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Light collection and solar sensing through the polar bear pelt

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The pelt of polar bears acts as a translucent insulation through the hairs of which diffuse light is transferred by a combination of scattered light and luminescence light collection. The optical and morphological differences with respect to the white hair of other mammals have been investigated by scanning light microscope and UV-laser-induced luminescence studies and model experiments performed which support the suggested mechanism. An evaluation of physiological information on the energy turnover and dissipation in the polar bear suggests that comparatively little additional energy can be gained by harvesting solar radiation. However, due to the peculiar energy transparent pelt of the polar bear and the significant cooling of peripheral tissues suffered during cold ambient conditions, solar irradiation may change subcutaneous temperatures by as much as 10 °C. It is suggested that the polar bear's skin, using the temperature pattern produced on its surface by scattered light, calibrated for wind chill against the body-temperature-controlled latissimus sheets, may be used as a kind of sensory system. This may help the polar bear to determine the approximate position of the sun and thus to navigate under diffuse arctic visibility but also to locate ice-free sea surfaces with significantly reduced light scattering properties as compared with ice-covered surfaces.

1. Introduction

In a recent short communication from our laboratory [1] it has been reported, that, in contrast to previous simplified concepts [2–4], the hairs of polar bears combine two distinct optical phenomena: light collection through optical scattering and luminescent light collection for a concentration of light on the hair basis, where it is converted into heat. As compared to white hair of other mammals evolutionary adaptation in optical key mechanisms has been demonstrated [1]. Although the advantage from the gain in thermal energy for a polar bear due to this light collection process appears to be moderate, the detected mechanism could create a temperature pattern on the skin, which could reflect the strongly asymmetric distribution of short wavelength light in polar environments. It has been speculated that the polar bear can use these stimuli for orientation and navigation. The present paper serves to provide a broader experimental basis, to understand the function of the light collecting hairs within the polar bear's pelt and to discuss consequences more in detail.

Some peculiar properties of the pelt of polar bears such as the strong absorption of UV light, as seen on UV photographs, the white appearance of the pelt and its solar thermal properties have been at the center of some scientific controversies [2–4]. It has been proposed that ultraviolet light may (by a complex process

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involving scattering from the inner cores and reflection from the outer surfaces) be preferentially conducted to the bear's skin explaining the strong UV absorption and the white appearance of the pelt [2]. An energetic advantage resulting from a conversion of UV light into heat was claimed although it was admitted that sufficient experimental and theoretical evidence is still lacking [4]. A different explanation attributed the UV absorption to ordinary absorption by proteins and the white colour to scattering phenomena similar to those which produce white colour in clouds, snow or milk and doubted any energetic advantage [3].

An interesting result of research on thermal properties of pelts of polar bears is the discovery of a comparatively low thermal insulation, both in contact with air and with water. This is thought to be necessary to allow sufficient heat dissipation during hunting [5]. Supporting this notion, a pair of muscle sheets (total area between 0.16 and 0.46 m^2), richly supplied with blood vessels, was found above the blubber directly under the skin above the dorsal latissimus and has been interpreted to be a specialized heat dissipating system [6].

2. Experimental

2.1. Hair samples

Hair samples from the polar bear have been obtained from four different sources: (a) Berlin Zoological Garden, (b) Frankfurt Zoological Garden, (c) Zircus Roncalli and (d) Eisrevue. They were cleaned with distilled water, but not treated with organic liquids. Some properties such as the luminescence appeared to vary according to the seasonal pelt and with the time passed since the taking of the sample. Sufficient systematic information is, however, not yet available. According to the specialized literature [17] the pelt of a polar bear may be completely white, yellowish or even grey to light brown with its colour depending on the season and on the way of life of the animal. It is usually clean white in late fall and in winter after the change of the hairs which occurs once a year. It becomes yellowish at the end of summer. Polar bears living in the pack-ice distant from open sea water are whiter than bears swimming frequently in the water. A gray or even light brown colour is reached with animals on land with little or no snow cover.

Only healthy hairs were included in the studies. One hair sample showed clearly fungal attack which affected the optical properties.

2.2. Optical studies

The refractive index of the hairs under investigation was determined using the method of index matching. A single hair was placed on a microscope slide, embedded in a fluid of known refractive index and covered with a cover glass. Upon observing the hair through a light microscope (Leitz Orthoplan, magnification $500\times$) index matching was achieved when the hair–fluid boundary during focusing and defocusing remains stationary.

Index matching was also used as a non-destructive method to look inside the hollow hair cylinder. By embedding the hair in a fluid of the same refractive index as the hair cylinder the hair becomes transparent and changes in the refractive index will be visible as dark areas or lines.

The wavelength dependent absorption of the hairs of different mammals were measured using a spectral photometer (Perkin Elmer Model 330) with an attached integrating sphere (range 350–1500 nm). Tuffs of hairs were either arranged in front of the integrating sphere with the axis of the hairs preferential parallel or perpendicular to the monochromatic collimated light beam. Scattered light is then collected by the integrating sphere and its intensity measured with a photomultiplier giving the transmission spectra.

To measure the reflection versus wavelength the hairs were attached on the backside of the integrating sphere and illuminated through a small opening. The opening was closed with a flat disc having the same surface coating as the inside of the integrating sphere. The incident angle was chosen to be approximately perpendicular to the hair axis.

The transmission curve of a single hair of a polar bear was recorded with a scanning light microscope (Zeiss). A diaphragm in the intermediate image plane allows only light coming from a small selected object area to enter the photomultiplier. The chosen diaphragm was 5×5 μm placed in the middle of the outer hair core. A condensor focuses light at angles between $60°$ and $90°$ to the hair axis.

The same arrangement was used to measure the light distribution in the base plane while illuminated with a tungsten iodine or xenon lamp. The whole object was moved with respect to the diaphragm in steps of ~ 5 μm and the measured light intensities were sampled and displayed as an image.

Luminescence spectra were taken in commercial luminescence spectral photometers. In one case a tuft of hairs ($\sim$ 100 single hairs) was aligned so that their bases approximately faced the entrance slit of the analyzing monochromator but the total luminescence light generated by the incident UV light (300 nm) is measured (Perkin Elmer). In another case only 7 hairs were excited by UV light but a diaphragm allows mainly the entrance of luminescence light originating from the basis of the hairs to enter the analyzing monochromator. In additional experiments UV laser light (352 nm) was used to excite luminescence in the hair of polar bear and, for comparison, of white goat (male and female) and pony.

The model experiments on light collection were performed with the following setup: (a) Glass capillaries (4.5 mm) and light from a tungsten iodine lamp passing through ground glass. The bases of the capillaries were directly attached to a Si detector which fit the needed area. Scattering centers within the capillary were produced by small KCl crystals, grown from a 0.1M aqueous solution (fig. 1a). (b) A mounting for the illumination, with diffuse light, of rectangular transparent plexiglass plates (fig. 1b), into the lower surface of which well defined concentrations of scratches were introduced for light scattering. Alternatively, plates containing luminescent molecules (e.g. perylene) were investigated for comparison. The measurement was performed in a black box with a black body absorber at the bottom of the plexiglass plate. The collected diffuse light was measured with a silicon detector at the edge of the plate along which the detector could be displaced.

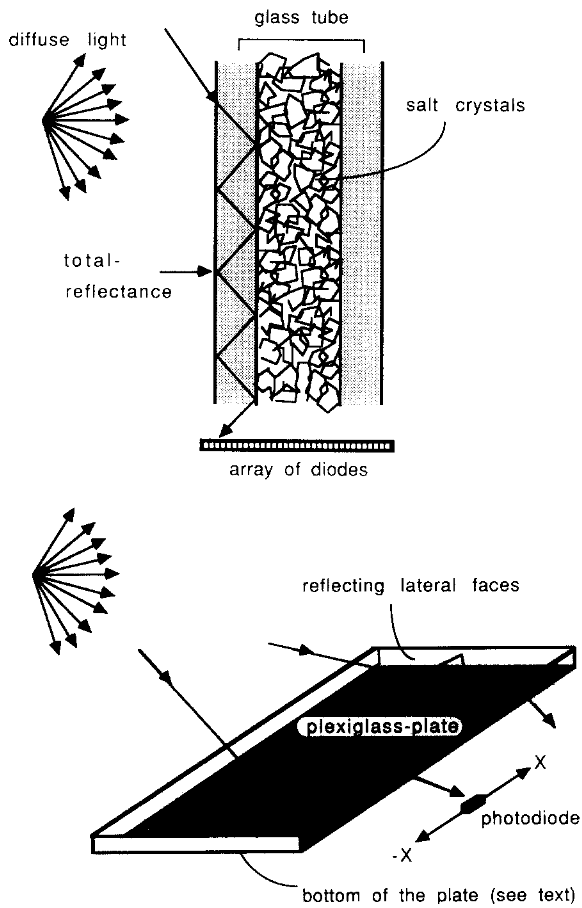

Fig. 1. Set-ups for model experiments on light collection using (top) a capillary with salt crystals forming scattering centers and (bottom) transparent plexiglass plates the bottom of which is modified by defined concentrations of scratches.

It should be emphasized that these measurements were not measurements of light concentration ratios but should simply provide qualitative information on light collection by light scattering processes and combined scattering–luminescence processes, respectively.

3. Results

3.1. Morphological studies

The difference of the morphology of hairs of polar bears, especially the structure of the inner channel, as compared to white hairs of other mammals has been

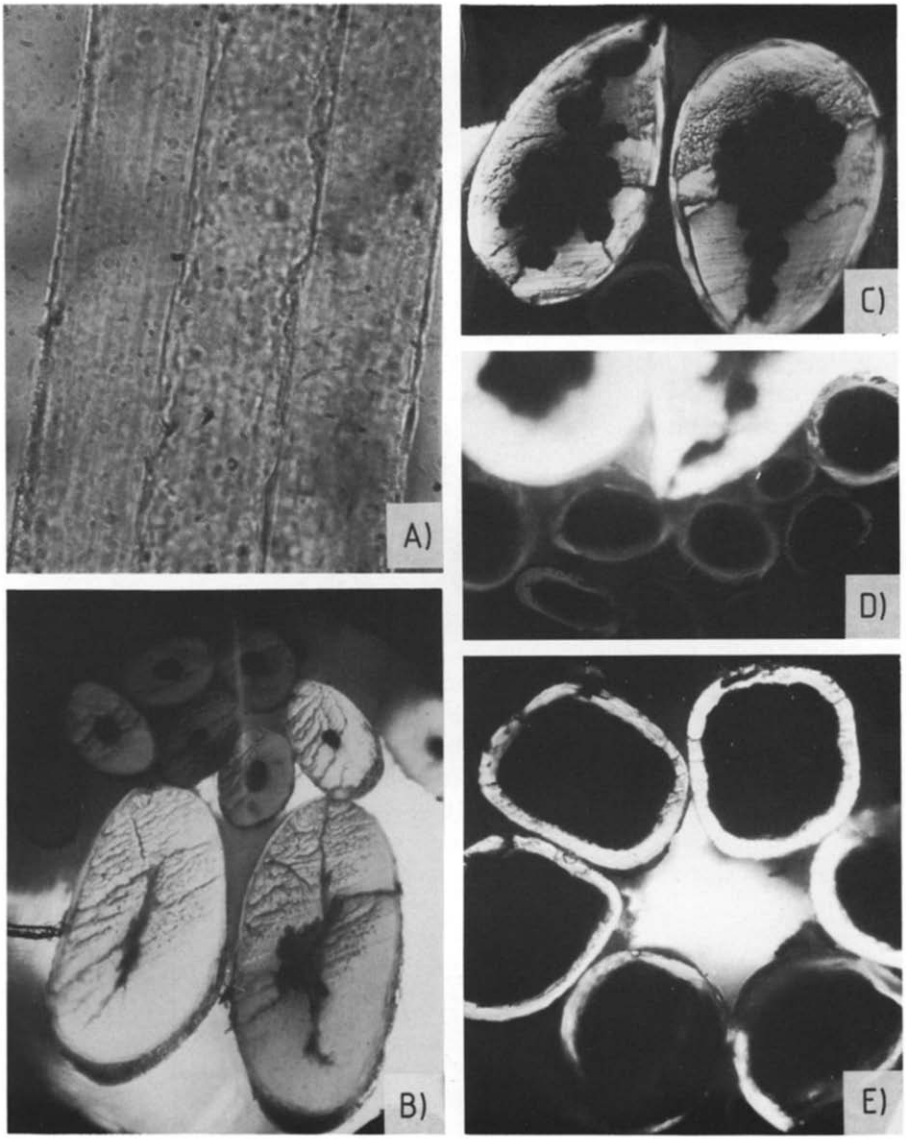

Fig. 2. Longitudinal cross section through hair of polar bear (A) compared with cross section through hair of polar bear and of two (thicker) hairs of pig (B), cross section of base of pig hair (C), of white horse (D) and male goat (E).

demonstrated [1]. Fig. 2 shows cross sections of white hairs of pig, white horse and goat and contrasts them with cross and logitudinal sections of hairs of the polar bear. As a remarkable detail and in contrast to other mammals scattering centers with a dimension of < 2 μm are visible in the hair channels of the polar bear.

3.2. Optical studies

The scattering centers have a refractive index which is different from that of the hair cylinder (which is $n = 1.559 \pm 0.002$, confirmed for 4 different polar bears). Fig. 3 shows a comparison of the transmission of light through white hair of pig, horse, sheep, polar bear and goat. It can be seen that in all these mammals the trend of spectral absorption is similar.

Fig. 4 compares the transmission curves of polar bear hairs measured in transmission–scattering (a) and reflection (b) with the curve published by Grojeen et al. [2]. In addition the transmission of a single hair measured parallel to the hair axis is shown (fig. 4d). It indicates a significant asymmetry in the optical properties of polar bear hair which might in part be due to light scattering in the hair core. In order to get complementary information on the optical properties of single polar bear hairs they were illuminated over a length of 3–4 cm parallel to the longitudinal axis with a tungsten iodine lamp and the light distribution in the basal plane was measured with a scanning light microscope. Fig. 5a shows the distribution of absorption after computer processing the signals to an image. It is seen that the visible excitation light incident on the hair at an angle between 60° and 90° to the hair axis is recovered at the hair base, except at the core and along a ring around the outer surface of the hair. The coupling of light into an optical fiber is not a trivial phenomenon. It is necessary that a mechanism is involved, which is able to redirect light propagation so that total reflectance from the inner hair surface is possible. Since visible light incident on polar bear hair does not produce significant luminescence, it is necessary to assume light capture in the hair occurs through scattering particles, evidently those visible in the core of the hair of polar bear [1].

When the tungsten iodine lamp is replaced by a source for UV light (xenon), the pronounced concentric absorption profile is somewhat faded, although still recog-

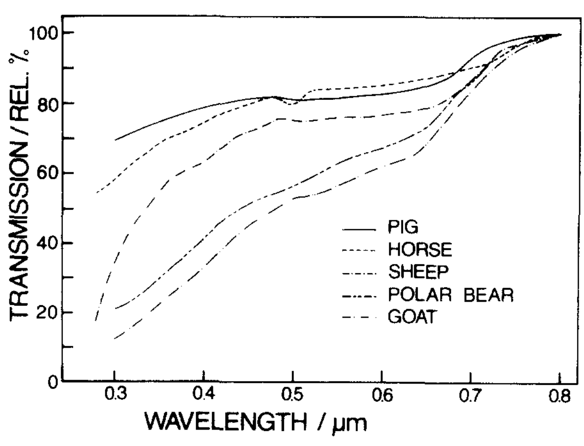

Fig. 3. Comparison of transmission of white hair bundles of different mammals (pig, horse, sheep, polar bear and goat). The value measured at 0.8 μm was calibrated to 100%.

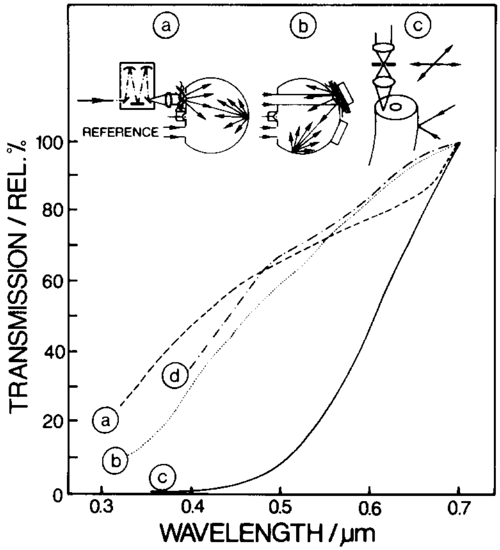

Fig. 4. Transmission–wavelength dependence for hair of polar bear (inserts explain set-ups for measurement): (a) in transmission–scattering, (b) in reflection, (c) transmission of a single hair measured parallel to the hair axis (transmission at 700 nm calibrated to 100%), (d) measurement of transmission of hairs of published by Grojean et al. [2].

nized (fig. 5b). A look at fig. 4, curve c, which demonstrates a strong absorption of blue and ultraviolet light parallel to the hair axis explains why less light now arrives at the hair bases. On the other hand, when UV light ($\lambda < 320$ nm) was incident, perpendicular to the hair axis, visible fluorescence light was emitted from the basal plain. This means that light coupling into the hair of polar bear through excitation of luminescent light has to be considered as a relevant factor determining the optical properties of polar bear hairs. It has been reported in the above mentioned short communication [1] that the luminescence of polar bear hairs is characteristically different from that of white hair of other mammals in that the onset of luminescence is shifted to longer wavelengths producing a characteristic luminescence gap between absorption and luminescence. Due to the significant light scattering properties of polar bear hairs and second-order diffraction from the grating, luminescence measurements with commercial luminescence spectrometers involved some difficulties. For this reason UV laser light ($\lambda = 252$ nm) was used as an excitation source in complementary experiments. Fig. 6 compares the luminescence induced with this 252 nm laser line in the hair of a polar bear with the luminescence of white hair from a male and female goat and a white pony. It is evident that only the hair of the polar bear shows a characteristic "luminescence gap" exceeding 1×10^{-14} s^{-1}, which is a precondition for efficient luminescent light collection (see later) and has been recognized as an evolutionary adaptation contributing to the polar bear's heat pump [1]. Compared to the next favourable luminescence spectrum of a mammal, that of a male goat, the luminescence spectrum of a polar bear hair is significantly

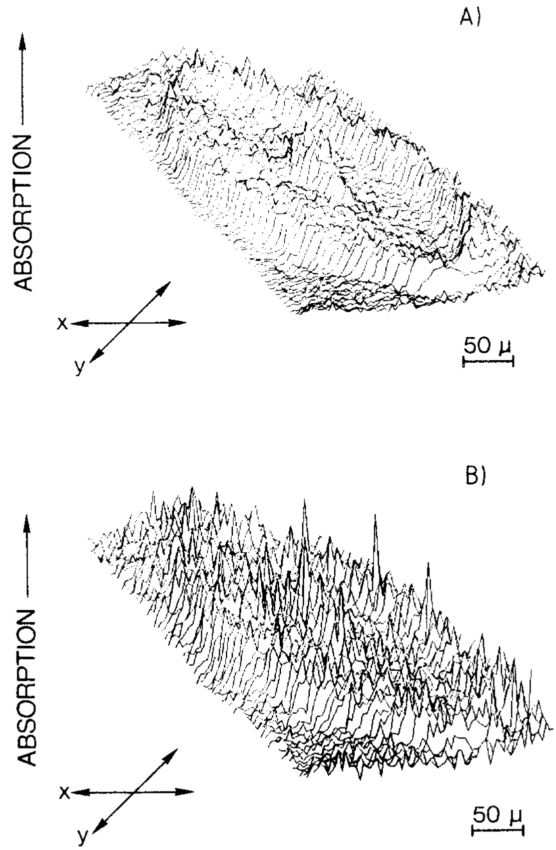

Fig. 5. Scanning light microscope profile of brightness of basal plain of hair of polar bear, computer-processed to an absorption profile: (A) using a W halogene lamp for illumination of a 3 to 4 cm long section of hair; (B) using a xenon lamp.

broader, which also constitutes a significant advantage for fluorescence light collection (see later). Not only is polar bear hair characterized by the shift of luminescence light towards longer wavelengths but it also emits stronger luminescence at the basal plains when mixed and compared with white hair of other mammals. Fluorescence light collection is therefore a mechanism which has to be considered in the optical properties of hairs of polar bears.

3.3. Model systems

The morphological, optical and scanning light microscopical studies performed with polar bear hair leave little doubt that light from the environment is coupled into the light conducting shaft of the hair by scattering processes. Since light collection by scattering processes is a little explored mechanism, model experiments

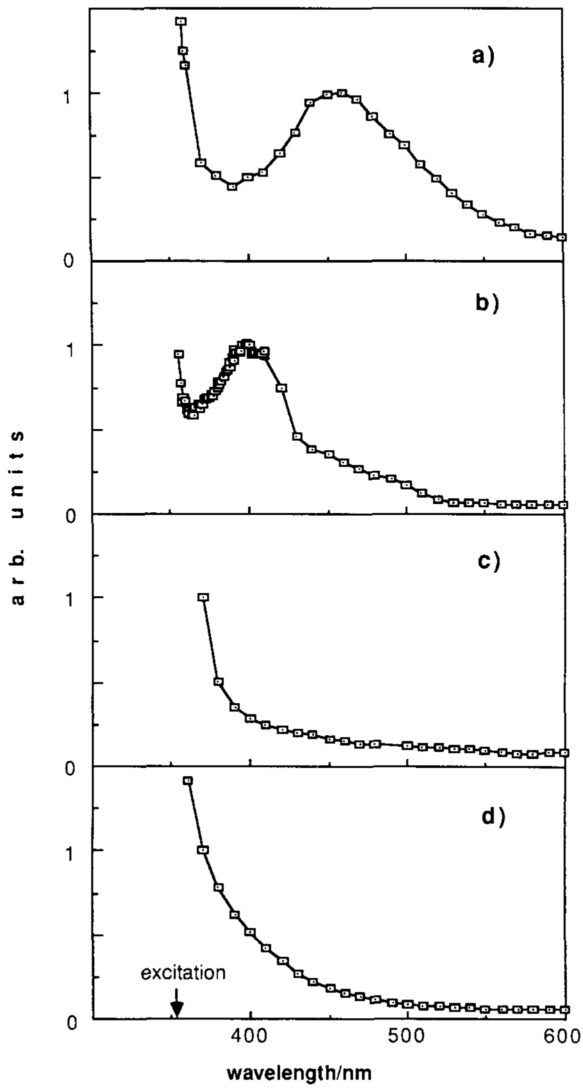

Fig. 6. UV laser-induced ($\lambda = 352$ nm) luminescence in hairs of polar bear (a), as compared to luminescence spectra produced with white hairs of male goat (b) and female goat (d) and of pony (c).

were performed (table 1). In one type of experiment, light collection by glass capillaries was investigated which superficially resemble polar bear hairs. Some light is indeed collected at the base of the capillary, but deposition of small salt crystals within the hollow core clearly doubled the collection efficiency. Scattering processes at the core of the capillary thus aid the coupling of light into the glass tube. Since scattering centers are difficult to control in a glass capillary, a two-dimensional geometry was chosen to study the effect of scattering centers more in detail. The results of light collection along transparent plexyglass plates with different scratch

Table 1
Experiments performed to study the coupling of light into light collecting structures (fig. 1)

Investigated light collecting structure	Experim. geometry	Coupling mechanism introduced	Introduced improvement of light collection
Glass capillary (4.5 mm)	Fig. 1a	Scattering on KCl crystals	2 times
Plexiglass plate (6 mm)	Fig. 1b	Scattering on scratches ($80/cm^2$)	230 times
Plexiglass plate (6 mm)	Fig. 1b	Scattering on scratches ($220/cm^2$)	150 times
Plexiglass plate (6 mm)	Fig. 1b	Scattering on scratches ($400/cm^2$)	80 times
Plexiglass plate (6 mm)	Fig. 1b	Scattering on scratches ($800/cm^2$)	33 times
Plexiglass plate (3 mm)	Fig. 1b	Luminescence red colour	300 times
Plexiglass plate (3 mm)	Fig. 1b	Luminescence yellow colour	200 times
Plexiglass plate (6 mm)	Fig. 1b	Scattering on white pigment	850 times

The numbers given do not indicate concentrations obtained, but improvements in light collection obtained due to scattering and luminescence processes.

densities on the bottom and illuminated with diffuse light are shown in table 1. It can be seen that light is efficiently deflected towards the rim of the plexiglass plate by the presence of scattering scratches. The maximum light deflection is achieved by scattering at a white paint applied to the plexiglass bottom. Luminescent light collecting plates (yellow and red) were studied for comparison and were found to be less efficient, which is partially due to the the narrower range of spectral activity. Their collection efficiency can be improved by introducing scattering scratches into their surface. The described experiments have shown that, with the simple geometry used (fig. 1), the coupling of light into light conducting structures by scattering processes is effective within the same order of magnitude as by fluorescence processes. Both mechanisms have, therefore, to be taken into consideration when discussing the light harvesting properties of the pelt of the polar bear.

4. Discussion

4.1. Light trapping in hair and solar heat pump

As already outlined in a short preceeding communication [1] the solar properties of polar bear hair can only be understood by considering both, its scattering and its luminescent behaviour. Provided the mechanism of light trapping in the polar bear hair would only involve scattering processes at the inner core, a principle which has technically been considered in very few applications such as solar cells supplied with a light scattering back contact [9–11], the thermodynamic limit for light collection (refractive index of air = 1) would be determined by [7,8]:

$$K_s = \beta n^2, \tag{1}$$

where β is a coefficient determining geometrical factors of light collection with $\beta = 4$ for three-dimensional (volume) light collection and $\beta = 2$ for two-dimensional light collection. The factor n^2 in formula (1) determines light concentration. This implies that with respect to the environmental solar radiation the light concentration through scattered light collection within the hair shaft cannot exceed the factor 9.72. In this case the polar bear adaptation takes advantage of the fact that diffuse radiation of unchanged frequency distribution can only be concentrated by passing it into another medium of higher refractive index.

The situation is clearly different and more favourable when the solar radiation is first converted into luminescence light through a Stokes process. This principle has been successfully applied in fluorescence light collectors [12]. This case implies that the number of photons (not, however, the energy flux) is conserved:

$$\nu_a \to \nu_e + \text{phonons (vibrational quanta)}.$$

The energy flow to the surroundings as heat Q_s is in this case related to the incoming radiation Q_a by the frequency shift $(\nu_e - \nu_a)$:

$$Q_s = Q_a(\nu_e - \nu_a)/\nu_a. \tag{2}$$

For terrestrial conditions of diffuse radiation (Wien approximation applicable) the highest obtainable optical concentration ratios are determined through the following relation [8]:

$$K_f = (\nu_e/\nu_a)^3\{\exp[-h(\nu_a - \nu_e)/kT_s] - \exp(-h\nu_a/kT_r)\}^{-1}, \tag{3}$$

where ν_a = frequency of absorbed light, ν_e = frequency of emitted light, T_r = temperature of absorbed radiation and T_s = temperature of emitted radiation.

Provided that the frequency shift $(\nu_a - \nu_e)$ is sufficiently large (order of magnitude 10^{14} s^{-1}), as in the case of polar bear hair, thermodynamic concentration ratios of several orders of magnitude can be expected. These concentration ratios drastically collapse with decreasing frequency shift.

It has, however, to be emphasized that eq. (3) in some respect resembles the open circuit voltage of a solar cell. It represents a thermodynamic quantity useful for the characterization of solar energy conversion. However, it does not describe the cell under working conditions. In other words, the concentration ratios calculated refer to solar radiation in equilibrium with the concentrator and in absence of any net radiation flux passing the concentrator system. A net radiation flux through the light collector involves irreversibilities such as molecular excitation and requires consideration of additional internal entropy production rates. For a net power flow equal to η_a times the total radiation flux arriving (η_a is equivalent to the efficiency of the absorption process) a correction for the maximum concentration ratio K_f (eq. (3)) of the form

$$K_f^a = (1 - \eta_a) K_f \tag{4}$$

has to be taken into consideration [8]. According to tables produced by Ries [8] for this concentrator mechanism, absorbed near-ultraviolet light of 0.38 μm, with an occurring frequency shift of $(\nu_a - \nu_e)$ of 10^{14} s^{-1} (corresponding to luminescence light of 0.43 μm) and an absorption efficiency of 0.9, on the basis of a black-body radiation of $T_s = 5762$ K at 200 W/m^2, could theoretically be concentrated by the ratio of 5.9×10^5. With a frequency shift $\nu_a - \nu_e$ exceeding 2×10^{14} s^{-1} (corresponding to luminescence light of 0.50 μm) the maximal concentration ratio rapidly approaches infinity. It is realized that a relatively small frequency shift results in quite high concentration ratios which explains the evolutionary pressure with respect to frequency shift of luminescence in poalr bear hair towards longer wavelengths as compared to the luminescence of white hairs of other mammals (fig. 6).

The temperature of solar and ambient radiation permits the treatment of radiation fluxes in a way analogous to the transport of heat in a temperature gradient. The temperature of solar radiation T depends strongly on the frequency ν but only weakly on the irradiance L_ν.

$$T(\nu, L_\nu) = (h\nu/k)\left[\log(2h\nu/3)\ c^2 L_\nu + 1\right]^{-1}. \tag{5}$$

Solar energy converting systems that use high radiance in a small aperture of direct solar radiation are therefore more unfavourable than high aperture selective systems in which a frequency shift compensates for an increase of radiance. A solar collector involving frequency shift must involve a minimum frequency shift of 5×10^{13} s^{-1} to 10^{14} s^{-1} and its emission band should not be too narrow as compared with the absorption band since this diminishes the area concentration ratios. Both conditions have been met by polar bear hairs and constitute a remarkable evolutionary adaptation as compared with the optical properties of white hair of other mammals.

The following mechanism of light collection in hairs of polar bears can therefore be taken into consideration (compare fig. 7): most of the light incident on the polar bear is coupled into the hair shaft by scattering processes at the hair core. Light collection via scattering processes occurs with only limited efficiency (the light collection factor in hairs of polar bear cannot exceed $K_s = 9.72$), but has the advantage of producing the white appearance of this mammal. If nature would have chosen the much more efficient luminescent light collection as the primary process for light capturing in the hairs of the polar bear, the animal would also have the optical appearance of a luminescence collector, that is it would emit a luminescence colour not compatible with the arctic environment. By converting scattered light within the hair shaft subsequently into luminescence light nature has nevertheless taken advantage of the favourable optical collection efficiency for luminescence light. Due to the cylindrical shape of the hairs, light scattered along the core can be collected by total reflection without a high probability for rescattering (which would be expected for a planar geometry). The same geometry would also favour lumines-

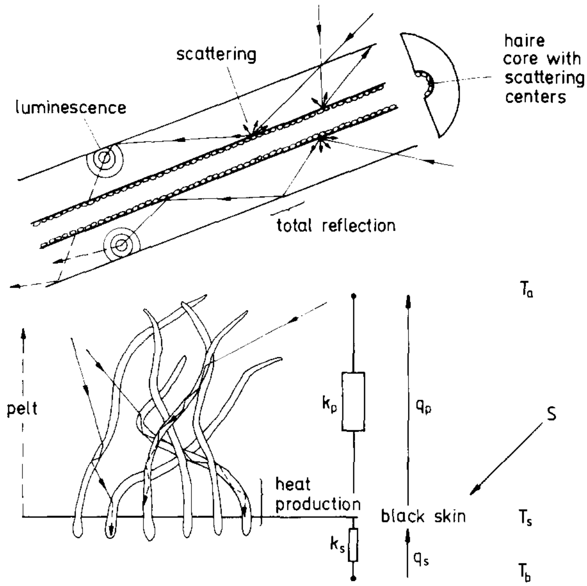

Fig. 7. Scheme explaining scattered light – luminescencent light collection in hairs of polar bear and function of pelt as transparent insulation (quantities inserted are described in the text).

cence light collection which cannot tolerate a high degree of scattering. Because of the strongly asymmetric and scattering properties of polar bear hair and their gradual alteration after cutting them from life animals, reliable quantitative data on luminescence efficiency could not be obtained. When mixed with white hairs of other mammals (e.g. pig) and illuminated with UV light they are clearly more luminescent at their base. Compared with well luminescent organic compounds luminescence appears to be relatively weak. While the efficiency of polar bear hairs as luminescence light collectors may still be moderate (in terms of evolution), the photon energy lost during conversion of scattered light into luminescence light is only lost for heat generation. It will therefore contribute to a favourable heat balance of the animal.

In order to facilitate the described light trapping mechanism there had to be an evolutionary adaptation both in the direction of a luminescence gap and of a broader luminescence band. With these important modifications the polar bear hairs have developed into heat pumps. They permit the funnelling of radiation to the lower regions or the base of the hairs where it is converted into heat which is trapped by the pelt which strongly limits convection losses. The scattering processes give, as already mentioned, the polar bear its characteristic whitish optical properties, but the fact that short wavelength blue and near-ultraviolet light is efficiently converted into trapped luminescent light adds a slightly yellowish appearance. Most important, it explains why polar bears, in spite of their white pelts, appear to be black when photographed with ultraviolet light. We have mentioned that there is a seasonal change in the colour of the pelt. It becomes more yellowish towards the end of summer with its high radiation intensity.

It has to be emphasized that, in our picture, light concentration will mainly occur on a microscopic level within individual hairs; macroscopically the long hairs of the polar bear are making his outer light collecting surface larger than the surface area of his skin.

4.2. Polar bear pelt as a transparent insulation system

The heat pump function of polar bear hair can macroscopically only adequately be described when considered as a part of the animal's pelt. Since the pelt is translucent for light and has insulating properties (it includes air spaces) it acts like a transparent insulation for passive solar energy utilization. Various types of such systems have been discussed in the literature [14–16]. A simplified theoretical concept developed for transparent insulating systems on buildings [16] can easily be applied to the pelt of the polar bear.

As indicated in fig. 7, k_p and k_s describe the reciprocal thermal resistances of the pelt and the peripheral tissues (skin and blubber), respectively, q_p and and q_s the corresponding heat fluxes (arrows mark the positive direction). T_a and T_b indicate the outside ambient and body temperature, respectively. S is the (averaged) radiative power absorbed by the black outer skin (and transformed into heat) and T_s the temperature it reaches.

After writing down the balance of heat flow $q_p = q_s + S$ and eliminating T_s from $q_s = k_s(T_b - T_s)$ and $q_p = k_p(T_s - T_a)$ we obtain

$$T_s = (k_p T_a + k_s T_b + S)/(k_s - k_p), \tag{6}$$

$$q_s = [k_s/(k_p + k_s)](k_p T_b - k_p T_a - S). \tag{7}$$

The heat flux is directed into the body when the radiative term S becomes greater than $k_p(T_b - T_a)$. When the heat flux in absence of radiation is q_p^*, the transparency of the pelt τ and the absorption in the skin α, the efficiency for solar energy utilization is

$$\eta = \tau\alpha(q_p^* - q_s)/S = \tau\alpha/(1 + k_p/k_s). \tag{8}$$

It can be concluded that an increase of the pelt's light transparency (τ) by combined scattered light and luminescence collection in its hairs as well as optimization of light absorption in the skin (which became black) have improved solar energy collection. Also a low heat conduction in the pelt (under dry conditions) and a comparatively high heat conduction through the skin and peripheral tissues would have improved light energy collection. The peculiar light collection system of the polar bear can be considered to be a compromise between his need to maintain a white pelt and the advantage of a translucent insulation for the harvest of light energy. Comparatively little visible light of all wavelengths is scattered to produce a white–yellowish colour while the polar bear's transparent insulation works mostly in the visible and near-UV. Since no IR photographs can be made of polar bears it must be concluded that re-emitted infrared radiation is trapped within the pelt. This will, of course, add to the performance of the animals translucent insulation.

4.3. Physiological advantages

Having discussed an evolutionary adaptation in the hair of the polar bear and his translucent pelt, we may address the complicated question of the use of this heat pump for the polar bear. Such an advantage is not entirely obvious as the following arguments will show: polar animals such as the polar bear must maintain, sometimes for weeks, temperature differences of up to 100 ° C between the environment and the interior of the body. Mammals accomplish this by two main adjustements, by lowering heat losses through increasing the insulation and by increasing the heat production though raising the metabolism. In addition advantages are drawn from skilled use of environmental opportunities which provide heating and protection from cold, as well as from postural thermoregulation.

In addition, researchers of the heat balance of polar bears such as Øritsland et al. [6] and Scholander et al. [5] have observed that polar bear furs are surprisingly course-haired and relatively poor insulators related to thickness. In fact polar bears suffer a considerable cooling of peripheral tissues during cold ambient conditions. Øritsland [6a] observed that subcutaneous temperatures of polar bears varied from 25 to 36 ° C depending on wind chill and that the subcutaneous-to-skin temperature difference increased to 10–14 ° C when the polar bear was immersed in water of 11–12 ° C. A further cooling finally started to depress the blubber temperature. Heat loss through polar bear skin increases considerably when immersed in ice water [5]. It has been argued that in order to be able to hunt the polar bear needs efficient heat loss mechanisms with high energy turnover. A pair of 2 mm thick sheets of striated muscles (0.16–0.48 m^2 in size) only 0.5–3 mm under the skin and richly supplied with blood vessels was discovered by Øritsland and was interpreted as being a heat dissipation device [6a].

The polar bear is a large animal with a relatively small surface area and should under normal feeding opportunities not be faced with serious problems of heat conservation. The experimentally measured local heat loss per surface area of polar bears has been provided by Øritsland and Lavigne [6b] and can be expressed by the formula (V_w walking speed in m/s.):

$$W_{hl} = 62.8 + 4V_w \quad [\mathrm{W/m^2}]. \tag{9}$$

A considerable effect of wind chill is to be expected. A comparable moderate wind chill of 780 W/m^2 (air temperature -2 ° C, wind velocity 1 m/s) depresses skin temperatures of polar bears to 27 ° C. Subcutaneous temperatures in calm air were about 2 ° C over the corresponding skin surface temperatures. Air movement could increase the surface-to-subcutaneous temperature difference up to 18 ° C [6a].

Let us now consider the effect of solar radiation on the energy balance of the polar bear. In the high arctic region up to 100% of the solar radiation may be present in the form of diffuse light [13], the spectral distribution of which is shifted to the blue with respect to the incident solar light (scattering proportional to λ^{-4}, Rayleigh scattering). Let us assume that only 10% to 20% of the total solar intensity (1350 W/m^2) may be available on the ground on a day with covered sky and that only approximately half of this scattered light is efficiently absorbed by the pelt of the polar bear. Under such conditions 67.5 to 135 W/m^2 of thermal energy will be transferred from outside to the skin of the polar bear, just about sufficient to compensate the heat loss due to the freezing environment (62.8 W/m^2 for a polar bear standing in quiet air and a multiple of this under conditions of severe wind chill). Such an energetic situation is reasonable well in agreement with experimental observations by Øritsland on a captured polar bear in Spitsbergen [6a]. While his body temperature measured 37° C and the skin above the latissimus sheet averaged a temperature of 33° C, the temperature in the flank lowered to 27° C (air temperature: −2 to 0° C). When, however, the sun came out behind clouds, the skin temperature in the flank of the bear increased by 10° C and thus reached the approximate body temperature while the temperature above the lattisimus sheets was practically unaffected. The richly supplied blood vessels close to the skin in this area had apparently no problems in regulating the skin temperature.

This simple consideration, which will have to be substantiated by further experimental research, suggests that the polar bear's solar heat pump cannot easily provide a significant contribution to the heat balance of this large arctic mammal (with its relatively small surface area). Because of the transparency of the polar bear's fur, however, the presence or absence of scattered light will lead to a significant variation of the polar bears skin temperature outside the region of the latissimus sheets. Since evolution of scattering centers in the core of hairs of polar bear and the development of a luminescence gap facilitating luminescence collection indicate an evolutionary advantage, for polar bears, to dispose of such an elaborate heat pump [1], it may be concluded that not the supplementary heat supply to the bear's metabolism but the induced temperature variations in the bears skin were the evolutionary driving force.

When eq. (8) is combined with eq. (6) the skin temperature T_s can be calculated:

$$T_s = T_a + (\eta/\tau\alpha)(T_b - T_a + S/k_s). \qquad (10)$$

A bear, standing in a dazzling white haze of an arctic plane, with eyes washed out and with an invisible positioned sun somewhere will experience a temperature pattern on his skin, generated by scattered light (fig. 8). According to eq. (10) the temperature T_s of the polar bear's black skin will not only depend on the air temperature T_a, the body temperature T_b and the quality of its transparent insulation pelt (η, τ, α), but also on the locally absorbed radiative power S and the reciprocal resistance of insulation k_s of the underlying tissues. Most of the light will arrive from the sky area around the position of the sun (Mie scattering) but also from directions allowing a rectangular deflection of sunlight towards the bear (Rayleigh scattering). The temperature pattern produced on the skin of a bear's body will accordingly change with its orientation towards the sun and largely differ between radiation exposed and non-exposed body regions. Temperature changes and fluctuations through wind chill could be compensated for by the latissimus sheet which is temperature-controlled by a rapid exchange of blood and may act as a reference. In other words, the polar bear's heat pump has to be understood as part of a sensory system for improved orientation in a hostile environment [1]. A polar bear would, after a hunting episode in a hazy environment, not only refind its

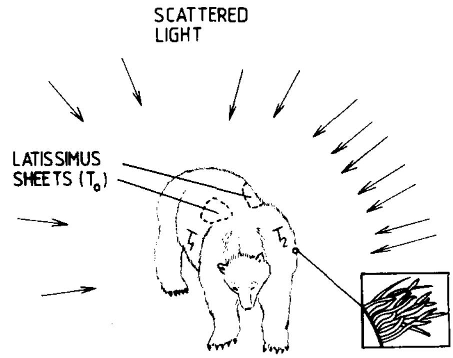

Fig. 8. Drawing explaining physiological situation of polar bear (latissimus sheets indicated) in diffuse light of the arctic with low positioned sun. The asymmetric temperature pattern developed on the skin is indicated.

orientation with respect to a hidden sun but also in principle be able to distinguish the presence of large obstacles and maybe their nature (ice or rock). Most interesting is also the possibility, that the polar bear uses its light collecting pelt for tracking down ice-free see areas, which is crucial for survival as a predacious animal. The polar bear's amazing skill in locating and straightforwardly approaching ice-free sea surfaces over larger distances has frequently been documented [17]. On clear days it may be possible to see light reflections from open water in the sky. In situations with moderate visibility less light may come from the direction of the open sea since a water surface will not scatter light to the extent observed from an ice- or snow-covered surface.

A sensory system of the type described has not been taken into consideration before and will have to be supported by field studies. The described sensory system may still be in a relatively early stage of evolution due to the comparatively young age of the polar bear species, which can still interbreed with the brown bear.

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