

## THE WATER-HOLDING MECHANISM OF SANDGROUSE FEATHERS

By A. M. RIJKE

*Department of Materials Science, University of Virginia,  
Charlottesville, Virginia 22901*

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### INTRODUCTION

The detailed studies of Cade & Maclean (1967) on the mechanism of water transport by the sandgrouse *Pterocles* have contributed important evidence to the long-standing controversy regarding the manner in which the young obtain their drinking water. The field observations of these authors have shown conclusively that the male of the species soaks his abdominal feathers by squatting down in water-holes, usually during the early hours. He then speeds off to the nesting site where the young gather around his exposed abdomen and obtain their water by stripping his belly feathers with their beaks.

In addition to this behaviour it has been noted that the abdominal feathers of the male, and to a lesser extent those of the female, show a number of structural characteristics which render the uptake of water particularly effective. The distal fifths of these feathers are very similar to the feathers of other parts of the sandgrouse body in that they show the conventional structural array of barbs and barbules with their characteristic water-repelling properties. The structural parameter  $(r+d)/r$  for both male and female rates between 5.5 and 6.2 with slightly higher values within this range for the dorsal side. This result is in line with similar data on other terrestrial birds, indicating an effective water repellency without the necessity of preventing water penetration (Rijke, 1970).

The proximal four-fifths of these feathers show a vastly different pattern. Microscopic investigation reveals that the barbs are not held together by the usual hook-and-flange mechanism of the barbules. Instead, a series of barbules, flat and ribbon-like along their basal parts, are coiled along the ventral side in a helical pattern and are effectively intertwined with neighbouring barbules of the adjacent barbs. This arrangement provides an unusually strong and springy quality; the barbs cannot be separated as easily as can those of other regions. Furthermore, they have a fringe of downy tufts at the ends on both sides of the rachis which is clearly discernible with the naked eye. Hair-like extensions of barbules cover most of the ventral side and their function becomes readily evident when water is applied to this surface. When the feather is dipped into the water and then withdrawn, the dorsal side appears to shed water effectively, but on the ventral side the downy tufts are drawn inward and hold a considerable amount of water due to capillary forces. Details on the water-retentive mechanism can be followed through a microscope of relatively low power. Water applied to the ventral side is readily drawn up into the hair-like extensions of the barbules and when it reaches the basal, coiled regions the helices abruptly uncoil and

proceed to expose their lengthy ends perpendicular to the plane of the feather. This arrangement of the barbules permits large quantities of water to be drawn up by capillary attraction. On subsequent drying the barbules will coil up again and intertwine with adjacent barbules, thus returning to the original feather structure. These microscopic observations have been described in detail by Cade & Maclean (1967) and re-examined and found to be correct for *Pterocles bicinctus* by this author.

It is the purpose of this paper to show that the structural mechanism of the water-holding barbules is a direct consequence of anisotropic, reversible dimensional changes of the feather keratin which are explicable on the basis of well-established physico-chemical principles appropriate to macromolecular systems.

#### THE STRUCTURE OF FEATHER KERATIN

Feather keratin, which in the native state possesses a  $\beta$ -type crystallographic structure, is similar to other fibrous proteins such as collagen,  $\alpha$ -keratin from hair and elastoidin in that it combines a macromolecular character with a high degree of axial orientation in the crystalline state. Upon melting (called shrinkage in this case) the individual long-chain molecules will coil up into statistically more probable configurations with concomitant changes in dimensional properties of the fibre. Subsequent recrystallization will normally not restore the original dimensions. Instead, small crystallites, formed at different positions along the protein chains, will be orientated in a crystallographically random manner and the fibrous characteristics will be permanently lost. The fibrous proteins as a class, therefore, possess the important initial structural requirements necessary for contraction to accompany melting.

In certain of these systems, particularly the keratins, chemical cross-links between units of the chains are also present. It is presumed in these cases that the cross-links are formed subsequent to fibre formation and are thus imposed on a previously axially orientated structure. Upon melting, the molecular chains between cross-links will again assume a randomly coiled configuration, but this time the chain ends have to meet the pre-requisite of retaining chemical linkage with the ends of three other chains at each cross-link. This will affect the configurational properties of these chains and thus the dimensional changes of the fibre, and will also provide the conditions for re-attaining at least part of the original anisotropic dimensions upon recrystallization. Hence, reversible contraction would be expected to accompany the crystal-liquid phase transition of highly cross-linked fibrous proteins.

It is well known that  $\alpha$ - and  $\beta$ -keratins exist in the orientated crystalline state, possess a high concentration of cystine residues and undergo contraction when subjected to the action of a wide variety of reagents (Alexander & Hudson, 1954). Two distinctly different types of contractile process are observed in keratin fibres. One of these involves the interaction with reagents known to sever disulphide cross-links between the cystine groups so that the dimensional changes observed are irreversible. In the other case, reversible anisotropic dimensional changes are observed without the breaking of intermolecular cross-links. This type of contractility is now recognized to be a consequence of melting and recrystallization. Examples of both types are reported in the literature (Whewell & Woods, 1946).

Melting and the accompanying contraction can also be produced by a diversity of

reagents. In Fig. 1 the shrinkage temperature of feather keratin from the quills of domestic turkeys is plotted against the concentration of lithium bromide in the supernatant liquid (Mandelkern, Halpin & Dioro, 1962). Increase of the bromide concentration causes the shrinkage temperature to drop, until the concentration reaches about 8 moles/l. With further increase of salt concentration the melting temperature rises again. Thus, according to the data plotted in Fig. 1, it should be possible to induce cyclic melting and recrystallization isothermally by changing the composition of the supernatant phase. Although an unphysiologically high salt concentration is appropriate to the occurrence of cyclic dimensional changes of keratin in the case of lithium bromide solutions, it should be pointed out that this does not detract from the usefulness of the principle involved. In fact, extremely small changes in concentration of

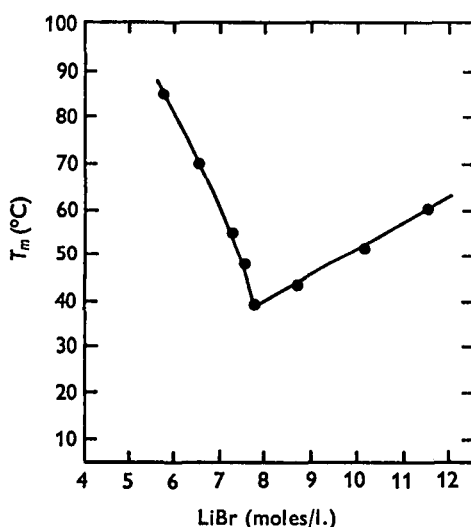


Fig. 1. Plot of melting temperature (shrinkage temperature) of feather keratin of domestic turkey against concentration of aqueous lithium bromide solutions (from Mandelkern *et al.* 1962).

adenosine triphosphate (ATP), a reagent presumed to be involved in the physiological action of muscle, have been found to be effective in reversible, rapid shortening of glycerinated muscle fibres (Mandelkern, 1964). Also, the particular chemical mechanism which causes melting with subsequent contraction is in no way uniquely related to the observed dimensional phenomenon which is a consequence of phase transition only. Despite the diversity of reagents that are known to induce contractility in the fibrous proteins, the same basic underlying mechanism can be shown to be operative. It is anticipated that the principles set forth above apply to a significant extent to such biological processes as muscle action, cell mitosis, chromosome movement and cell motility, although no direct evidence of such involvement exists at present.

#### STRUCTURAL PROPERTIES OF THE BARBULES

The principles outlined in the previous section find their origin in the macromolecular character of fibrous proteins and are not peculiar to chemical composition or biological origin. In fact, any macromolecular material that can be crystallized follow-

ing dimensional extension is expected to show this behaviour, as indeed is found for such materials as polyethylene and synthetic rubber (Mandelkern, 1964). Reversible contraction and elongation in these cases can be achieved by introduction of cross-links through X-ray irradiation. In advancing an explanation for the unusual behaviour of the barbules of sandgrouse, it will be sufficient to consider only those properties of feather keratin related to its macromolecular nature without recourse to specific biological aspects.

The reversible structural changes of the barbules of the abdominal feathers when in contact with water follow directly from the above considerations if we assume that a melting–recrystallization transition is involved in the process. The actual percentage of dimensional recovery after each cycle is determined by the degree of axial orientation and the extent of crystallinity and/or cross-linking between the cystine groups. It is only in this respect that the barbules need to be different from keratin of other feathers in order to exhibit their remarkable nature.

It is immaterial whether the immersion in water (dilution) causes the barbules to melt or crystallize. As shown in Fig. 1 for keratin of the rachis, dilution of the ambient salt solution can induce both melting and crystallization, depending on the prevailing concentration range.

In an effort to verify the above-mentioned principles the proximal four-fifths of abdominal feathers of *P. bicinctus* and *P. namaqua* were investigated by X-ray diffraction to discover whether there is any morphological transition of the keratin on wetting. The material was packed in thin-walled glass capillaries of 1 mm diameter and mounted in the beam of a XRD-5 diffractometer. Nickel-filtered  $\text{CuK } \alpha$ -radiation was employed, and samples of the same dimensions were mounted in a stage to facilitate identical position for scattering. The diffraction patterns were determined over an angular range which corresponds to  $2\theta = 10\text{--}60^\circ$ . Water was added through the open tops of the capillaries and the samples were wetted thoroughly by capillary activity. Separate runs on dry and wet capillary tubes without sample were performed in order to determine the contribution of glass and water to the overall scattering.

The results are shown in Fig. 2 for *P. bicinctus*. A peak can be discerned at  $2\theta = 19.5^\circ$  due to the presence of crystallinity in the keratin. From the surface areas under the curves, it can be calculated that the crystalline fraction in the dry sample is not more than 22%, which reduces to about 3% when the samples are wetted. It should be emphasized that these figures have at best approximate value only because of the large contribution to the scattering of glass and water, the small samples sizes and the relatively small percentage of crystallinity present. They do, however, clearly indicate that the crystallinity decreases on wetting. After the samples had been dried, the original diffractograms were again obtained. Similar results were found for *P. namaqua* in which the respective percentages of crystallinity are somewhat smaller than in *P. bicinctus*. These results show clearly that the mechanism of reversible melting–recrystallization cycles in barbule keratin upon wetting is qualitatively supported by X-ray analysis in analogy with similar findings on axially oriented, crystalline macromolecules.

When the degree of crystallinity or cross-linking is not homogeneous throughout a cross-section of the barbules, twisting and turning of the fibre will accompany the transition as a result of unequal contraction or elongation of different sections of the

fibre. Provided that the cross-links are not severed, all processes are completely reversible.

The essential difference between the abdominal barbules of the sandgrouse and other feather components is therefore determined by a variation of structural parameters of the feather keratin only, without the necessity of invoking evolutionary innovations in structural design.

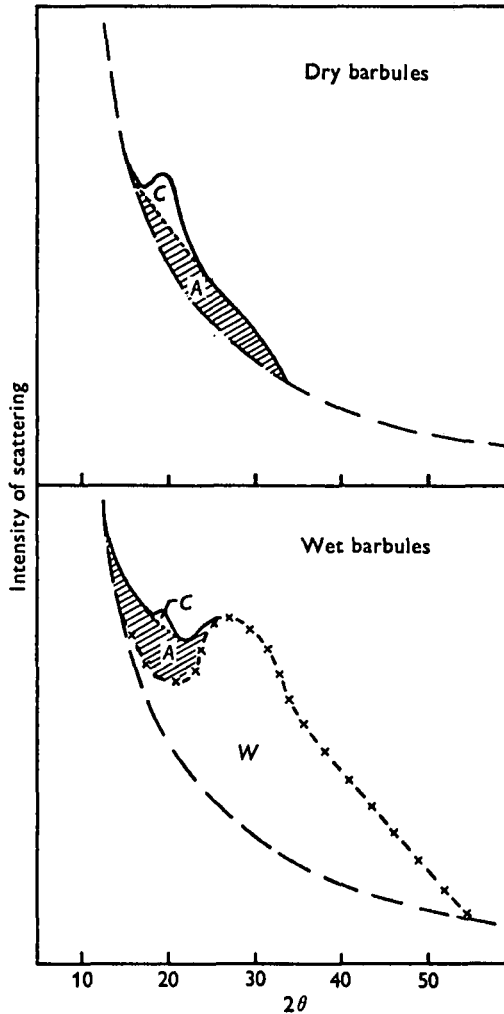


Fig. 2. X-ray diffractograms of abdominal barbules of *P. bicinctus*. —, Base-line due to scattering of empty glass capillary; + — +, scattering due to glass and water; — —, separating amorphous from crystalline scattering of sample. *W*, Scattering due to water; *A*, amorphous scattering of sample; *C*, crystalline scattering of sample.

It is unlikely that the water-holding mechanism of the abdominal barbules is based on any other mechanism. Dimensional changes can in principle be brought about by imbibition of a swelling agent, but such a process is slow and diffusion-controlled and fails to show the abrupt mechanical transformation so evident in sandgrouse barbules.

## SUMMARY

1. The barbules of the abdominal feathers of sandgrouse exhibit structural characteristics which are favourable for the uptake of large quantities of water. This feature greatly assists the male of the species in his efforts to bring water to the young.
2. The structural details of feather keratin, peculiar to many fibrous proteins, provide a straightforward explanation of the mechanical transformation of sandgrouse barbules, when wetted, in physico-chemical terms appropriate to macromolecular systems.
3. X-ray analysis of dry and wetted sandgrouse barbules qualitatively support the proposed mechanism of a reversible melting-recrystallization cycle for the barbule keratin.

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