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The structure and mechanical design of rhinoceros dermal armour

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SUMMARY

The collagenous dermis of the white rhinoceros forms a thick, protective armour that is highly specialized in its structure and material properties compared with other mammalian skin. Rhinoceros skin is three times thicker than predicted allometrically, and it contains a dense and highly ordered three-dimensional array of relatively straight and highly crosslinked collagen fibres. The skin of the back and flanks exhibits a steep stress–strain curve with very little 'toe' region, a high elastic modulus (240 MPa), a high tensile strength (30 MPa), a low breaking strain (0.24) and high breaking energy (3 MJm^{-3}) and work of fracture (78 kJm^{-2}). By comparison, the belly skin is somewhat less stiff, weaker, and more extensible. In compression, rhinoceros skin withstands average stresses and strains of 170 MPa and 0.7, respectively, before yielding. As a biological material, rhinoceros dorsolateral skin has properties that are intermediate between those of 'normal' mammalian skin and tendons. This study shows that the dermal armour of the rhinoceros is very well adapted to resist blows from the horns of conspecifics, as might occur during aggressive behaviour, due to specialized material properties as well as its great thickness.

1. INTRODUCTION

Regional variations in skin thickness and mechanical properties occur over the body of all mammals, but many large herbivores have specific zones of the integument that are markedly thickened (Harkness 1968). Jarman (1989) advanced the hypothesis that such areas act as shields against blows received during intraspecific combat, and that the position of the shield areas is related to the fighting style and weaponry of the species in question. Supporting evidence for this idea comes from earlier studies of mountain sheep and goats (Geist 1967, 1971), impala (Jarman 1972), pronghorn antelope (Kitchen & Bromley 1974), roe deer (Sokolov & Danilkin 1979) and the boar (McCarthy & Howlett 1988). As part of his hypothesis, Jarman (1989) proposed that the skin's increased thickness alone, rather than any structural modifications within, was the significant factor in providing the mechanical shielding function. However, he did not examine either the histological details nor the mechanical properties of the skin of the species in which he was interested, so the latter postulation remains moot.

The dermal shields of large herbivores are collagen-rich tissues that are amenable to mechanical testing for comparison with other mammalian skin and collagenous tissues. In order to evaluate the hypothesis that thickness alone is sufficient to explain the shielding function of thickened dermal patches of mammals, we examined both the structural and material properties of the skin of the white rhinoceros (*Ceratotherium simum*), generally regarded as the third-largest species of living terrestrial mammal (Owen-Smith 1988). It is well known that these animals use their horn in intraspecific combat and have conspicuously thickened skin (Cave & Allbrook 1959). Although Jarman (1989) did not make any direct observations on rhinoceroses, he did refer to Cave & Allbrook's (1959) work as an example of skin thickening in the Perissodactyla. The specific predictions arising from Jarman's hypothesis on dermal shields that we tested are: (i) the skin of the white rhinoceros should be structurally similar to that of other mammals; and (ii) the mechanical properties of the thickened skin should scale in proportion to thickness when compared with skin of other mammals, i.e. their material properties should prove to be identical.

2. MATERIALS AND METHODS

Skin samples were taken from the back and flanks (referred to as dorsolateral skin), and the belly of Duncan, an adult male white rhinoceros of mass 1600 kg, that died at the Calgary Zoo. This animal was at least 28 years old and somewhat lighter than the average field mass for adult bulls (Owen-Smith 1988). We were unable to extend the sample size beyond this one individual, due to the rarity of the species.

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Dimensional measurements of whole skin samples were made and tested against allometric predictions of skin thickness. Histological preparations were made to investigate details of collagen fibre morphology and orientation. Tissue samples were fixed in 10% (by volume) formalin and sectioned on a freezing microtome for observation and photography on a Wild M5 stereoscope with polarizing optics. Other samples were weighed and freeze-dried, hydrolysed in 6N HCl for 24 h, and subjected to a colorimetric hydroxyproline assay (Berg 1982) to determine the collagen content. Skin collagen was digested by cyanogen bromide, and the resulting peptides were separated by sodium dodecyl-sulphate polyacrylamide gel electrophoresis according to published techniques (Light 1982) as a means of qualitatively assessing the extent of intermolecular collagen crosslinking.

Mechanical tests of dorsolateral and belly skin pieces were done on a Monsanto 10 kN capacity Tensometer as follows:

1. Tensile tests were conducted on strips of skin cut in a standard dumbell shape (figure 1*a*) in order to provide large gripping surfaces and ensure that failure occurred in the central section. This sample configuration is commonly used in engineering tests on sheet materials and has been used previously in studies of skin mechanics (Ridge & Wright 1966; Veronda & Westman 1970). Test pieces were clamped in vice-type grips and stretched at rates of 5 mm min^{-1} or 10 mm min^{-1} in the tensometer. Samples were taken from mid to deep regions of the dermis, in transverse, longitudinal and diagonal directions, with respect to the body long axis. Before each test, vernier calipers were used to measure the initial width and thickness, as well as the distance between two parallel markers that were glued directly onto the narrow central portion of the sample (figure 1*a*). Tensile tests consisted of cyclic extensions to strains of about 0.10, until 5–10 stable force–extension cycles were recorded, followed by stretching the sample to the point of rupture. The force was recorded by an electronic load cell mounted in the travelling crosshead of the tensometer, while extension between the markers was determined by a video dimension analyser (VDA). Both signals were recorded simultaneously on an *x–y* plotter and digitally on a Digital PDP-11/23 minicomputer or an 80386-based micro-computer. Data from the destructive tests were normalized to stress (= force/initial cross-sectional area), measured in megapascals (1 MPa = 1 MNm^{-2}) and strain (= change in length/the initial length), from which the following material properties were derived. The tensile strength and the breaking strain are, respectively, the maximum stress and strain achieved before tensile rupture. The modulus of elasticity, a measure of the material stiffness, was calculated (in megapascals) as the slope of the linear portion of the stress–strain curve. The total area under the stress–strain curve is W, the energy required to break a unit volume of material, and is a measure of the material toughness (Gordon 1978). W was calculated by integrating the stress–strain curves digitally, and expressed in megajoules per cubic metre. Subsequently, some fractured specimens were routinely fixed and prepared for viewing with a scanning electron microscope in order to assess the mode of fracture.

2. The work of fracture (G) was determined from controlled tear-tests of dorsal skin strips, taken from superficial and deep regions. A short cut was made along the longitudinal axis of non-tapered skin specimens (figure 1*b*) to initiate the fracture. The specimen was torn by pulling the ends of the two 'legs' formed by the cut with the tensometer so that the crack was propagated in a controlled fashion at a relatively constant force. The work done (in kilojoules per square metre) to create the new fracture surfaces was calculated using a formula described by Purslow (1990) as $G = 2F/t$, where F is the mean plateau force and t is the sample thickness.

3. Compressive tests were conducted on cylinders of skin cut with a cork borer from superficial and deep regions (figure 1*c*). These tests enabled determination of compressive strength, stiffness and mode of compressive failure. Stress in megapascals was recorded by way of a load cell, and strain was calculated by measurements made from video images.

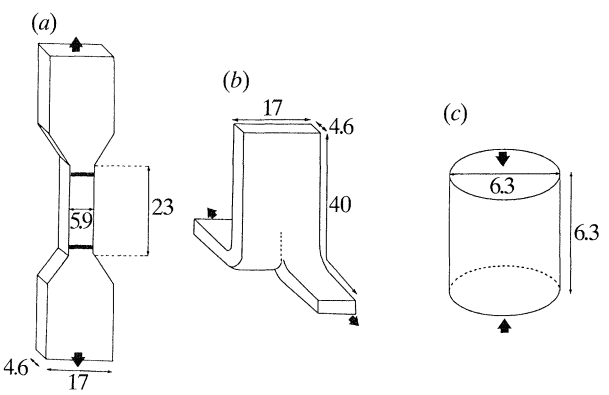

Figure 1. Diagrams to illustrate the form of pieces of rhinoceros skin used for mechanical tests. (*a*) Tensile samples were cut in a typical 'dumbell' shape, to provide large surfaces for gripping and to ensure that fracture would occur in the narrow central region. Two parallel strips of black tape (1 mm wide) were glued onto the surface for strain determination by the VDA. (*b*) The 'trouser-tear' specimen. (*c*) Cylindrical pieces cut with a cork borer used in compression tests.

For comparative purposes, we also conducted mechanical tests on the flank skin of a 220 kg persian wild ass (*Equus hemionus onager*) that died at the San Diego Zoo. This is a large herbivore with no specialized weaponry, such as horns, and with skin that does not appear to be thickened beyond what is predicted by allometry (see Results section).

3. RESULTS

(*a*) *Gross morphology of the skin*

From allometric relations (Calder 1984), the total skin mass (M_s) of a mammal can be predicted from body mass (M) as $M_s = 0.106\ M^{0.94}$ (mass in kilograms), and the surface area is given as $A = 0.111\ M^{0.65}\ m^2$.

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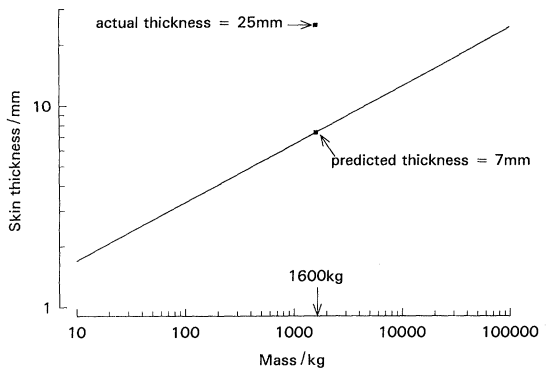

Figure 2. Allometric prediction of mammalian skin thickness as a function of body mass, $t = 0.87\ M^{0.29}$, based upon data taken from Calder (1984). For an adult white rhinoceros weighing 1600 kg, the predicted skin thickness is 7 mm, yet the actual measured thickness was 25 mm on the back and flanks, and 15 mm on the belly. Clearly, compared with other mammals, the rhinoceros has disproportionately thick skin for its body mass.

Assuming a density of 1100 kg m^{-3}, the average skin thickness (t) can then be calculated as the volume divided by the area, i.e. $t = 0.868\ M^{0.29}$ mm. For a 1600 kg adult male white rhinoceros, the predicted skin thickness is 7 mm (figure 2), but the actual thickness of skin along the back and flanks averaged 25 mm, whereas that for the belly skin was about 15 mm. Thus, the skin is much thicker than would be predicted from simple allometry. Further extrapolation of the allometric relationship (figure 2) predicts that a mammal having skin as thick as the white rhinoceros would weigh 50 000–100 000 kg! By comparison, the thickness of the flank skin of a 220 kg wild ass averaged 3.6 mm, close to the 4.1 mm thickness predicted by the allometric relation. Clearly scaling alone does not account for the extreme thickness of the skin of the white rhinoceros. A functional explanation lies in the hypothesis put forward by Jarman (1989) that increased skin thickness provides a protective dermal shield.

(*b*) *Skin histology*

The dermis of the white rhinoceros is composed of a dense feltwork of thick collagen fibres whose orientation and dimensions vary with position and depth (figures 3 and 4). In the dorsum and flanks the collagen fibre diameter averages 70 μm and 100 μm in superficial and deep regions, respectively (table 1). This fibrous network seems highly organized, and fibres can be seen oriented diagonally through the skin thickness in each of the three orthogonal planes of sectioning. These features contrast with those typically seen in other, so called 'normal' mammalian skin (Harkness 1968) and suggest that specialized mechanical properties may occur. Belly skin is thinner and has superficial fibres averaging 60 μm in diameter and deep fibres of 200 μm diameter (table 1). These are markedly crimped and more loosely arranged than those of the back and flanks (figure 4 and table 1).

(*c*) *Collagen characteristics*

The water content of dorsolateral and belly skin was 60.9% (± 1.2%). Collagen comprised 85% of the dry fraction, or 33.2% of the tissue wet mass.

Skin collagen was digested into peptide fragments by cyanogen bromide to make a qualitative assessment of covalent crosslink density, an important factor contributing to the tensile strength of the fibrils. Skin collagen is primarily Type I, and the peptide designated α1-CB6 is the major one involved in the extracellular crosslinking between collagen molecules. Initially, crosslinks form between a site on this peptide and a much smaller one in an adjacent collagen molecule. With maturation, the α1-CB6 peptide is incorporated into large molecular mass polymers of CB6 plus smaller peptides, as intermolecular crosslinking proceeds to adjacent molecules (Light & Bailey 1979). The rhinoceros skin collagen shows an abundance of high molecular mass peptides and virtually none of the monomeric α1-CB6 (figure 5). In contrast, the skin collagen from an adult rabbit has a large proportion of α1-CB6 monomer, but virtually none of the large polymeric peptides present in the rhinoceros collagen. These results demonstrate that the rhinoceros skin collagen is extensively stabilized by mature crosslinkages.

(*d*) *Mechanical tests*

Tensile tests revealed that the skin of the white rhinoceros has relatively high stiffness and low extensibility. The dorsolateral and belly skin display substantially different mechanical behaviour, although the stress–strain curves for each do not vary significantly among the three orthogonal directions (figures 6 and 7), nor between the mid and deep regions tested. These curves show the nonlinearity that is typical of soft connective tissues. The 'toe' region of the dorsolateral skin curve is extremely short with the linear portion occurring after strains of about 0.04, and failure beginning after strains of about 0.20. Tensile fracture is primarily a result of breakage of individual collagen fibres, rather than failure by fibre pull-out (figure 8). The elastic modulus averaged 237 MPa, whereas the mean breaking stress and strain were, respectively, 30.5 MPa and 0.24 (table 2). These properties are quite different from those of the skin of other mammals such as the rabbit, cat (Veronda & Westman 1970; see figure 11), and the wild ass used in this study (see table 2 and figure 7), all of which have higher extensibility and lower strength and elastic modulus. The stress–strain curve for the rhinoceros belly skin also becomes linear after strains of about 0.04, but exhibits about one half the elastic modulus and breaking stress, and 1.5 times the breaking strain of the dorsolateral skin (table 2). It should be noted that the strain is calculated from the initial, unstressed sample length but the skin, particularly on the sides of the body, is probably pre-stressed to some extent *in vivo* due to the great mass of the tissue itself. Thus, it is likely that the extensibility of the skin on the animal is somewhat less than for the test samples.

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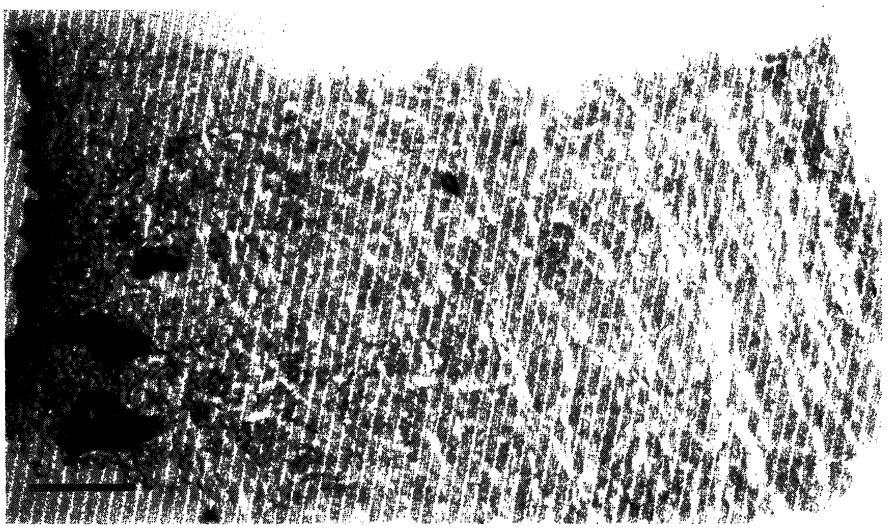

Figure 3. A polarized light micrograph showing an entire transverse section of the skin from the belly of the white rhinoceros (epidermal surface on the left). The highly birefringent collagen fibres are prominent throughout, being somewhat thinner and more regularly arrayed in the outermost region of the dermis. Scale bar is 2.0 mm.

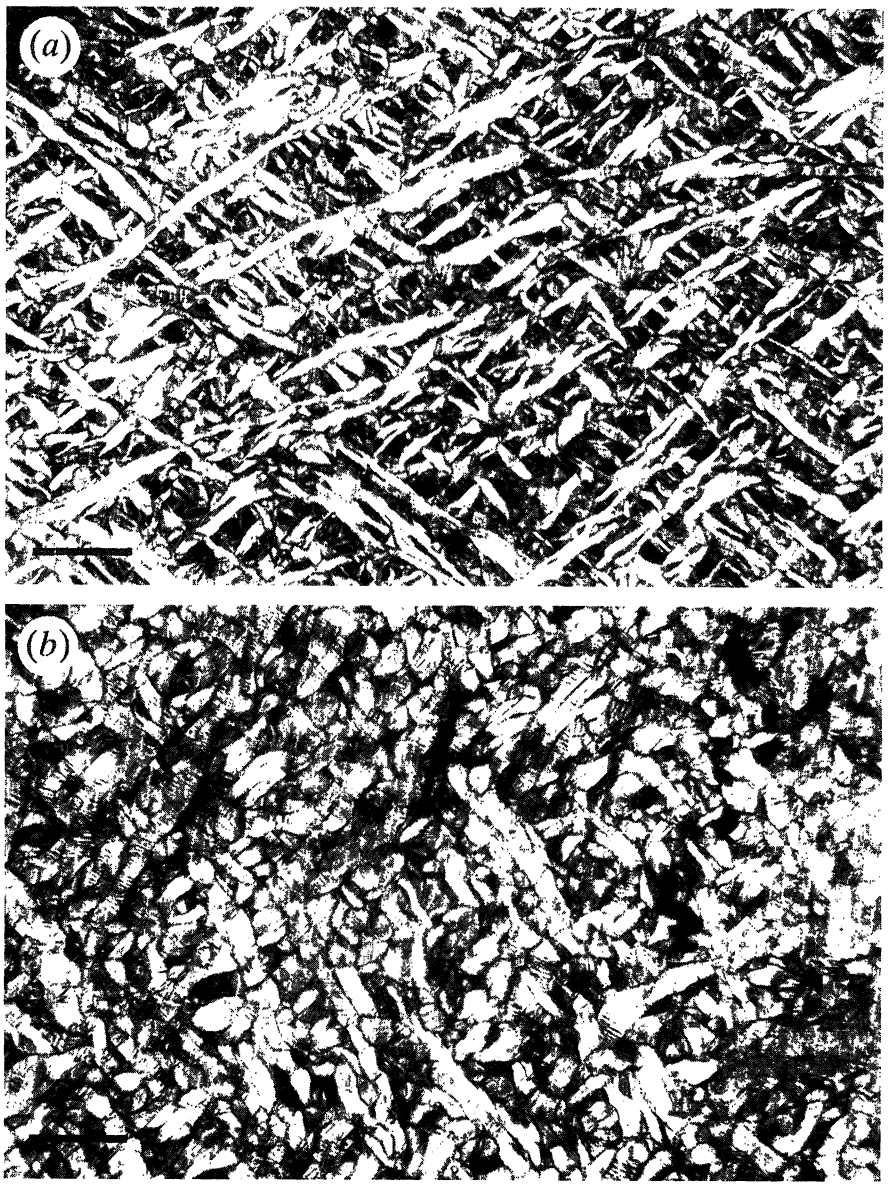

Figure 4. Polarized light micrographs of transverse sections of white rhinoceros skin showing the arrangement of collagen fibres in the deep dermis of (*a*) the flank and (*b*) the belly. Fibres in the former are relatively straight and average 90 μm in diameter, whereas those in the latter are crimped and average 200 μm in diameter. Scale bars are 1.0 mm.

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Table 1. *Collagen fibre morphology in rhinoceros skin*

	dorsolateral ($n=9$)		belly ($n=15$)	
	mean	± s.e.m.	mean	± s.e.m.
fibre diameter/mm				
superficial	0.07	0.01	0.06	0.01
deep	0.10	0.02	0.20	0.02
crimp period/mm	—	—	0.82	0.01

The mean breaking energy for rhinoceros dorsolateral and belly skin were similar and averaged about 3.1 MJm^{-3} (table 2). This is slightly lower than the breaking energy of the flank skin from the wild ass and higher than the breaking energy of cat skin (Veronda & Westman 1970). Controlled tear tests revealed that rhinoceros dorsolateral skin resists tear propagation relatively well, with a work of fracture in the superficial portion that is about twice that of rat skin (Purslow 1983). Figure 9 shows a typical tear test record obtained from back skin of the white rhinoceros. The initial region of the curve represents elastic deformation of the two arms of the test piece. When the force is sufficient to propagate the tear, it proceeds in a relatively steady fashion with no additional force required. The plateau region is not completely smooth but oscillates about a mean value (F) in a 'stick-slip' behaviour typical of fibrous biological materials (Purslow 1983). In this type of controlled fracture, the strain energy input within the plateau region is approximately equal to the work done to form the new surfaces. Values of the work of fracture (G) for the dorsolateral skin of the white rhinoceros averaged 77.6 kJm^{-2} in superficial samples and 43.0 kJm^{-2} in the deep layer (table 2). By comparison, the average work of fracture of the wild ass flank skin was 33 kJm^{-2}, whereas that for rat skin is reported to

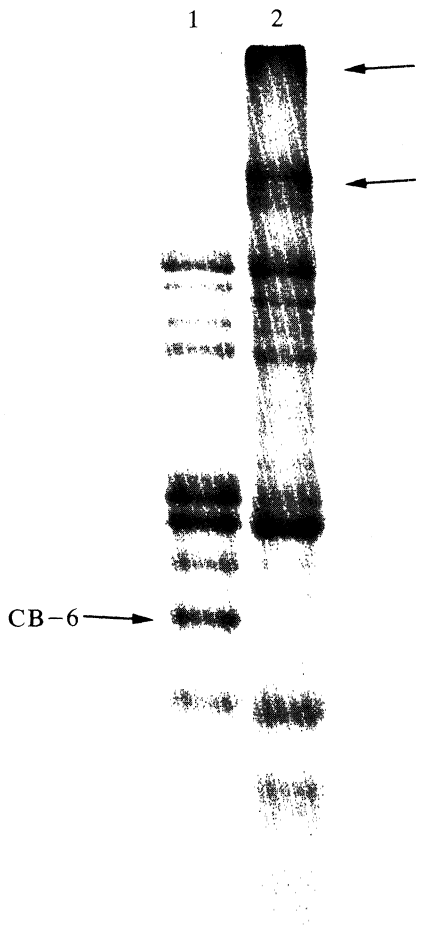

Figure 5. Cyanogen bromide peptides of skin collagen from rabbit (lane 1) and rhinoceros (lane 2), stained with Coomasie Blue R250 after gel electrophoresis. The peptides are separated by decreasing molecular mass from top to bottom on the gel. The 19 kDa peptide labelled as CB-6 is from the C-terminal region of the α1 (type I) molecule and contains a site of intermolecular covalent crosslink formation. With ageing, these crosslinks join together adjacent collagen molecules which, after cyanogen bromide digestion, yield large polymers of CB-6, rather than the monomeric form. Thus, the presence of heterogeneous high molecular mass material near the top of the gel (arrows) and virtually no monomer CB-6 suggest that the rhinoceros collagen is extensively crosslinked (see Light (1985) and Light & Bailey (1979) for details of this technique).

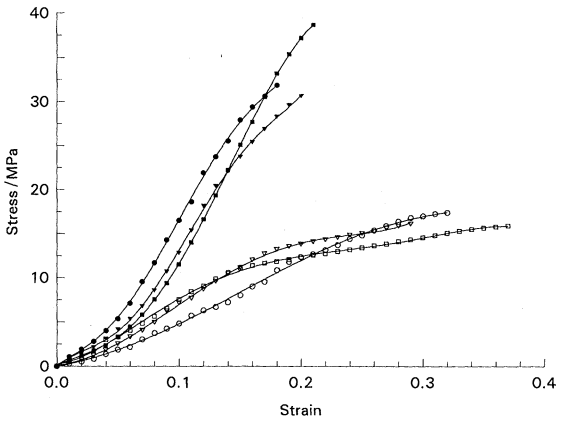

Figure 6. Examples of digitized stress–strain data from tensile tests to failure of longitudinal (triangles), circumferential (circles) and diagonal (squares) strips of rhinoceros dorsolateral (filled symbols) and belly (open symbols) skin. While the dorsolateral skin is substantially stiffer than the belly skin, the effect of test direction is insignificant in each location.

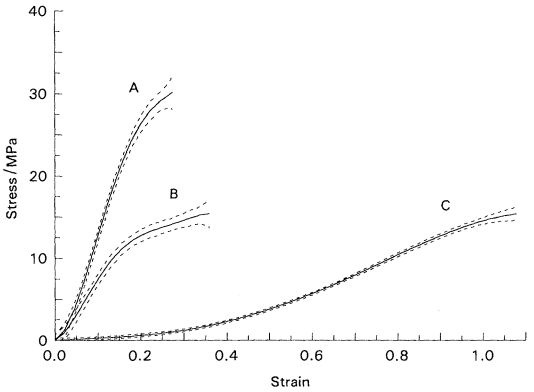

Figure 7. Stress–strain curves and their 95% confidence limits, fitted by polynomial regression, for pooled tests on (A) rhinoceros dorsolateral skin ($n=23$), (B) rhinoceros belly skin ($n=9$), and (C) flank skin from the wild ass ($n=5$).

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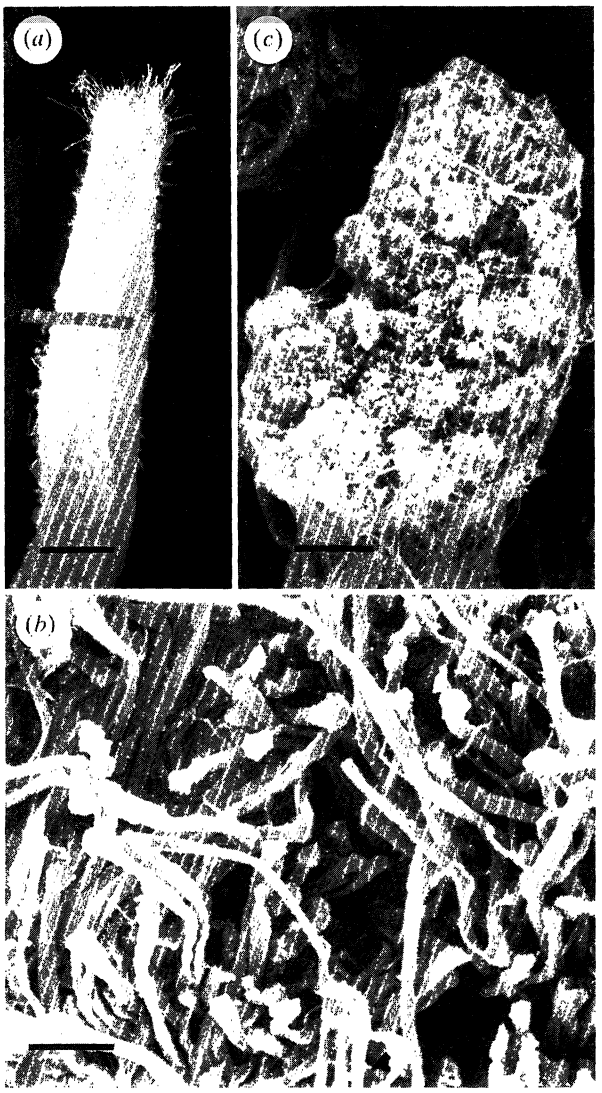

Figure 8. (*a*) A photograph of one portion of a test specimen of dorsal skin that was broken in tension. The broken surface is at the top. Scale bar is 5 mm. (*b*) A scanning electron micrograph of the fracture surface. Scale bar is 500 μm. (*c*) A higher-magnification view of one of the collagen fibre ends in (*b*). The bulbous appearance of the ends of the collagen fibres shows that the specimen broke by fracture of the fibres rather than by disruption of the network by fibre pull-out. Scale bar is 25 μm.

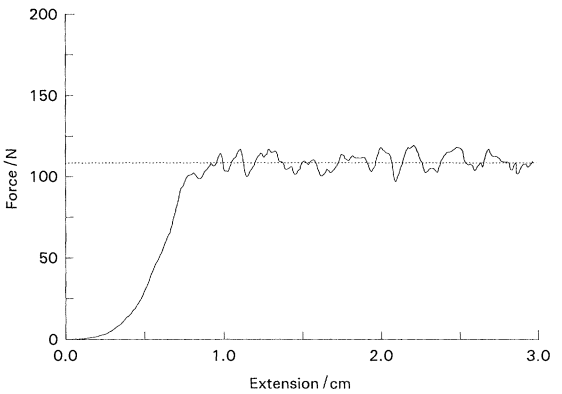

Figure 9. A typical record from a trouser-tear experiment to determine the work of fracture ($G = 77\ \mathrm{kJm^{-2}}$) of a skin sample from the back of the white rhinoceros. Initial deformation of the two arms of the test piece is followed by controlled tearing at a force that oscillates about a mean value F, indicated by the broken line.

range from 15 $\mathrm{kJm^{-2}}$ to 30 $\mathrm{kJm^{-2}}$ (Purslow 1983). Thus, in addition to being exceptionally thick, the skin on the back and flanks of the white rhinoceros has material properties that provide a higher resistance to catastrophic rupture than is typical of other mammalian skin.

In compression, rhinoceros skin fails at very high stresses (figure 10), and is much stiffer than in tension (table 3). No significant difference was found between samples taken from superficial and deep regions. Dorsolateral skin samples failed explosively, as indicated by the sharp peak in the stress–strain curve, at a mean stress and strain of about 170 MPa and 0.7, respectively (table 3). This appeared to be coincident with expulsion of most of the interstitial water, as indicated by comparing the mass of the samples before and after tests. Belly skin fails at similar stress and strain, but not explosively, as can be seen by the more rounded peak in the stress-strain curve (figure 10). For both dorsolateral and belly skin, the compressive stiffness was approximately 700 MPa (table 3). For comparison, the compressive modulus of hyaline cartilage is about 500 MPa, whereas that for bone is at least tenfold higher (Vincent 1982). The great resis-

Table 2. *Mechanical properties of skin: uniaxial tensile tests*

(Data for skin from the white rhinoceros (*C. simum*) and the wild ass (*E. hemionus*) are compared.)

	C. simum				*E. hemionus*	
	dorsolateral ($n=23$)		belly ($n=9$)		flank ($n=5$)	
property	mean	± s.e.m.	mean	± s.e.m.	mean	± s.e.m.
breaking stress/MPa	30.5	1.08	14.5	1.59	13.1	± 1.63
breaking strain	0.24	0.01	0.33	0.02	0.86	± 0.08
breaking energy/$\mathrm{MJm^{-3}}$	2.89	0.16	3.28	0.43	3.7	± 0.58
elastic modulus/MPa	237.3	9.75	107.8	± 13.9	31.1	± 3.4
work of fracture/$\mathrm{KJm^{-2}}$						
superficial ($n=6$)	77.6	4.35	—	—	—	—
deep ($n=9$)	43.0	2.3	—	—	33.0	—

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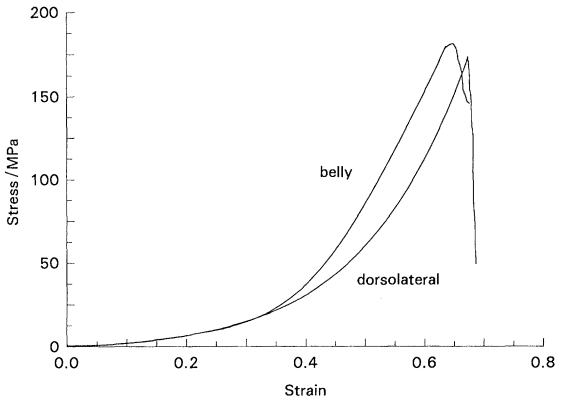

Figure 10. Examples of compressive stress–strain curves for cylindrical samples of skin from dorsolateral and belly skin of the white rhinoceros. The major difference between these is that compressive failure was explosive in the dorsolateral skin but more gradual in the belly skin.

tance to compressive stress of the rhinoceros skin is another indication of the unusual mechanical properties of this dermis.

4. DISCUSSION

The evidence from this study does not support the hypothesis suggested by Jarman (1989) that the armour-like protection provided by the dermis of the rhinoceros arises solely from its great thickness. Instead, we find that this skin has additional structural and mechanical specializations that make it stronger and stiffer and, therefore, much better suited to act as a physical shield compared with the skin of other mammals. These remarkable properties are more pronounced in the areas of the back and flanks of the animal than on the ventral surface. The relatively stiff rhinoceros skin is not merely a thicker version of 'normal' mammalian skin (Harkness 1968), as would be predicted from Jarman's (1989) hypothesis, but a much different material. Like that of the walrus and hippopotamus, rhinoceros dorsolateral skin can be described qualitatively as a 'solid, relatively inextensible slab of collagenous tissue' that is rigid enough to 'be cut into a shape quite easily' (Harkness 1968).

The major component of mammalian dermis is collagen, a stiff, fibrous protein that typically accounts for 70–80% of the tissue dry mass (Neuman & Logan 1950; Harkness 1971). Elastic fibres comprise only about 4% of the dry dermis (Tregear 1966). In general, collagen is present in skin as a feltwork of markedly convoluted fibres that are randomly oriented in many directions, (Shelac 1957; Gibson 1977). These fibres straighten out as the tissue is stretched, and an increasing proportion become aligned toward the direction of stretch as the load is increased. Ultimately, this realignment results in a structure of parallel fibres that is relatively stiff and resistant to further extension (Wright & Ridge 1965; Ridge & Wright 1966; Gibson 1977), giving rise to the typical J-shaped stress–strain curve. The collagen content of rhinoceros dermis is near the upper end of the range cited above. Crosslinking is extensive, suggesting that the fibres are very strong indeed. Major structural differences are most evident, however, in the high degree of order and relative straightness of the collagen fibres, particularly in dorsolateral locations. Consequently, rhinoceros skin is relatively inextensible and the stress–strain curve enters the high stiffness region at much lower strains than does the skin of other mammals. Tendons and ligaments are also collagen-based tissues, but the fibres are essentially parallel in the unstressed state and, consequently, these structures become very stiff at strains of only a few percent (figure 11). Clearly, the material properties of collagenous tissues are highly dependent on the architectural arrangement of the constituent fibres (Viidik 1980). Figure 11 depicts how the tensile mechanical properties of such tissues change with the degree of fibre organization, relative to the direction of the applied force. In mechanical terms, we may regard rhinoceros dermis as a structure that is intermediate between 'normal' mammalian skin and tendon.

Table 3. *Compressive properties of rhinoceros skin*

	dorsolateral ($n=52$)		belly ($n=25$)	
property	mean	± s.e.m.	mean	± s.e.m.
failure stress/MPa	172.7	7.5	169.1	9.4
failure strain	0.68	0.01	0.73	0.02
failure mode	explosive		non-explosive	
compressive stiffness/MPa	700	5.3	667	9.6

The three-dimensional organization of the collagen fibres in the dorsolateral and belly skin, as shown in figures 3 and 4, endow it with tensile properties that are similar in directions orthogonal to the body long axis. The collagen molecules are highly crosslinked, and the fibres are closely packed (figures 3, 4 and 8b) and appear to be well-connected internally because tensile failure requires relatively large stresses that cause fibre rupture rather than 'pull-out'. This structural arrangement also provides a very great resistance to compressive loading, presumably by holding interstitial water relatively tightly within the fibre network, and generating tension in fibres perpendicular to the compressive force. We do not yet know what structural changes coincide with compressive failure of the dermis.

The mechanical protection that the dermal armour provides to the rhinoceros may be most relevant in the context of resisting blows from the horns of conspecifics. The tensile strength, elastic modulus and work of fracture are relatively high, compared with values for other mammalian skin (Tregear 1966; Veronda & Westman 1970; Purslow 1983). These properties, coupled with the extreme thickness of the skin and the tight arrangement of its constituent collagen fibres, enhance the resistance of this tissue to compressive failure and, thus, to penetration or tearing by a horn in combat.

The horns of white rhinoceroses are foil-like weapons, and the shoulders, flanks and rump of the opponent are the main targets of attack with the horn.

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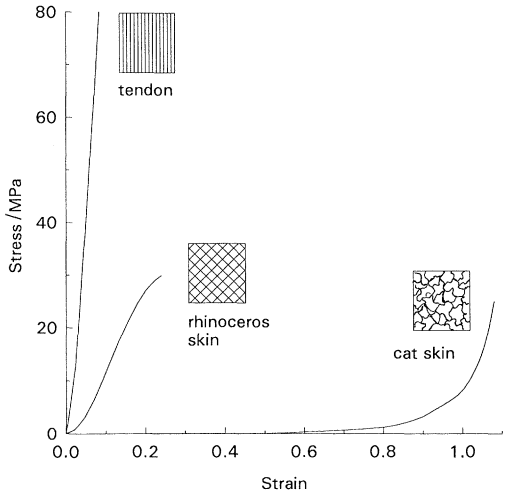

Figure 11. A schematic representation of how the tensile material properties of collagen fibre-reinforced connective tissues are influenced by their fibre orientation. Typical mammalian skin, such as that of the cat, consists of randomly arrayed, convoluted collagen fibres. It is very extensible and does not enter its high modulus phase until stretched by more than 80% of its initial length (data from Veronda & Westman (1970)). Tendon, which consists of bundles of relatively straight, parallel collagen fibres, enters the high modulus phase almost immediately and is very stiff. The dorsolateral skin of the white rhinoceros consists of a highly ordered network of relatively straight collagen fibres that becomes very stiff at strains above about 0.04. Thus, by virtue of its peculiar fibre architecture, rhinoceros skin is highly modified to act as an armour-like shield.

These are also the areas that bear markedly thickened skin. There are few reports describing intraspecific combat between white rhinoceroses; the best accounts are those of Owen-Smith (1973), who conducted a five-year study of the behaviour of this species. Out-and-out combat bouts are apparently rare, but when they do occur they can be very vigorous and involve blows of great force, considering that the combatants may have a mass of thousands of kilograms. Horn clashes occur between all combinations of individuals and have been interpreted as weapon threats (Owen-Smith 1973). Charges, where one individual advances at a rapid trot towards another, are made only by territorial bulls (Owen-Smith 1973). This action leads either to a brief clash of horns or to horn-to-horn confrontation. Sometimes adult bulls attack each other using successive horn-jabbing movements, clearly directed towards the body of the opponent. In some prolonged clashes, the combat is essentially head-to-head, involving a great deal of fencing with the horns and often resulting in gashes being incurred around the eye region. Sometimes violent horn-to-body blows are struck (Owen-Smith 1973), with individuals being oriented in a more sideways-on fashion and the blows being administered by upward and backward raking movements of the head.

In discussing combat between black rhinoceroses, Carter (1965) comments that the horn is positioned to deliver the upper cut, with the tremendous power of the heavily muscled neck behind it. Blows can be delivered in very rapid succession. Carter (1965) also notes that the hide of the white rhinoceros 'is identical in texture to that of the black, and of about the same thickness.' Owen-Smith (1973) described an encounter between two territorial bull white rhinoceroses in which the horn was dug repeatedly into the side of the opponent, resulting in numerous bloody gashes. These detailed accounts of combat bouts indicate that blows may be severe and that it is possible for the horn to puncture the skin as well as tear it. However, because the head of the aggressor is moved in an arc, the most likely wound may well be a gash rather than a deep puncture, as direct observations of battles and scars indicate (Carter 1965; Owen-Smith 1973). A consideration of the mechanical properties of the skin also suggests that tearing might be the most likely mode of failure from blows with a horn. Interestingly, although rhinoceros skin is stronger, stiffer, and has a higher work of fracture than that of other mammals, the force of tearing a sample is relatively low compared with that required to cause its failure in tension or compression. Tearing may provide a defensive advantage, namely that when serious combat occurs the resulting wounds may be superficial gashes rather than deep punctures that could cause lethal damage to internal organs. If so, this presents a rather different mechanical design strategy than that found in many other soft biological materials (including 'normal' mammalian skin) in which a relatively low stiffness and large extensibility together provide the means to absorb a large strain energy and thus prevent fracture (Gordon 1978; Denny 1988).

It seems likely that the skin of other large mammals that indulge in intraspecific combat with piercing horns or tusks might also have special structural and mechanical features, in addition to increased thickness, to minimize the risk of wounding in the areas prone to attack. Although no detailed studies of the mechanical properties of skin from such animals have been reported, there is some evidence that supports this idea. For example, the skin of the hippopotamus is comparatively thin and pliable over the belly but very thick (*ca.* 15–20 mm), stiff and relatively inextensible along the flanks, back and rump (Verheyen 1954; Luck & Wright 1964; Tregear 1966; Harkness; 1968). This tissue is composed of 50–100 μm thick, straight collagen fibres arranged in a three-dimensional network (Tregear 1966) that resembles the rhinoceros dermis microscopically. Harkness & Harkness (1965) reported that the breaking strength of the back and flank skin of the hippopotamus was about 35 MPa (twice the strength of the belly skin), and that the properties in the longitudinal and circumferential directions were comparable. Harkness (1968) also described walrus skin as being very stiff, and often severely scarred from attacks by the tusks of conspecifics. Fradrich (1974) reported that the thickened skin along the sides of the head, neck and body of male wild boars reduces the lethality of slashing blows with the tusks that often result in deep, elongated lacerations. Dubost (1979) described the thickened dermal shield of water chevrotains as being reinforced with very thick, straight connective tissue fibres, also

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reported by Jarman (1989). It is interesting to note that the largest terrestrial mammal, the african elephant, does not have the thickest skin. According to Harkness & Harkness (1965), elephant skin thickness varies from about 10 mm to 15 mm on the sides and back. This is not substantially different from the thickness predicted by the scaling model of figure 2, based on a body mass of 5000–6000 kg (Owen-Smith 1988). This suggests that elephant dermis may not be highly modified as an armour to protect against the tusks of conspecifics. Indeed, serious fighting between adult elephants is extremely rare (Douglas-Hamilton & Douglas-Hamilton 1975). More commonly, disputes between elephants are settled by threatening displays, although occasions where cows inflicted bloody wounds on calves have been observed (Douglas-Hamilton & Douglas-Hamilton 1975). Recently, Lillywhite & Stein (1987) have shown that elephant skin has a relatively thick epidermis and surface sculpturing that is designed to provide an effective barrier to water loss.

Further studies on the structure and mechanical properties of the skins of these various animals are needed before more general conclusions can be made concerning the evolution and mechanical design of dermal shields in mammals.

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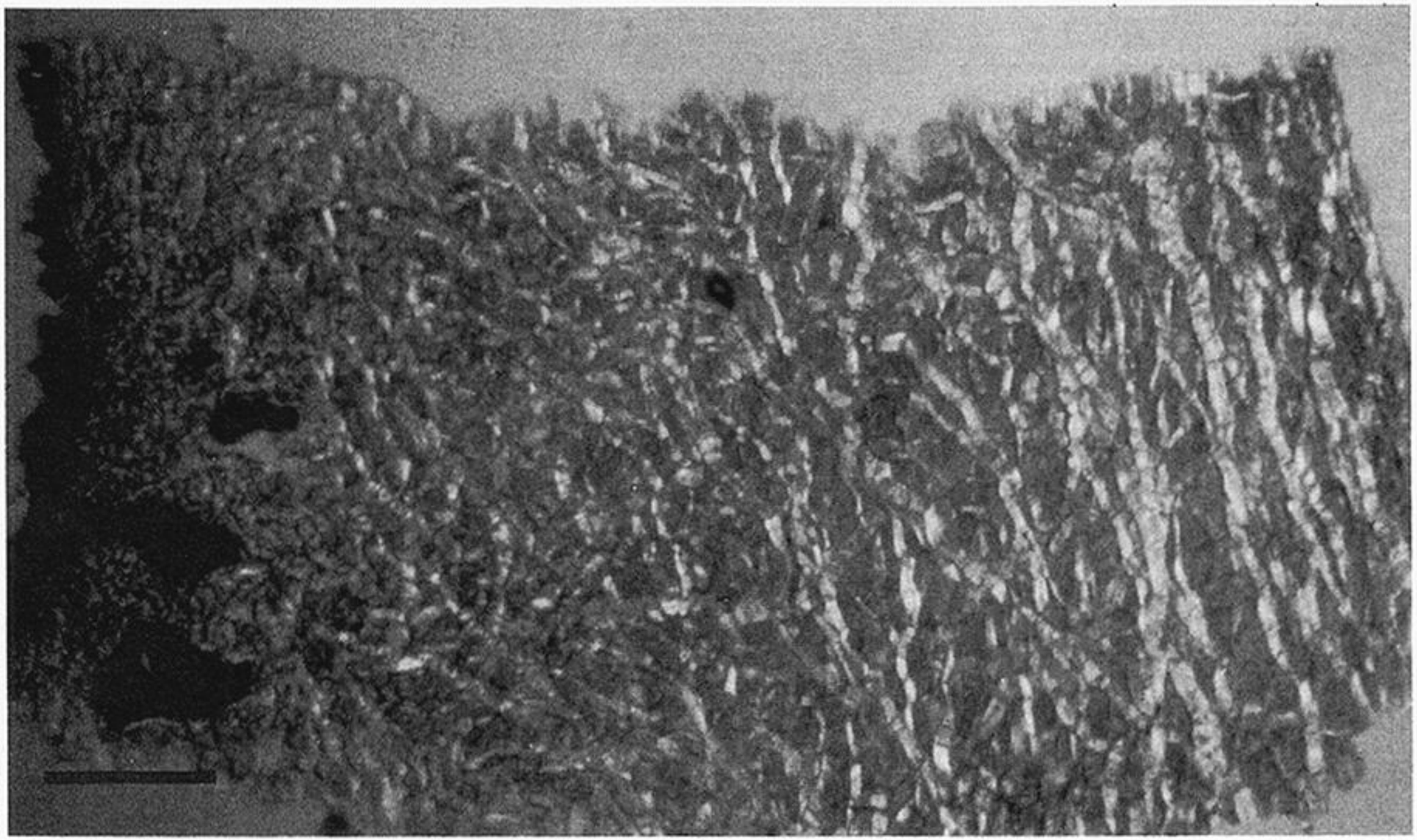

gure 3. A polarized light micrograph showing an entire transverse section of the skin from the belly of the white inoceros (epidermal surface on the left). The highly birefringent collagen fibres are prominent throughout, being mewhat thinner and more regularly arrayed in the outermost region of the dermis. Scale bar is 2.0 mm.

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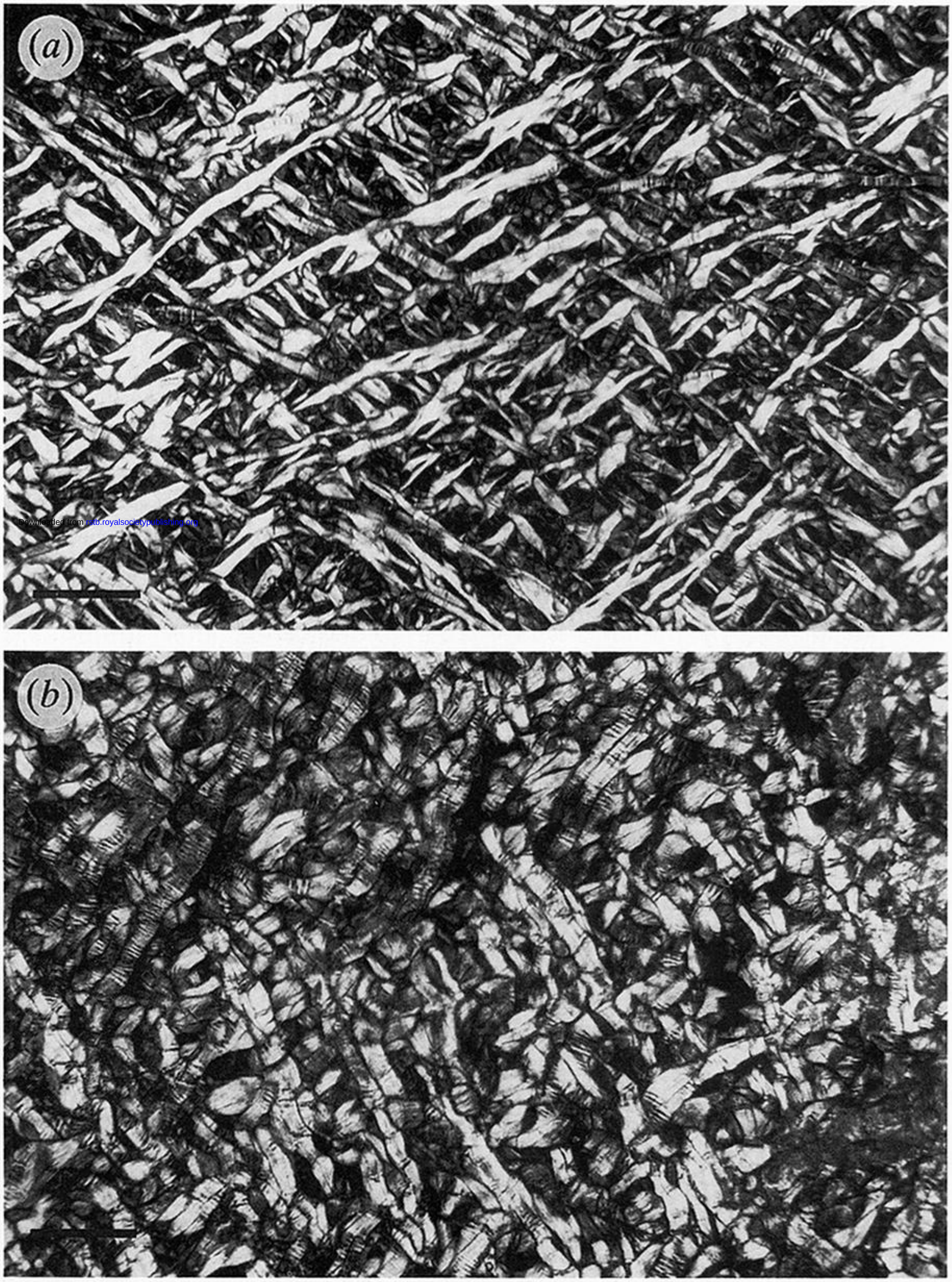

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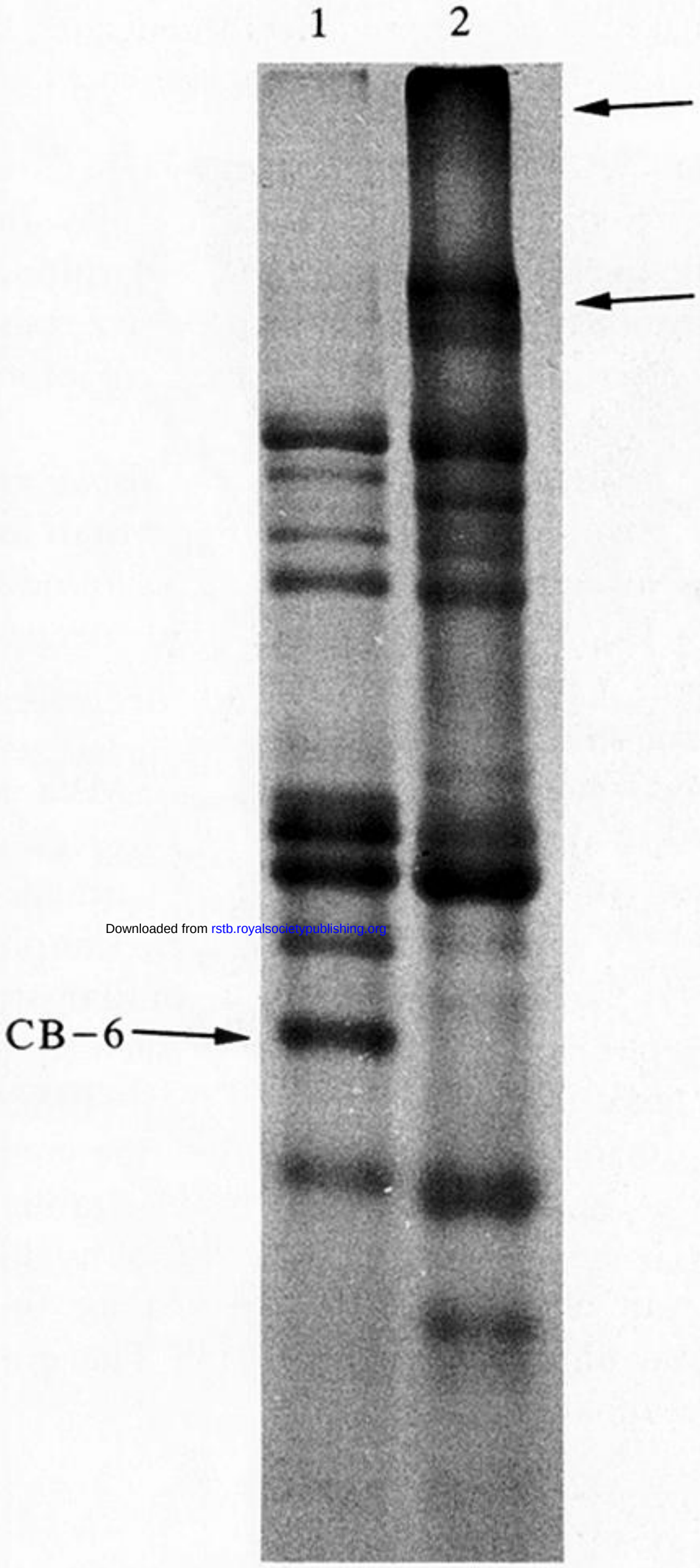
igure 4. Polarized light micrographs of transverse sections of white rhinoceros skin showing the arrangement of ollagen fibres in the deep dermis of (*a*) the flank and (*b*) the belly. Fibres in the former are relatively straight and verage 90 µm in diameter, whereas those in the latter are crimped and average 200 µm in diameter. Scale bars are 0 mm.



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gure 5. Cyanogen bromide peptides of skin collagen from bbit (lane 1) and rhinoceros (lane 2), stained with oomasie Blue R250 after gel electrophoresis. The peptides e separated by decreasing molecular mass from top to ottom on the gel. The 19 kDa peptide labelled as CB-6 is om the C-terminal region of the $\alpha 1$ (type I) molecule and ntains a site of intermolecular covalent crosslink forma- on. With ageing, these crosslinks join together adjacent llagen molecules which, after cyanogen bromide digestion, eld large polymers of CB-6, rather than the monomeric rm. Thus, the presence of heterogeneous high molecular ass material near the top of the gel (arrows) and virtually monomer CB-6 suggest that the rhinoceros collagen is tensively crosslinked (see Light (1985) and Light & Bailey 979) for details of this technique).

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igure 8. (*a*) A photograph of one portion of a test specimen dorsal skin that was broken in tension. The broken surface at the top. Scale bar is 5 mm. (*b*) A scanning electron icrograph of the fracture surface. Scale bar is 500 µm. (*c*) higher-magnification view of one of the collagen fibre nds in (*b*). The bulbous appearance of the ends of the llagen fibres shows that the specimen broke by fracture of e fibres rather than by disruption of the network by fibre ll-out. Scale bar is 25 µm.