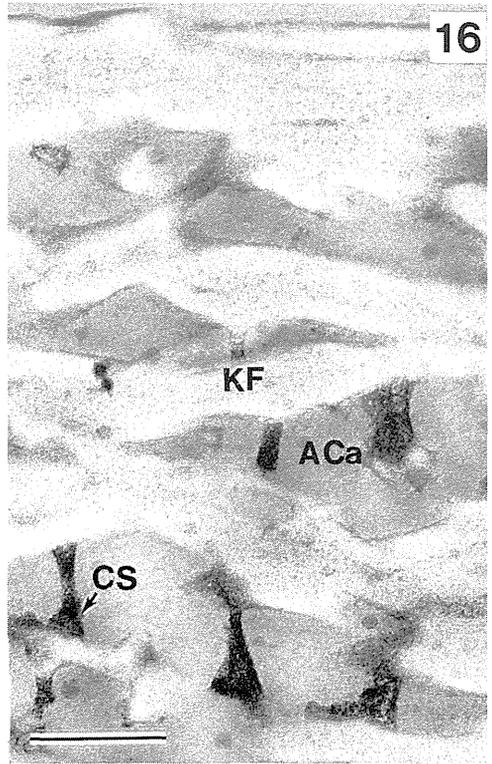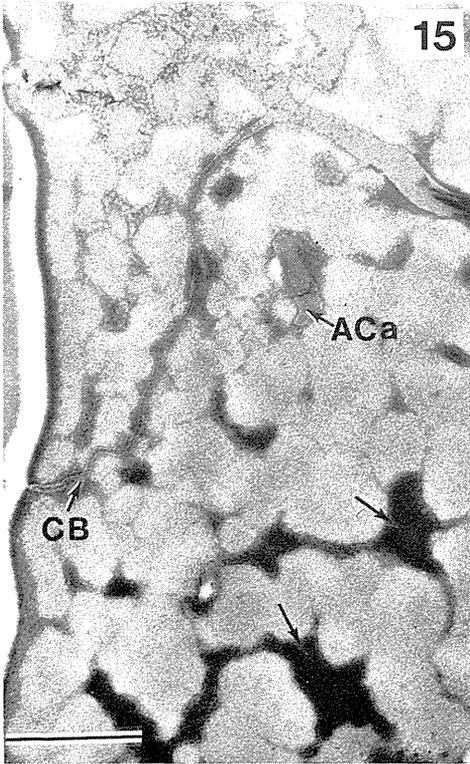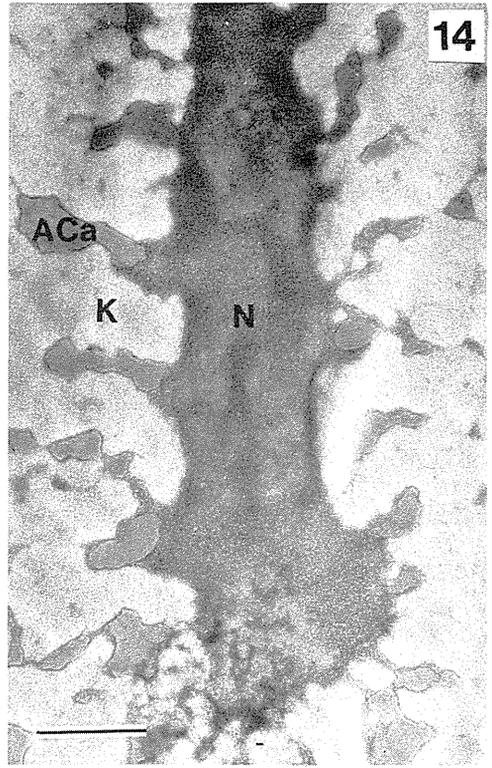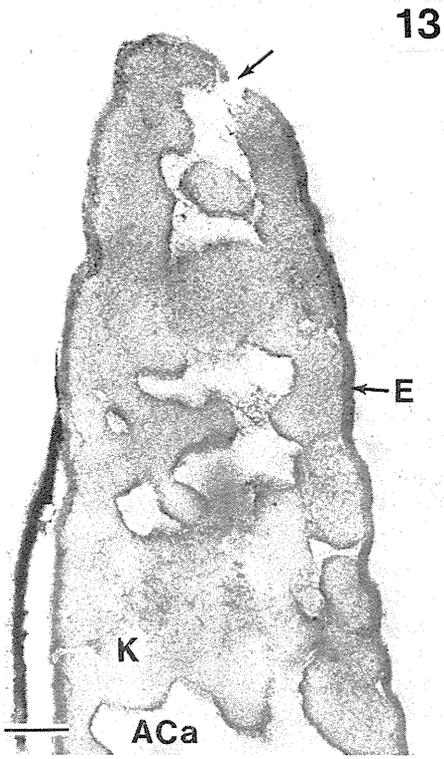
These measurements were performed with light impinging vertically on the feather sample surface. The conditions equal not too well the natural situation, where diffuse daylight is always present in addition to direct sunlight and often is the sole light source. Some measurements using obliquely incident light (corresponding to diffuse daylight) were made on the ptarmigan feather sample. No large differences in the shapes of the spectra were noted compared to the spectra obtained with vertical illumination, and so the shapes of the spectra in Fig. 21 probably are representative for the spectral reflection of the ptarmigan plumage under a number of conditions. With obliquely incident light reflectance of the ptarmigan feathers was about 85%. This probably corresponds to the reflectance of an intact plumage, since the ptarmigan plumages visually judged were somewhat lighter than white bellies of the Great Black-backed Gull *Larus marinus,* and since the reflectance of such feathers is 65−80% (unpublished measurements with a Beckmann DK-2A spectrophotometer, which yields reflectance spectra which correspond to colours as perceived under normal viewing (»macro«) conditions). The lower reflectance values with vertical illumination of the ptarmigan feather sample is probably due to some light having being transmitted through the feathers, and it is probable that the lower reflection of the hen compared to the ptarmigan feather sample is mostly due to a larger transmission of light (rather than to the light being reflected in other directions than from the ptarmigan feather sample).

DISCUSSION

Air in barbules

The present findings confirm Chandler's observation (1916) that the barbules of white ptarmigan feathers are air-filled. His observation referred to *Lagopus lagopus;* the present to *Lagopus mutus.* Probably does the same hold for *L. leucurus.* According to Chandler (1916) the barbules of white feathers are usually compact, transparent, the reflection from the numerous surfaces of barbs, barbules and barbule outgrowths in an unpigmented plumage being sufficient for creating a white

colour. I observed barbules of white feathers of *Spheniscus demersus, Cygnus olor, Larus ridibundus, Ptilinopus rivoli, Cacatua moluccensis* and *Delichon urbica* in reflected light; they all appeared transparent, reflecting light only from their edges like the barbules of the hen and the pheasant. It thus appears that the structure of the ptarmigan barbules is relatively unique among white feathers. It would be interesting to know whether other species from habitats with much snow and with white in their plumage have a similar structure.

Pigmented barbules are as a rule compact without air (personal observations). A few instances of air-containing barbules are known, however. Among galliform birds in the Blood Pheasant *Ithaginis cruentus* and in the Indian Peafowl *Pavo cristatus.* From the observations (with the light and the polarization microscope) by Schmidt (1961) on the green pigmented barbules of *Ithaginis* it appears that the arrangement of the air-filled cavities in these is the same as in the ptarmigan. In the same paper Schmidt proposes a classification of the various relationships which air within a feather may bear to the different feather components. According to this the air-filling of the ptarmigan barbules is of the »permoenial or interfibrillar« type.

Fig. 17. Ptarmigan barbule, longitudinal section. The oblong air-filled cavities are found between the interwoven keratin fibrils. TEM. Scale: 0.2 μm.
Rypebistråle, længdesnit. De aflange luftfyldte hulrum ligger imellem de sammenvævede keratin fibriller. TEM. Målestok: 0,2 μm.

Fig. 18. Ptarmigan barbule, longitudinal section. A nuclear remnant is suspended between keratin fibrils. TEM. Scale: 0.5 μm.
*Rypebistråle, længdesnit. En kærnerest er ophængt mellem keratin fibriller. TEM. Målestok: 0,5 μm.*

Fig. 19. Part of a transverse section of a dark ramus of a fruit dove. Many melanin granules are present in the air-filled medullary and in the keratin-filled cortex cells. TEM. Scale: 1 μm.
Del af tværsnit af mørk fjerstråle af en frugtdue. Der er mange melaninkorn både i de luftfyldte marv- og i de keratinfyldte barkceller. TEM. Målestok: 1 μm.
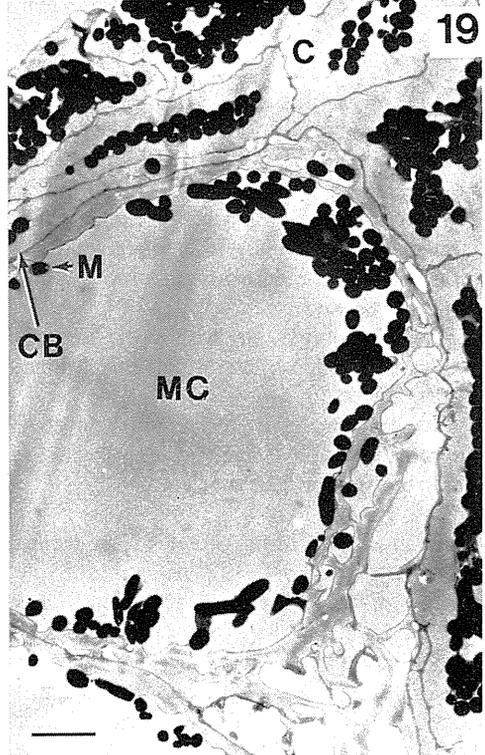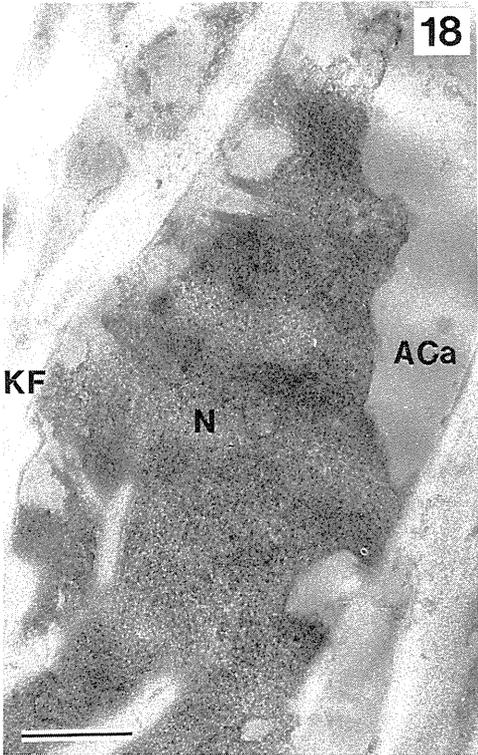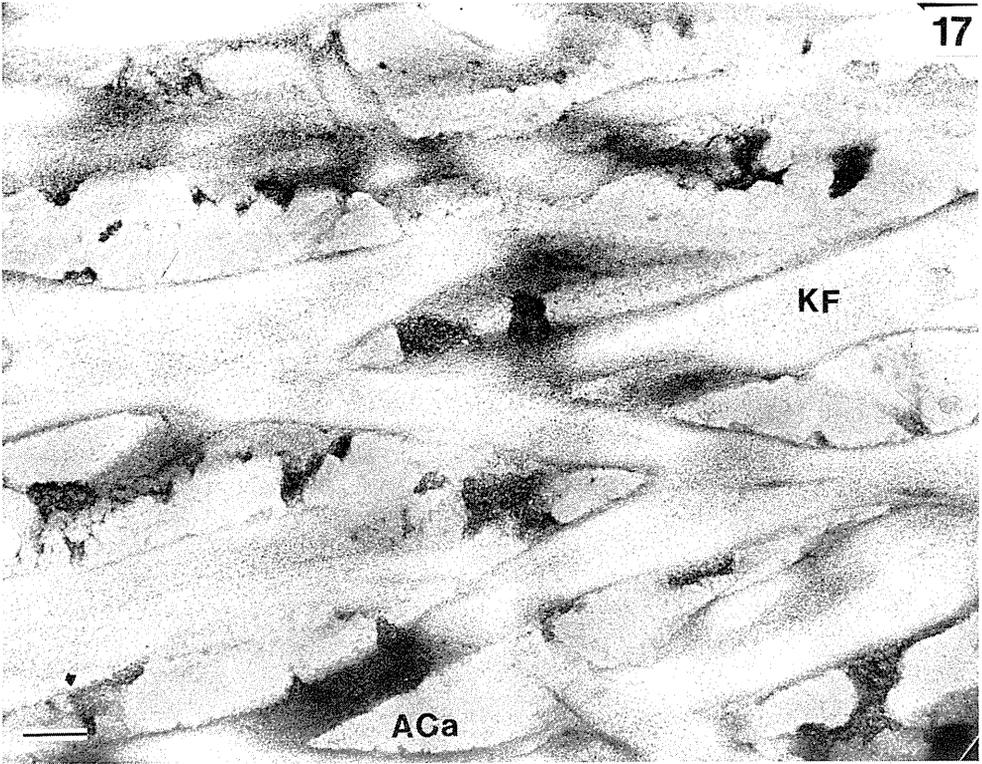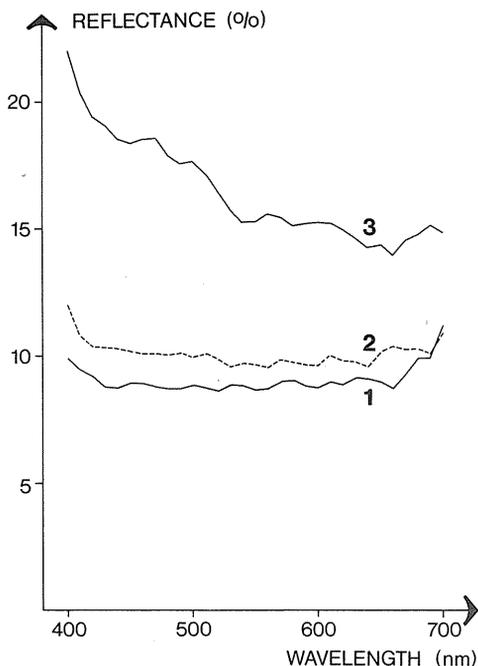
Fig. 20. Reflectance spectra of single barbule cells of white feathers. 1: Domestic Hen, 2: Pheasant, 3: Rock Ptarmigan (belly).
Refleksionsspektre af enkelte bistråleceller af hvide fjer. 1: Tamhøne, 2: Fasan, 3: Fjeldrype (bug).

In *Pavo cristatus* air is a component in the three-dimensional lattice producing the colour of »the eye« (Durrer 1962) and so is much more regular distributed than in the Ptarmigan.

In several pigeons (Häcker & Meyer 1902, Schmidt 1961) there is, within the barbules, air which is of importance for the production of structural colours.

Finally, there is air within the melanin granules of some structural coloured feathers (review: Dyck 1976).

Further examples are certainly to be uncovered in the future, but clearly air in barbules is a rather uncommon phenomenon.

Function of the white colour of the winter plumage

The air in the barbules of white ptarmigan feathers clearly represents a specialization. Two possible causes for this will be discussed: Energy economy and better colour resemblance to snow. (A third possibility: Weight reduction is discounted on the grounds that it is

extremely unlikely that such a specialization should take place in a genus which is so little dependent on flight ability, when it has not (as far as is known) taken place in other species much more dependent on their flying ability; furthermore weight reduction must be very slight).

Energy economy:
The argument of Salomonsen that white feathers improve insulation relative to pigmented feathers, is that »the cells of white . . . feathers are filled with air, which is a nonconductor, and white coloration, therefore, serves to keep the body warmth inside the . . . plumage« (Salomonsen 1972). The air-content of the barbules clearly can be explained in accordance with this argument.

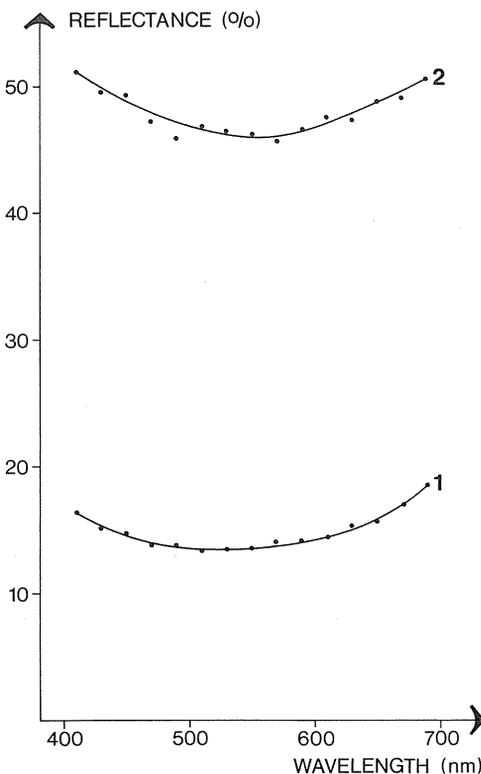But let us consider how much the air-content

Fig. 21. Reflectance spectra of samples of white feathers. 1: Domestic Hen, 2: Rock Ptarmigan (back).
Refleksionsspektre af hvide fjer. 1: Tamhøne, 2: Fjeldrype (ryg).

of the total plumage is increased. The air-content varies with location within a barbule, so an accurate estimate is difficult to obtain. But it would appear that 50 % (by volume) is not an underestimate. If we disregard the air content of shaft and rami and consider the pennaceous portion of the feather to be representative of the entire feather we may then very roughly state that an unspecialized white feather contains no air and a white ptarmigan feather 50 %.

Prenglowitz (1933) determined the amounts of keratin and air in plumages of four species. From his figures I have calculated the ratios air volume : total volume, again assuming that the feathers are compact, all air being present between the feathers. The lowest ratio is that of a grebe (95.1 %), the highest that of an owl (98.8 %). Applying a mean value of 97 % to a ptarmigan a change from an air content of 0 to 50 % in the feathers will mean an increase in the overall air content of the plumage from 97 % to 98.5 %; a moderate increase.

Complementary to the argument that white feathers are air-filled and non-conductive is the argument that »in the coloured . . . feathers the cells are filled with melanin granules which are able to conduct heat» (Salomonsen 1972).

This statement may give an exaggerated impression of the density of melanin granules in the cells. I have not sectioned pigmented ptarmigan feathers but refer to Fig. 19, which shows a medullary cell of a ramus with melanin granules in it. The section originates from a portion of a transverse section of a dark ramus of an unrelated species, a Fruit Dove *Ptilinopus (Leucotreron) cincta,* but in my experience it is a typical example of a rather heavily pigmented ramus (there is no air in the barbules of this species). It will be seen that although many melanin granules are present in the medullary cells, air is still the principal component. In the cortex, however, the melanin granules constitute a substantial fraction of the total volume.

It is likely that there is a difference in the conductivity of unpigmented and melanin pigmented keratin parts, especially as melanin possibly is a semiconductor (Needham 1974, p. 62), but I do not know of any experimental determinations.

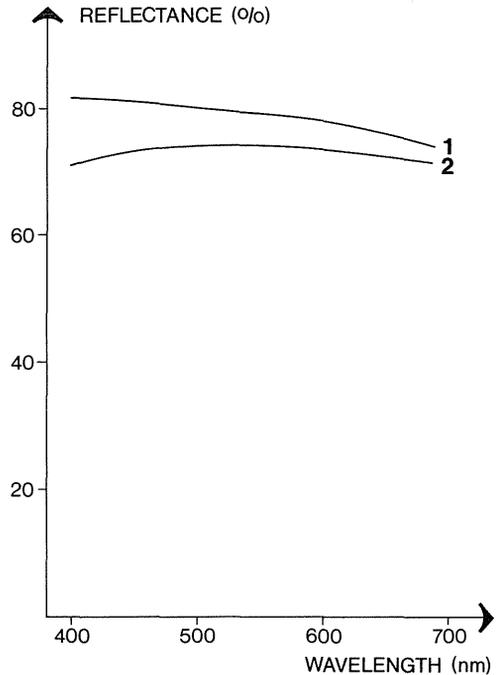The experiments of Veghte & Herreid (1965) give some indirect evidence, however. These

Fig. 22. Reflectance spectra of (1) fresh snow and (2) snow with an ice film. Redrawn after Wyszecki & Stiles (1967).
Refleksionsspektre af (1) frisk sne og (2) sne med et overfladisk islag. Omtegnet efter Wyszecki & Stiles (1967).

workers determined, by infrared radiometry, the surface temperature of the plumage of living individuals of four arctic species *(Parus atricapillus, Perisoreus canadensis, Lagopus leucurus, Corvus corax)* exposed to environmental air temperatures between −7 and −41° C. The surface temperature of the black raven was very close (1–2° C below) to air temperature when this was −41° C. The ptarmigan when kept at −34° C likewise had surface temperatures only a few degrees below air temperature. At air temperatures of −29° C and −18° C the ptarmigan surface was warmer than the raven surface but this could be ascribed to locomotor activity of the ptarmigan. At an air temperature of −8° C surface temperatures in the two species were similar. It would thus appear that the two species did not differ with respect to heat loss, but since the data suggest a tendency for heat loss to be higher the smaller the species, and since the ptarmigan is smaller

than the raven, the ptarmigan may be slightly more effective than the raven in reducing heat loss. It is noteworthy, however, that the deep black raven shows surface temperatures closely similar to that of very cold air; this indicates that heavy melanin pigmentation is not a hindrance for having a very efficient insulation. The two small species with their patterned plumages offer theoretically better opportunity for evaluating the relationships between colour and surface temperature. The thermograms do not suggest a positive correlation between darkness of plumage region and surface temperature, but an evaluation is made difficult by the extreme fluffing of the plumage, which occurred at very low temperatures.

It seems likely that the movements of the feathers associated with the fluffing will result in heat loss through convection rather than through conductance within the feathers.

It thus appears doubtful whether the air in the barbules of white ptarmigan feathers helps to increase the insulation of the plumage, and the argument may be carried a step further: Would it not be energetically more efficient for a ptarmigan to be dark during winter?

It is generally acknowledged that it is advantageous for poikilothermic animals to be dark in cold regions in order to increase heat absorbtion of radiation, while this is not the case for homoithermic animals (Needham 1974, p. 160). There are some results, however, which indicate that also dark birds profite from absorbtion of heat through radiation. Morton (1967) observed that White-crowned Sparrows *Zonotrichia leucophrys* during winter fed less on days with sunshine than on days with overcast. In a laboratory experiment he found that at 7° C birds exposed to near-infrared radiation in addition to illumination from incandescent lamps had a lower food intake than controls receiving no near-infrared radiation. At 20° C there was no difference between experimental birds and controls. Hamilton & Heppner (1967) obtained similar results when they compared food intake of Zebra Finches *Taeniopygia castanotis* dyed black with that of undyed light ones. Calder & King (1974) mention further experiments.

Also the reverse situation is possible, however; namely that a light plumage is more advantageous for the absorbtion of heat-radiation than is a dark one. In an experiment

on excised pieces of skin of the Harp Seal *Pagophilus groenlandicus,* Øritsland (1970) found that skin with light hairs became warmer when exposed to sunshine than did skin with dark hairs. The probable explanation is that in the dark pelage solar radiation is absorbed in the outer part of the hair layer, while in the light pelage radiation is mainly absorbed in the deeper layers close to the skin. A significant factor in heating probably is that in the light pelage the outer part of the hair layer prevents transmission of long-wave heat-radiation in the outward direction.

Such a »greenhouse theory« is attractive in that it provides a possible explanation of some examples of white colouration which are difficult to explain as cryptic colouration. Some of these examples refer to the fact that »among the boreal birds of the Old World the general tendency is that they are paler in East Siberia, where the winter temperatures are lower than farther west where, however, the snow cover is much more considerable« (Salomonsen 1972). Other examples refer to the fact that some arctic birds have developed white colour in concealed parts of the plumage. This applies f.inst. to the bases of the tail feathers of the Rock Ptarmigan (the visible part of these feathers is black) and to the downy bases of the body feathers of the Willow Ptarmigan in winter plumage (Salomonsen 1972).

Whether any light is transmitted through a white Ptarmigan plumage is not known, but since probably reflection is about 85 % and absorption by the unpigmented keratin negligible there presumably is some transmission of light through the plumage to the skin.

Absorption of solar radiation is of course of no relevance for ptarmigans during periods of constant darkness. But in northeastern Greenland the white plumage is assumed already in early autumn and retained until May-July (females change first) (Salomonsen 1939), so even in a higharctic population there are several months during which birds in winter plumage are exposed to radiation from the sun and the sky.

The question as to whether it pays for a species to be dark or light in order to maximize heat absorption through radiation, then may be related to the thickness of the plumage. In a tropical species like the Zebra Finch or in a temperate species like the White-crowned

Sparrow with a presumably rather thin plumage it may pay best to be dark since heat absorbed by the feathers can be transferred to the skin. In an arctic species like the Rock Ptarmigan where the plumage has to be thick in order to have a sufficiently thick layer of air between the feathers to prevent excessive heat loss, particularly during periods of darkness, it may pay best to be light so that the proportion of the light which is absorbed, although rather small, is absorbed by the skin rather than by the outer layers of the plumage. (It appears, however, that the difference in plumage thickness between tropical and arctic birds is less marked than the corresponding difference in pelage thickness of mammals (Irving 1972, p. 107). Other factors, like the proportion of the plumage being downy and the structure of the downs, may play a role here, however. Avian orders vary much with respect to the structure of the downy barbules (Chandler 1916). According to Salomonsen (1939) the feathers of the winter plumage are denser and more downy than those of the other plumages; he considers this an adaptation to the cold. Johnson (1968) likewise is of the opinion that the insulation of the White-tailed Ptarmigan is greater during winter.)

Clearly measurements of the reflection and transmission of intact plumages are needed.

Since the air in the Ptarmigan barbules seems to increase reflection throughout the visible spectral region, whereby transmission must be reduced, the air seems not to be an adaptation in accordance with such a »greenhouse theory«.

In his doctoral thesis Salomonsen (1939) also suggests that a white plumage is advantageous over a dark plumage in reducing heat loss due to thermal radiation, but quotes Loewe (1933) for stating that no such advantage exists. More recent experiments confirm Loewe's statement (Kelly *et al.* 1954, Hammel 1956) in that the colour of a plumage or a pelage bears little or no relation to its reflectance in the far-infrared region (4–40 µm). Regardless of colour little or no radiation is reflected in this spectral region, the surfaces are »black« and behave like black-body radiators. It is of special interest that this also holds for a white Willow Ptarmigan skin (Hammel 1956).

Colour resemblance to snow:
Fresh snow reflects about 80 % of incident light (Fig. 22). Reflectance increases slightly with decreasing wave-length, corresponding to a bluish white colour. In contrast snow with an ice film shows a weak reflectance peak in the green part of the spectrum (Fig. 22).

It fits with this that a ptarmigan feather sample is very slightly bluish (p. 48), but the agreement between the snow and the ptarmigan spectra (Figs. 21 & 22) is not good. A hen feather sample is very slightly yellowish and so there is an indication that the function of the air in the ptarmigan barbules is to make the white colour bluish in accordance with the colour of fresh snow.

Further measurements are needed, however, to verify this. The feather samples used are probably not completely representative of intact plumages and the measuring method (»semi-micro« conditions) is not completely representative of conditions in the field. The hen feathers which were somewhat soiled when collected, were thoroughly rinsed (ultrasonic treatment in water with detergent added) before the feather sample was prepared. A few brown particles still adhered then, however, but it is considered improbable that they have contributed significantly to the yellow tint of the sample. It is astonishing that short-wave reflection, which is so marked on the spectra of single ptarmigan cells, is so much less prominent on the spectra of the feather sample, and that there is increased reflection in the long-wave region from the feather sample, when the barbule cells reflect little in this region. In a general way it can be said that when the number of non-absorbing feathers stacked above each other is increased, reflectance will eventually approach 100 % in the entire visible region.

With respect to overall reflection (lightness) it is very probable that a ptarmigan plumage is lighter than a hen plumage and that the air-filling of the barbules is an adaptation for providing the ptarmigan plumage with a lightness similar to that of snow. But also here further measurements are needed. There can be no doubt that the intact plumage of a white hen is not so much darker as a white ptarmigan plumage as indicated by Fig. 21. More feathers under each other in the intact plumage than in the feather samples will tend to make the

difference in lightness between a hen and a ptarmigan plumage less.

Reflectance values of the ptarmigan feather sample about 85 % when measured under »semi-micro« conditions with obliquely incident light are in relatively good agreement with the snow reflectance spectra (Fig. 22).

It is not certain that air in barbules is necessary for obtaining a plumage reflection similar to that of snow, since white gull feathers (with no air in barbules) reflect up to about 80 % (p. 50). But gull feathers have many outgrowths from the barbules in order to be water-repellent (Rutschke 1960) and it may be additional reflection from these outgrowths which provide such a high overall reflection.

Besides influencing hue and lightness of the plumage, the air of the barbules may also change the angular distribution of the light reflected by the plumage, so that it resembles the angular distribution of light reflected from snow more than that of other white plumages do. At a close view the appearance of a ptarmigan plumage surface is markedly different from that of a white pheasant or a gull.

To conclude this section it can be said that there are indications that the air-filling of ptarmigan barbules is an adaptation for providing a resemblance of the plumage colour to snow colour which goes further than the resemblance of other white plumages.

Concluding remarks:

When I set out with this investigation I was fairly convinced that the white colour was to be understood solely as camouflage. Now, I agree with Salomonsen that both energy economy and camouflage are involved. I do not agree with Salomonsen, however, as to how it is that a light plumage is more energy economical than a dark one; I find an explanation in accordance with the »greenhouse theory« much more likely.

But it is the merit of Finn Salomonsen to have demonstrated that whiteness is not always closely correlated with snow cover. In particular he demonstrated this in his brilliant analysis of the moult in the Rock Ptarmigan (Salomonsen 1939), and supported it by arguments such as those cited above (p. 54).

In his doctoral thesis Salomonsen clearly considers heat conservation as the primary function. I do not agree, but consider camouflage the primary function. Mainly, because many recent studies indicate the extreme importance of camouflage in the survival of many species (f.inst. Tinbergen *et al.* 1962). With respect to desert colouration there has been a similar discussion as to the relative importance of camouflage and thermal relations. A recent review (Cloudsley-Thompson 1976) states that camouflage is the principal factor governing colourations.

With reference to the ptarmigan specifically I can offer no further arguments − with the exception of one, namely the air of the barbules − which leads us back to our starting point.

Since the air probably diminishes the transmission of light through the plumage it possibly reduces heat absorption from radiation and thereby is unfavourable with respect to the energy budget of the bird. On the other hand there is some evidence, although not conclusive, that the air is improving colour resemblance to the snow.

So it appears that where selection with respect to energy economy and to camouflage come to a conflict, selection with respect to camouflage is given first priority.

ACKNOWLEDGMENTS

SUMMARY

The white feathers in the winter plumages of ptarmigans are unique among white feathers in that the barbules contain air-filled cavities. The building of the Rock Ptarmigan *Lagopus mutus* barbules is described from electronmicroscopical findings. The air content increases light reflection from the barbules over that from barbules containing no air.

Salomonsen (1939, 1972) has argued that the white colour is more important for heat conservation than for camouflage. Some of the available evidence is discussed and it is concluded that the white colour probably is of importance for camouflage as well as for energy economy, but that the former function is the most important. The air

in the barbules is probably an adaptation for increasing visual resemblance to snow. Based on an experiment by Øritsland (1970) it is suggested that the white colour permits some absorption of solar radiation (the plumage acting as a greenhouse), while the white colour has no function in increasing the conservation of heat.

DANSK RESUMÉ

Fjeldrypens vinterdragt: De luftholdige bistrålers struktur og funktionen af den hvide farve.

I sin doktorafhandling (Salomonsen 1939) over Fjeldrypens fældning og dragter behandler Finn Salomonsen bl.a. spørgsmålet om hvorfor ryperne er hvide om vinteren. Han hævder, på basis af sine undersøgelser, at de hvide fjer har deres væsentligste betydning ved at nedsætte varmetabet, snarere end ved at kamouflere fuglene i sneen. I sin åbningsforelæsning ved den internationale ornithologkongres i Haag i 1970 påpegede Salomonsen (1972) at spørgsmålet stadig er uafklaret. I denne artikel belyses spørgsmålet udfra bygningen af de hvide fjer.

I de fleste tilfælde dannes hvide fjerpartier simpelthen ved at fjerene mangler pigment; refleksionen fra de utallige overflader som en fjerdragt består af (stråler, bistråler og bistrålernes udvækster) er tilstrækkelige til at give det hvide indtryk. Hvide rypefjer er unikke derved, at bistrålerne indeholder luft i form af aflange hulrum imellem hornfibrene. Billederne viser lys- og elektronmikroskopiske optagelser af disse bistråler samt af tilsvarende bistråler fra hvide høns og en hvid, albinistisk fasan, hvor bistrålerne imidlertid helt består af horn. Målinger af fjerenes lysrefleksion gør det sandsynligt at luften i rypefjerene gør rypedragten hvidere end de fleste andre hvide fjerpartier, og måske også mere blålig. Da sne er svagt blålig (eller grønlig, alt efter omstændighederne) er der visse holdepunkter for at antage at fjerenes specielle bygning er sket som en tilpasning til sneens farve og altså som kamouflage.

Det diskuteres endvidere om luften i rypefjerene kan tænkes at forbedre fjerdragtens isolerende evne. Da langt det meste luft i en fjerdragt befinder sig imellem fjerene og ikke i fjerene, og da varmetabet antagelig sker ved at varm luft imellem fjerene nær huden udskiftes med kold luft fra omgivelserne snarere end ved varmeledning igennem fjerene, anses det for usandsynligt at rypefjerenes specielle bygning er en tilpasning til at reducere varmetabet.

Imidlertid er der, som påvist af Salomonsen, en række ejendommeligheder i udbredelsen af hvidt i fjerdragten, såsom at de hvideste bestande ikke altid lever i de snerigeste egne, men i de koldeste, sådan at temperaturen åbenbart også må spille en eller

anden rolle for hvidheden. På basis af undersøgelser af norske forskere fremsættes den formodning at rypedragtens hvide fjerdragt virker som et drivhus, der tillader en vis udnyttelse af solstrålingen. Havde rypedragten været mørk, ville der ganske vist kunne absorberes mere stråling fra solen, men strålingen ville væsentligst opsuges af de mørke fjer, og det ville antageligt være vanskeligt i den tykke fjerdragt at få varmen transporteret fra de mørke fjer og ind til huden, således at varmen kunne komme rypen til gavn. I en hvid fjerdragt, derimod, vil en vis varmeabsorption muligvis kunne ske i de dybe lag af fjerdragten eller direkte i huden og dermed kunne komme rypen til gode.

Det forekommer herefter sandsynligt at rypevinterdragtens hvide farver har betydning både for kamouflage og for energibudgettet. I modsætning til Salomonsen anser jeg dog kamouflagefunktionen som den vigtigste, bl.a. fordi luften i bistrålerne formodentlig snarere modvirker end fremmer en eventuel drivhusfunktion.

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