

## MECHANICAL PROPERTIES AND MORPHOLOGICAL CORRELATES OF FRAGILE SKIN IN GEKKONID LIZARDS

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### Summary

The mechanical properties of gekkonid lizard skin are investigated for the first time. Although the skin of certain geckos, such as *Gekko gekko*, behaves in 'typical' vertebrate fashion, that of others, such as *Ailuronyx seychellensis*, exhibits unusual properties associated with identifiable morphological specializations. Light and scanning electron microscopy reveal that *Ailuronyx* dermis is functionally bilayered; the stratum compactum is divided into inner and outer layers by intervening loose connective tissue. The inner layer is strong and tough and does not differ significantly in its properties from that of *Gekko gekko* whole skin. The much thicker outer layer, however, is only 1/20 as strong and 1/50 as tough as the inner layer, and exhibits preformed zones of weakness. In nature, *Ailuronyx* parts with considerable portions of the outer components of the skin as an antipredator escape mechanism. Skin samples from 17 additional gecko species varied considerably in their strength, stiffness and toughness. None of the forms with tough skin employs regional integumentary loss as a predator escape strategy. Weak skin alone is not sufficient to permit regional integumentary loss, as the capability to lose the skin involves not only inherent properties of the tissue, but also features of the mechanical interaction of skin layers with one another and with the underlying body wall.

### Introduction

Autotomy, or the ability to 'shed' or 'drop' portions of the body, is a widely employed antipredator strategy among vertebrates. Caudal autotomy is the most common manifestation of this phenomenon among tetrapods. It occurs in certain salamanders (Wake & Dresner, 1967), rodents (Mohr, 1941; Dubost & Gasc, 1987) and a great many lepidosaurian reptiles (Arnold, 1984, 1988; Bellairs & Bryant, 1985). In those forms in which the tail is autotomized intravertebrally (except amphisbaenians, see Gans, 1978), loss is followed by regeneration. Other

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forms of autotomy are necessarily rare as animals cannot dispense with body parts that are absolutely essential to survival (Goss, 1969; Reichman, 1984).

Autotomy, in the literal sense, pertains to self-induced loss. However, the concept as currently employed has been extended (e.g. Dubost & Gasc, 1987) to include losses induced by an external agency but facilitated by the structural properties of the organism in question. Within this broader context, the ability of certain lizards to exfoliate large portions of their integument in response to physical contact by a putative predator may be construed as autotomy. We prefer, however, to restrict the term autotomy to its more literal meaning with its implications of neurological control. The expression 'regional integumentary loss' is used instead for the phenomenon described herein.

Regional integumentary loss is found only in certain species of the scincid lizard genera *Ctenotus* and *Lerista* (Greer, 1986), and a number of taxa of gekkonid lizards in the subfamily Gekkoninae. Such an antipredator mechanism has been reported in all or most members of the genera *Aristelliger* (Grant, 1941; Greene, 1988; A. M. Bauer, personal observations), *Geckolepis* (Schmidt, 1911; Mertens, 1955, 1960; Bellairs, 1969; Anderson, 1972; Meier, 1980; Schubert & Christophers, 1985), *Gehyra* (Bustard, 1970; Anderson, 1972; McKeown, 1978; A. M. Bauer, personal observation), *Perochirus* (J. V. Vindum, personal communication), *Teratoscincus* (Minton, 1966; Anderson, 1972), and insular populations of *Thecadactylus* (T. J. Papenfuss, personal communication). It is also typical of some members of the genus *Phelsuma* (McKeown & Miller, 1985; Greene, 1988) and of *Pachydactylus namaquensis* (Greene, 1988). Such regional integumentary loss also occurs in the large Seychelles gecko *Ailuronyx seychellensis* (Honegger, 1966; Evans & Evans, 1980; McKeown & Miller, 1985), and it is in this taxon, along with *Geckolepis*, another Indian Ocean island endemic, that this ability is most clearly manifested.

The anatomy of the integument of *Geckolepis typica* has been investigated by Schubert & Christophers (1985) who found a preformed zone of weakness lying in the fatty subcutis. On the basis of transmission electron microscopy, they identified a network of myofibroblasts which they believed actively initiated integumentary autotomy. Their work attempted to provide a precise mechanistic explanation for the fragility of the dermis of *Geckolepis*. While convincing at one level, however, their concentration on ultrastructural details is unsatisfying from the perspective of whole-organism biology as it fails to address the properties of the integument as an organ system with inherent mechanical properties.

In this paper we examine the skin of geckos in general, and *Ailuronyx seychellensis* in particular, in an attempt to characterize the properties of fragile skin and delineate their morphological correlates.

In this regard we distinguish fragile skin (which may be easily torn and the outer layers released from the body as a result of specific morphological modifications) from weak skin (which is more uniform in its structural properties and only fails under relatively low induced loading when removed from contact with underlying tissues). Little is known about the biomechanical parameters of tetrapod skin

except in relation to a limited number of laboratory mammals (e.g. Fung, 1981; Purslow, 1983). This general paucity of information makes it difficult to place the details of particular observed phenomena into a more general mechanical and morphological context. To attempt to overcome this we have examined the pertinent properties of a variety of geckos that do not have fragile skin. This has enabled us to outline the basic mechanical and morphological parameters of gecko skin.

## Materials and methods

### *Animals*

Specimens of *Ailuronyx seychellensis* were collected on Aride Island, Republic of Seychelles, in August 1987, killed with T-61 solution (Hoechst Pharmaceuticals, Montreal), fixed in 10 % neutral buffered formalin, and stored in 70 % ethanol. *Gekko gecko* were obtained from a commercial dealer and prepared as above. Skin strips were also obtained from similarly fixed and preserved specimens of 17 other gekkonid taxa (see Table 2 for listing). Skin samples for mechanical testing and light and electron microscopy were excised in strips of approximately 20 mm  $\times$  70 mm and subsequently trimmed for the required purposes. Strips of fresh *Gekko gecko* skin were also taken from freshly killed specimens, and either tested immediately or after formalin fixation.

### *Mechanical testing*

Strips for mechanical testing were held in metal vice-type clamps with hard rubber faces which prevented slippage, and stretched at a rate of 20 mm min<sup>-1</sup> on a Monsanto T10 tensometer. This gave strain rates in the range 0.02–0.04 s<sup>-1</sup>. Fixed samples were rehydrated in distilled water before use and kept moist during the tests. For each sample the width and length between clamps were measured with vernier calipers before the test, while the thickness was determined afterwards from frozen transverse sections using a light microscope with a digital micrometer eyepiece. Signals for force and cross-head movement from the tensometer were recorded as force vs displacement on an x,y plotter. These data were normalized to stress ( $\sigma$  = force per cross-sectional area), measured in pascals (1 Pa = 1 N m<sup>-2</sup>), and strain ( $\epsilon$  = the increment in length divided by the initial length).

Loading was applied to skin strips taken either parallel with or at 90° to the body long axis. The skin of *Ailuronyx seychellensis* was tested intact and also after separating the outer from the inner layer of the dermis (see Results). Most commonly, the sample was stretched to the break point and from the data the failure strain ( $\epsilon_f$ ) and tensile strength (i.e. the maximum stress achieved prior to failure,  $\sigma_m$ ) were determined. The modulus of elasticity ( $E$ ), a measure of the material stiffness, was calculated from the slope of the linear portion of the stress-strain curve. The total area under the stress-strain curve is the energy required to break a unit volume of material ( $W$ ), expressed in J m<sup>-3</sup>, and is a measure of toughness (Gordon, 1978). This was calculated by cutting out

photocopies of the stress-strain curves and comparing their weights with the weight of a calibrated area of paper.

For the specimens of *G. gecko* and *A. seychellensis* the work of fracture ( $\Gamma$ ) was also determined by using a 'trouser tear' technique (Purslow, 1983; Biedka *et al.* 1987). A short cut was made along the longitudinal axis of a skin specimen 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 a crack was propagated in a controlled fashion at a relatively constant force (see Fig. 7). The work done was calculated as the mean plateau force ( $\bar{F}$ ) times the tear length ( $L$ ). This was divided by the area of the two new surfaces formed (i.e.  $2Lt$ , where  $t$  is the sample thickness) to yield the work of fracture in  $\text{J m}^{-2}$ . Owing to limited availability of *Ailuronyx* skin, trouser tear tests were conducted only longitudinally as this orientation accords with the direction of greatest strength predicted from collagen fibre orientation and thickness, and from tensile tests. All mechanical tests were recorded on a VHS video system and still photographs were taken from stop-frame video images with a 35 mm format camera.

### Microscopy

Material for light microscopy was embedded in Paraplast and sectioned on a rotary microtome at a thickness of 8–10  $\mu\text{m}$ . Stains used were haematoxylin and eosin, Masson's trichrome and Mallory's azan trichrome (Humason, 1979).

Specimens for scanning electron microscopy (SEM) were critical-point dried, mounted so as to expose the cut surface of the skin, sputter coated with gold-palladium alloy, and examined using a Hitachi S-450 SEM. Skin samples fractured as a result of mechanical testing (see above) were similarly prepared for SEM examination.

Collagen fibre angles in the skins were measured by viewing wet-mounted samples under a Wild M5 polarizing microscope fitted with a graduated rotating stage.

## Results

### Field observations

As reported by McKeown & Miller (1985), wild-captured specimens of *Ailuronyx seychellensis* readily part with extensive pieces of skin. Even gentle handling of these animals frequently resulted in extensive cutaneous trauma, as *Ailuronyx* tends to twist its body when restrained, inducing torsional stress on the integument.

The integumentary fragility of *Ailuronyx* was verified in the course of procurement of specimens for this project. Initial attempts to capture specimens by hand were unsuccessful as skin loss, although expected, proved distracting enough to collectors to allow the escape of the wounded animal. Ultimately, undamaged specimens were obtained with a butterfly net.

The common invocation of regional integumentary loss as a defence in

*Ailuronyx seychellensis* is attested to by the prevalence in museum collections of specimens with fresh or healed wounds. Twenty-four of 30 specimens examined [British Museum (Natural History), California Academy of Sciences, Zoologisches Forschungsinstitut und Museum Alexander Koenig] exhibited such wounds, all of which were confined to the dorsal and lateral surfaces of the trunk and head.

### Skin mechanics

Mechanical tests revealed major differences between *Ailuronyx seychellensis* and *Gekko gecko* in the strength, stiffness and toughness of their skins (Fig. 1). In both species the load curves are J-shaped, consisting of an initial 'toe' region followed by a linear portion, as is typical of soft biological materials. The peak in stress ( $\sigma_m$ ) occurs at the limit of elastic deformation, where the skin structure begins to fail ( $\epsilon_f$ ). Fig. 1A indicates that the dorsal skin of *A. seychellensis* is relatively weak, with the longitudinal elastic modulus ( $E$ ) and tensile strength ( $\sigma_m$ ) being about an order of magnitude lower than in *G. gecko* (Fig. 1B). Differences are also seen in the way the skin from these species breaks. Tensile failure in *A. seychellensis* skin begins as a tear at a strain of about 0.28, which propagates further with continued extension. This is shown by the gradual decrease in stress to zero beyond  $\epsilon_f$  in Fig. 1A. In contrast, the skin of *G. gecko* breaks catastrophically, as indicated by the sharp drop in stress at  $\epsilon_f$ , and at a failure strain which is twice as high as in *A. seychellensis* (Fig. 1B). The breaking energy ( $W$ ), determined from these specimens, is only  $0.25 \text{ MJ m}^{-3}$  for *A. seychellensis* compared with  $2.6 \text{ MJ m}^{-3}$  for *G. gecko*. This shows that the dorsal skin of the

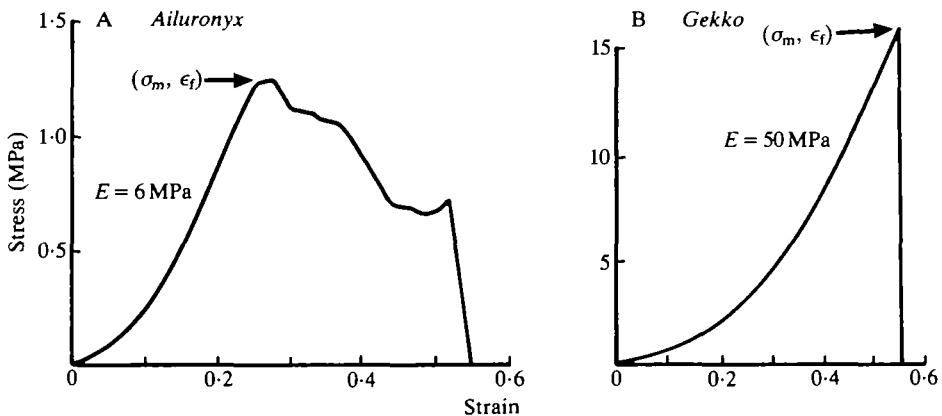


Fig. 1. Stress-strain curves for dorsal skin of (A) *Ailuronyx seychellensis* and (B) *Gekko gecko* stretched longitudinally to the breaking point in the tensometer. The modulus of elasticity,  $E$ , is calculated as the slope of the linear portion of the load curve. Peak stress  $\sigma_m$  occurs at the limit of elastic extension,  $\epsilon_f$ , the failure strain. The skin of *G. gecko* breaks suddenly as a catastrophic rupture, while the skin of *A. seychellensis* tears gradually with extension beyond  $\epsilon_f$ .

Table 1. Summary of the longitudinal mechanical properties of dorsal skin samples from *Ailuronyx seychellensis* and *Gekko gekko*

Sample	N	Thickness (mm)	$\epsilon_f$	$\sigma_m$ (MPa)	E (MPa)	W (MJ m <sup>-3</sup> )	$\Gamma$ (kJ m <sup>-2</sup> )
<i>Ailuronyx seychellensis</i>							
Whole skin	8	0.36	0.31 ± 0.06	1.28 ± 0.34	7.2 ± 1.6	0.27 ± 0.17	0.5
Outer layer	6	0.30	0.29 ± 0.08	0.9 ± 0.2	4.6 ± 1.0	0.13 ± 0.05	0.22
Inner layer	6	0.02	0.85 ± 0.17	21.0 ± 3.8	52 ± 15	6.5 ± 1.5	12.5
<i>Gekko gekko</i>							
Whole skin	10	0.22	0.57 ± 0.09	11.5 ± 2.5	42 ± 7.1	2.4 ± 0.4	2.0

Values are means ± S.E.M.

$\epsilon_f$ , failure strain;  $\sigma_m$ , maximum stress prior to failure; E, modulus of elasticity; W, area under the stress-strain curve;  $\Gamma$ , work of fracture.

former species is only one-tenth as tough as that of the latter. Mean values of the tensile mechanical properties of the skins of these two species are given in Table 1.

Fig. 2 compares the mechanical properties of skin samples taken longitudinally and transversely from the dorsal and ventral surfaces of *Ailuronyx seychellensis*. These data show that the failure strains are virtually the same in all cases, but that tensile strength and elastic moduli are only half as great in the longitudinally oriented dorsal skin samples as in the other samples. That the skin is preferentially weakest dorsally in the direction of the body long axis is consistent with the observation that the occurrence of natural skin wounds in *A. seychellensis* is most prevalent on the dorsum (see above). In contrast, similar tests on the skin of

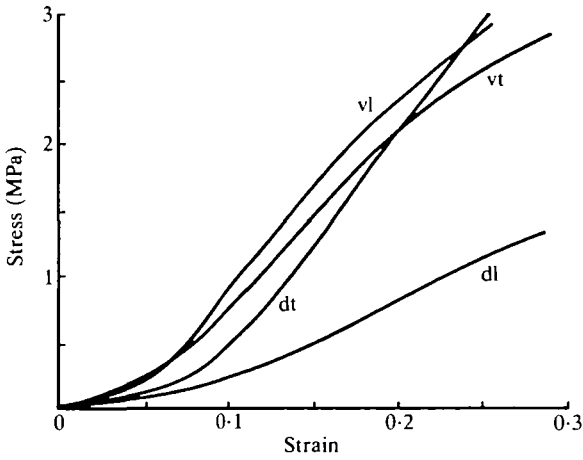


Fig. 2. Stress-strain curves for skin samples from *Ailuronyx seychellensis* comparing dorsal (d) and ventral (v) skin tested transversely (t) and longitudinally (l).

*Gekko gecko* indicate that there are no major differences in mechanical properties between dorsal and ventral locations or transverse and longitudinal orientations.

The difficulty in obtaining the exotic species for this study necessitated the use of preserved material. To determine what effect formalin fixation might have on the mechanical properties of lizard skin, fresh and preserved skin samples from an individual specimen of the commercially available *G. gecko* were compared. Examples of stress-strain plots for dorsal longitudinal skin samples shown in Fig. 3 reveal no major differences in mechanical behaviour attributable to fixation. This is surprising since the effect of formalin fixation on mammalian skin is significant. Viidik (1980) found that rat skin  $\sigma_m$  and  $E$  were increased by about 50 % following formalin fixation. It was not possible to assess the preservation effects on the skin of *Ailuronyx seychellensis* and the other species tested (see Table 2) but, based on the results from *G. gecko*, we have operated under the assumption that the mechanical data obtained are fairly representative of the properties of fresh skin, and that comparisons within a group of preserved specimens should still yield qualitatively, if not quantitatively, valid conclusions.

Two distinct dermal layers are present in *Ailuronyx seychellensis* dorsal skin, a thick outer layer and a much thinner underlying layer (see below). These are easily separable upon dissection and were tested individually. It was found that these two layers were mechanically quite different. The thin inner layer, which is not ruptured during regional integumentary loss, is much stronger, stiffer and tougher than the thick outer layer. Fig. 4A shows three longitudinal force-extension curves: one for a test on the outer skin layer obtained from the dorsum of *A. seychellensis*, one for the inner layer of the same skin strip, and one for an equivalent sized strip of whole skin from the same animal. Up to an extension of about 4mm, at which point the outer layer broke, the force-extension

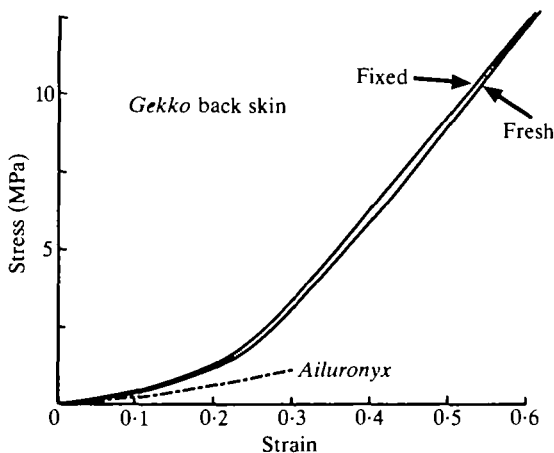


Fig. 3. Examples of stress-strain curves for fresh and fixed dorsal skin taken from adjacent sites of a single individual of *Gekko gecko*, tested longitudinally. The broken line is the load part of the stress-strain curve for *Ailuronyx seychellensis* redrawn from Fig. 1A.

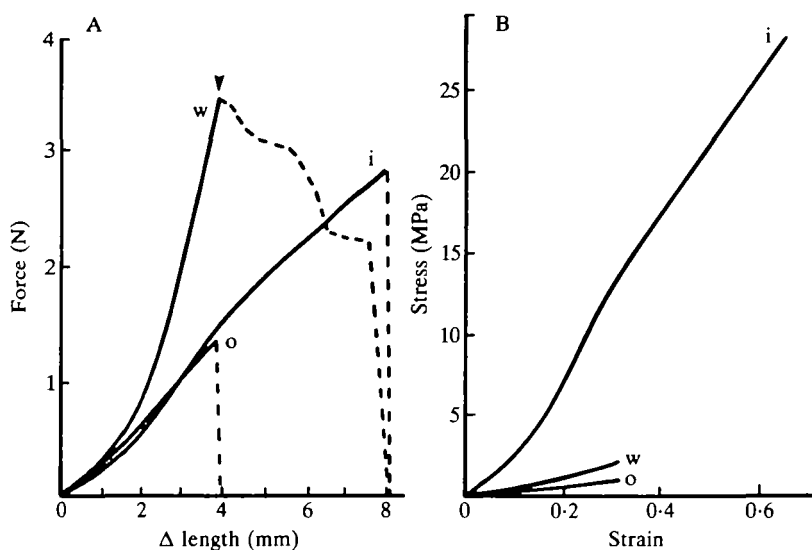


Fig. 4. (A) Longitudinal force-extension curves for *Ailuronyx seychellensis* dorsal skin tested whole (w) and after separation of the outer (o) and inner (i) layers. Each sample was initially 12 mm long and 5 mm wide. Failure of whole skin began (arrowhead) at an extension where the outer layer ruptured and was complete when the inner layer broke at about twice that extension. (B) Data from A normalized to stress and strain. The outer skin layer has a low elastic modulus ( $E = 4$  MPa), tensile strength ( $\sigma_m = 1$  MPa) and breaking energy ( $W = 0.15$  MJ m $^{-3}$ ) compared with the very thin and tough inner layer ( $E = 57$  MPa,  $\sigma_m = 27$  MPa,  $W = 6$  MJ m $^{-3}$ ).

curves for both layers are almost identical. This indicates that the total force to stretch whole skin up to 30 %, where it began to fail, was shared equally by these two layers, even though the inner layer was only 1/15th as thick as the outer layer (see Table 1). When the forces are normalized (Fig. 4B) it can be seen that the inner layer sustains much higher stresses at all strains than does the outer layer. The tensile strength, yield strain, breaking energy and elastic modulus are all much greater for the inner layer than for the outer one (see Table 1 for summaries). In fact, the inner layer of *A. seychellensis* resembles the whole skin of *G. gecko* in its mechanical integrity, with no apparent modifications for regional weakness. While the outer layer broke at a strain of 0.3, the inner layer broke only after being strained to about 0.7 (Fig. 4B). Failure of the whole skin sample reflected the combined properties of both inner and outer layers acting in parallel. The peak stress coincided with fracture of the outer layer and the transfer of the entire stress to the remaining inner layer, which subsequently broke under further extension. This can be seen in the visual records of extension of a longitudinal strip of whole *A. seychellensis* dorsal skin (Fig. 5).

The mechanical differences between the inner and outer layers of *Ailuronyx seychellensis* dorsal skin are illustrated qualitatively in Fig. 5C–G. While the outer layer tears at low strain, the inner layer is highly extensible. The decrease in width



seen in the inner layer as it is stretched (Fig. 5G) indicates the reorientation of its constituent collagen fibres. These fibres are 15–20  $\mu\text{m}$  in diameter and occur as criss-cross arrays which make angles of about  $55^\circ$  with the body long axis when the skin is unstrained (Fig. 6). From this angle it can be predicted that a strain of 0.74 would occur before the collagen fibres were reoriented directly along the axis of tension. Fig. 5G shows a strip of the inner layer that was strained up to 0.9 just before breaking. The average value of  $\epsilon_f$  for the inner layer was 0.85 (Table 1). The outer layer has thick collagen fibres (40–60  $\mu\text{m}$  in diameter) oriented at about  $90^\circ$  to the body long axis, and much thinner fibres at  $0^\circ$  (Fig. 6). This fibre arrangement should reinforce the outer layer transversely and provide lower strength longitudinally, as is indeed the case (Fig. 2). Fig. 5C,D,E shows one example of an outer layer strip that fractured at a tensile strain of 0.20. The average value of  $\epsilon_f$  for the outer layer was 0.29 (Table 1). Fig. 5H–J shows a strip of *G. gecko* skin which was extended and broke at a strain of 0.6. The lateral

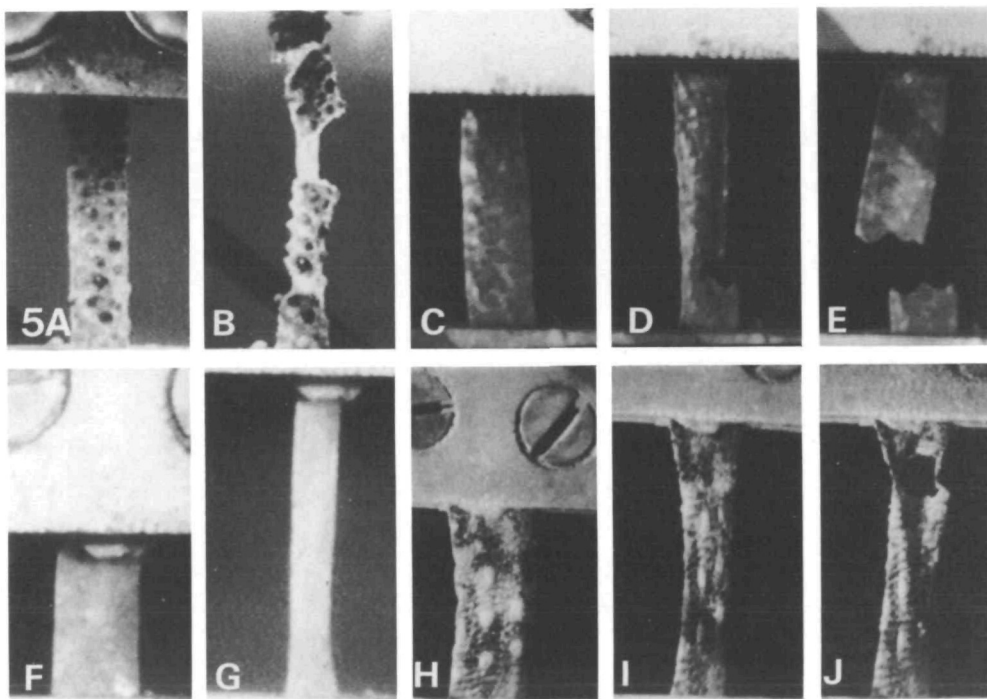


Fig. 5. Video frames of tensile tests on dorsal longitudinal skin samples from *Ailuronyx seychellensis* (A–G) and *Gekko gecko* (H–J). (A) Whole skin unloaded. (B) Sample A extended to  $\epsilon = 0.36$ . The outer layer has fractured in several places revealing the thin underlying layer which is still intact. (C) Sample of the outer layer unloaded. (D) Sample C extended to  $\epsilon = 0.20$ . A transverse tear has been initiated. (E) Fracture occurring in sample C. (F) Sample of the inner layer unloaded. (G) Sample F stretched to  $\epsilon = 0.9$ , just before breaking. (H) Sample of skin from *Gekko gecko* unloaded. (I) Sample H stretched to  $\epsilon = 0.6$ . (J) Fracture occurring in sample H.

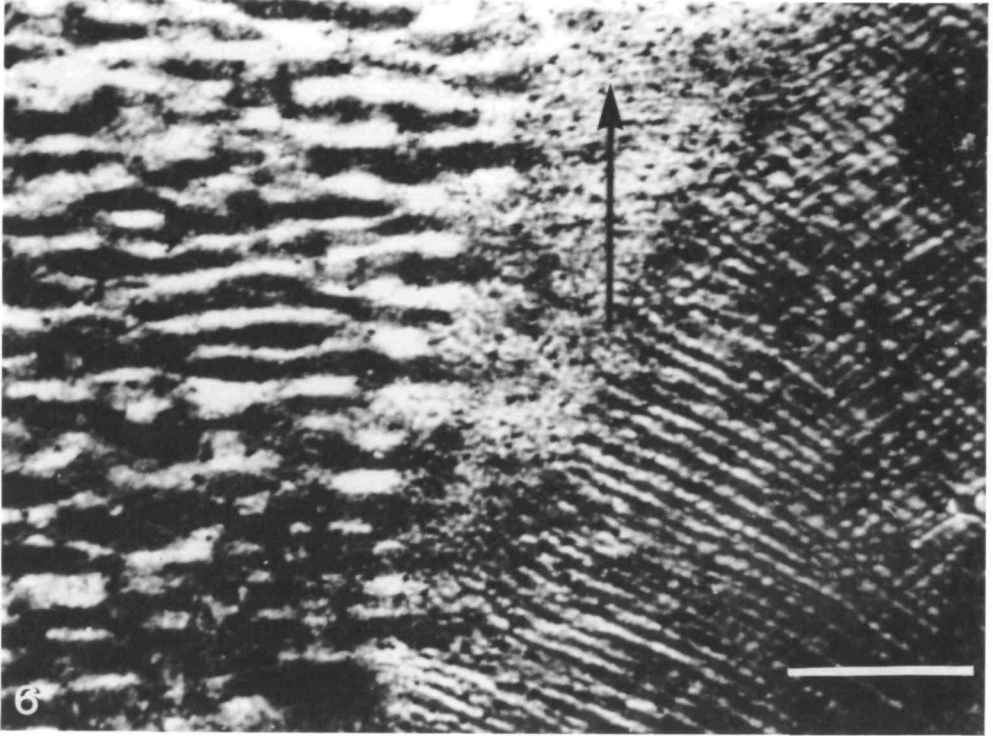


Fig. 6. A polarized light micrograph of dorsal skin from *Ailuronyx seychellensis* showing collagen fibre organization in the outer layer, on the left, and in the inner layer, on the right, where the outer layer has been removed. The outer layer consists of large fibres (40–60  $\mu\text{m}$  in diameter) oriented  $90^\circ$  to the body long axis (indicated by arrow), and smaller fibres which lie at  $0^\circ$  to this axis. The inner layer has a criss-cross array of collagen fibres, 15–20  $\mu\text{m}$  in diameter, which lie at approximately  $55^\circ$  to the body long axis. Scale bar, 0.50 mm.

'necking' of the sample at high strains suggests, as with the inner layer of *A. seychellensis* skin, that the fibre component has reoriented towards the axis of stress. Collagen fibres in *G. gecko* skin were in crossed arrays with an average fibre angle of  $50^\circ$  to the body long axis. From this angle it may be predicted that a strain of 0.56 would be possible before the fibres were loaded directly along their axis. The average value of  $\epsilon_f$  for *G. gecko* skin is 0.57 (Table 1). The mechanical properties of these tissues are highly dependent on the fibre morphology and are consistent with the behaviour of fibre-reinforced composite materials.

From tear tests on skin samples, the work of fracture ( $\Gamma$ ), an indication of the fracture toughness of a material, was determined. Typical force–extension records are shown in Fig. 7. In each case the initial region of the curve represents elastic deformation of the two arms of the test piece. When the force is high enough to propagate the tear, it then proceeds in a stable fashion with no additional force required. The plateau region is not smooth but oscillates about a mean value  $\bar{F}$  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  $\Gamma$  for the skin of *Ailuronyx seychellensis* and *Gekko gecko* are provided in Table 1. Not surprisingly, these results indicate that the outer layer of *A. seychellensis* skin could be torn longitudinally with very little energy input. The cracks so propagated are not straight but follow the fibre pattern. We would not expect any major differences if the skin was torn transversely, although, if anything, it may be slightly less tough. However, the inner layer of the skin of this species had a high work of fracture, indicating that it is a very tough material. The skin of *G. gecko* is also much tougher than the outer layer of *A. seychellensis*, although not as tough as the inner layer of this species.

Finally, we compared the mechanical properties of the skin of 17 other species of gekkonid lizards, some of which have been described as having fragile skin or exhibiting regional integumentary loss. The results are summarized in Table 2. Based on the mechanical properties of the skin, we have arbitrarily divided these species into two groups. Group A represents species having skins of relatively low strength and toughness ( $\sigma_m < 10$  MPa and  $W < 2$  MJ m<sup>-3</sup>). Group B contains species having skins of relatively high strength and toughness ( $\sigma_m > 10$  MPa and  $W > 2$  MJ m<sup>-3</sup>). *Ailuronyx seychellensis* is included in group A, and *Gekko gecko* in group B. Only two species, *Cosymbotus platyurus* and *Tarentola mauritanica*, exhibit the toughness characteristic of one group and the strength characteristic of the other. In general, skin thickness and failure strains do not appear to be correlated with strength and toughness. The species previously described as exhibiting fragile integuments (see Introduction) all fit into group A, thus establishing a correlation between this characteristic and the mechanical properties of the skin. Interestingly, it may also be noted that the tensile failure behaviour of skin samples from most of the species suspected of having fragile skins (marked by asterisks in Table 2) resembles that of *A. seychellensis* (see

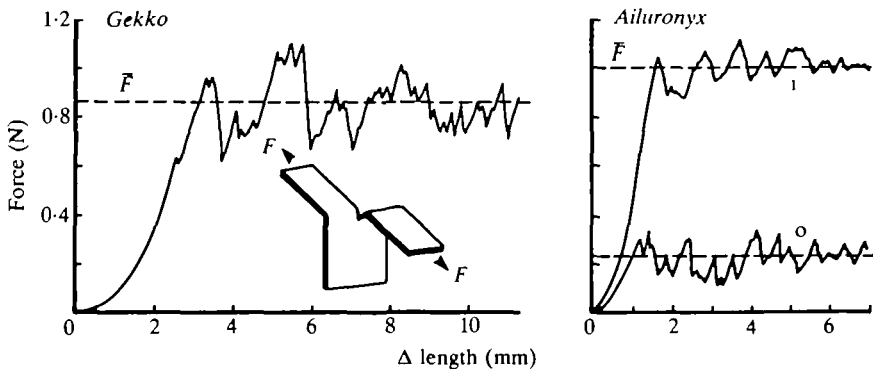


Fig. 7. Typical records from 'trouser tear' experiments to determine the work of fracture of skin samples from (A) *Gekko gecko* and (B) *Ailuronyx seychellensis* inner (i) and outer (o) layers. The configuration of the test sample is shown in A. In each test the tearing force oscillated about a mean value  $\bar{F}$ , indicated by the broken line.

Table 2. *Mechanical properties of various gekkonid skins*

Species	Thickness (mm)	$\epsilon_f$	$\sigma_m$ (MPa)	$E$ (MPa)	$W$ (MJ m <sup>-3</sup> )
Group A					
<i>Ailuronyx seychellensis</i> (Duméril & Bibron)*†	0.36	0.31	1.3	7.2	0.3
<i>Geckolepis maculatus</i> Peters*†	0.08	0.65	1.3	2.6	0.3
<i>Teratoscincus scincus</i> (Schlegel)*†	0.11	0.32	3.3	13.7	0.6
<i>Gehyra mutilata</i> (Wiegmann)*†	0.08	0.36	5.1	18.5	1.1
<i>Stenodactylus sthenodactylus</i> (Lichtenstein)	0.06	0.55	4.4	10.3	1.3
<i>Hemidactylus fasciatus</i> Gray†	0.05	0.36	7.2	38.0	1.2
<i>Nactus pelagicus</i> (Girard)	0.06	0.55	6.5	17.6	1.3
<i>Pachydactylus bibronii</i> (A. Smith)	0.08	0.41	7.3	23.7	1.5
<i>Aristelliger praesignis</i> (Hallowell)*†	0.09	0.58	5.6	14.9	1.9
<i>Phelsuma madagascariensis</i> (Gray)*	0.11	0.42	6.3	18.7	1.9
<i>Cosymbotus platyurus</i> (Scheider)	0.05	0.71	9.4	19.6	3.2
<i>Tarentola mauritanica</i> (Linnaeus)	0.10	0.38	12.0	46.4	1.7
Group B					
<i>Gekko gekko</i> (Linnaeus)	0.22	0.57	11.5	42.0	2.4
<i>Cyrtodactylus malayanus</i> (de Rooij)	0.07	0.50	10.6	34.9	2.2
<i>Geckonia chazaliae</i> Mocquard	0.11	0.37	16.9	75.7	2.4
<i>Aeluroscalabotes felinus</i> (Günther)	0.05	0.36	17.0	68.5	2.5
<i>Homopholis fasciata</i> (Boulenger)	0.06	0.46	19.0	62.4	2.9
<i>Phelsuma quadriocellata</i> (Peters)	0.05	0.58	19.3	49.6	4.1
<i>Thecadactylus rapicauda</i> (Houttuyn)*	0.06	0.49	25.8	82.5	5.2

\* Previously considered fragile.  
† Failure behaviour like that of *A. seychellensis*.  
See Table 1 for an explanation of the abbreviations.

Fig. 1A), while failure in skin from all other species resembles the catastrophic type of rupture seen in *G. gekko* (see Fig. 1B).

### *Morphology of the integument*

#### *Gekko gekko*, surficial morphology

The integument of *Gekko gekko* is typical in structure of that of gekkonid lizards in general. Dorsal scalation is heterogeneous, consisting of juxtaposing granules and tubercles of varying size. Weakly keratinized hinge regions between the scales provide flexibility to the skin as a unit (see Maderson, 1965). The granules themselves are generally flattened and polygonal in outline, and form rosettes around the caudally directed, regularly arranged, subconical tubercles. Certain of the more anterior mid-dorsal tubercles are underlain by osteoderms (Bauer & Russell, 1989). Ventral scales are somewhat more imbricate and less heterogeneous in both shape and surface relief (see Maderson *et al.* 1978a).

*Gekko gecko*, histology

The epidermis of the dorsum is noticeably thicker on the exposed scale surfaces than it is in the hinge regions, and is underlain by pigment cells in the outer region of the dermis. On average, the epidermis accounts for approximately 4 % of total integumentary thickness. The underlying dermis may be divided into a thicker (approx. 90 % of total skin thickness) outer region and a thinner (approx. 6 % of total skin thickness), but distinct, inner region (Fig. 8A), with little loose

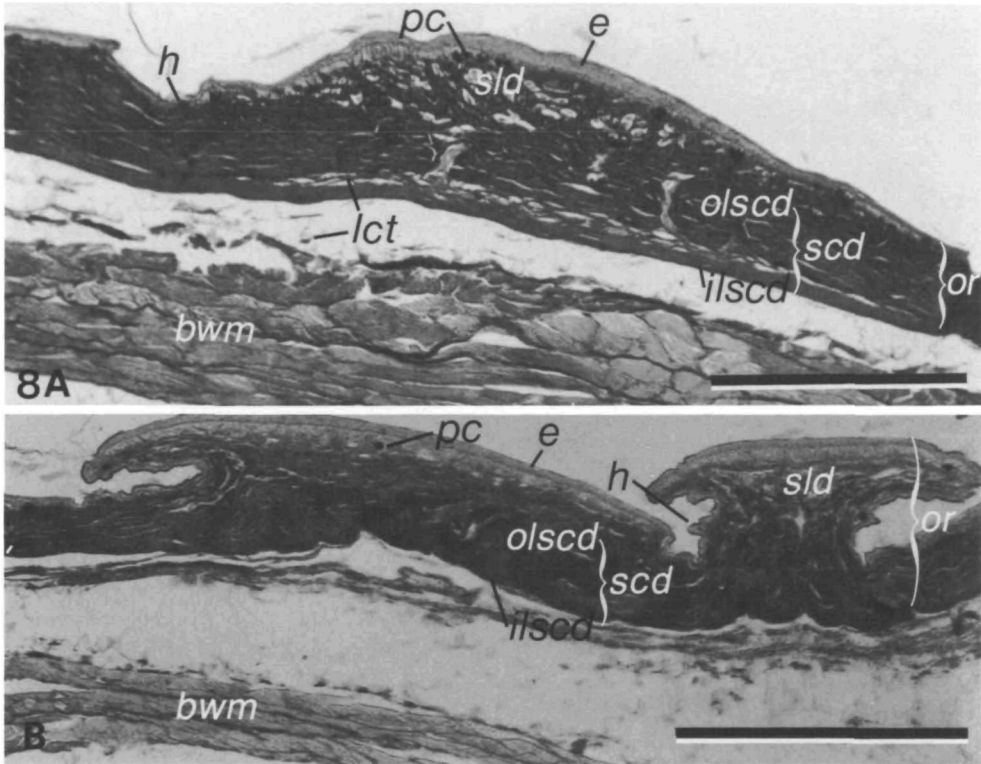


Fig. 8. (A) Longitudinal section through the dorsal skin of *Gekko gecko*. The epidermis (*e*) is thicker on the exposed scale surface than in the hinge region (*h*). The stratum laxum of the dermis (*sld*) includes pigment cells (*pc*) and is underlain by the thicker stratum compactum (*scd*). The thicker outer layer of the latter (*olscd*) combines with the stratum laxum and epidermis to make up the composite outer region (*or*) of the integument. The thinner inner layer of the stratum compactum (*ilscd*) is closely applied to the outer layer of the stratum compactum, with small amounts of loose connective tissue (*lct*) intervening between the two. The body wall muscles (*bwm*) lie deep to the stratum compactum and are segregated from the latter by another layer of loose connective tissue. Scale bar, 0.5 mm. Haematoxylin and eosin stain. (B) Transverse section through the ventral skin of *Gekko gecko*. The stratum laxum of the dermis (*sld*) is somewhat more extensive than in the dorsal skin, and the inner layer of the stratum compactum (*ilscd*) is more closely adpressed to the outer layer (*olscd*). Other abbreviations as in A above. Scale bar, 0.5 mm. Haematoxylin and eosin stain.

connective tissue intervening between the two. The outer region is a composite of the thin stratum laxum and the majority of the collagenous matrix of the stratum compactum. The inner region consists of the deepest layers of the stratum compactum and possesses prominent pigment cells associated with its outer periphery (Fig. 8A). A thin layer of loose connective tissue separates the base of the dermis from the body wall musculature.

The ventral skin (Fig. 8B) differs from that of the dorsum in terms of the heterogeneity of the scales outlined above. Further, the stratum laxum is somewhat more extensive and the inner layer of the stratum compactum is more closely adpressed to the outer layer.

*Ailuronyx seychellensis*, *surficial morphology*

The dorsal scalation of original skin consists of pronounced conical tubercles arranged in an alternating pattern of large and smaller units (Figs 9, 10A,B). Narrow hinge regions appear as grooves within the high relief of the conical scales (Fig. 9). The larger tubercles are characterized by their generally circular bases,

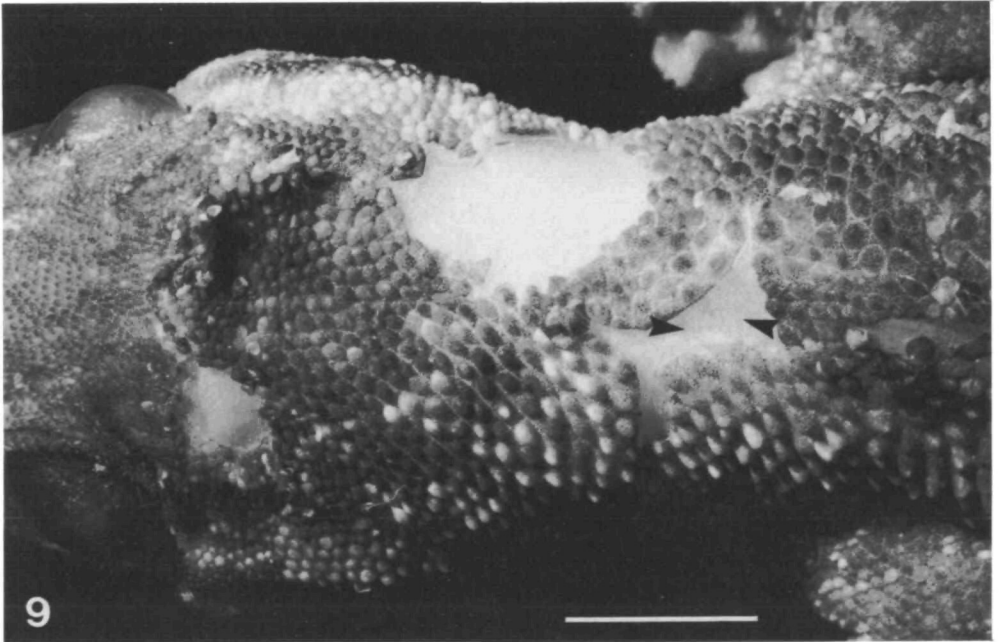


Fig. 9. Dorsal view of the neck of *Ailuronyx seychellensis* showing regions of fractured skin. Note the large conical tubercles and the grooved hinge regions between them. Arrowheads point to regions where the pigment cells of the deep stratum compactum have been exposed. Scale bar, 10 mm.

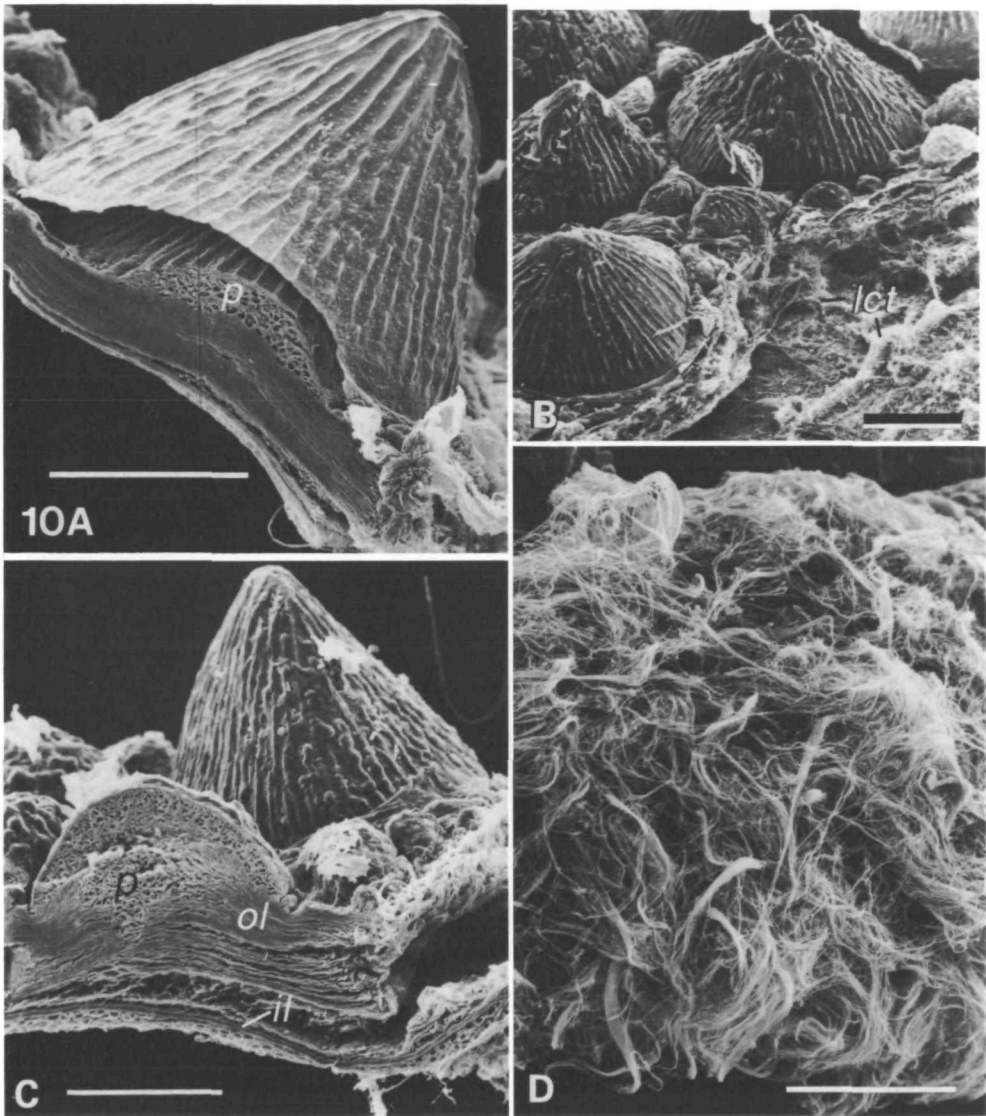


Fig. 10. Scanning electron micrographs of the skin of *Ailuronyx seychellensis*. (A) Large dorsal tubercle (prior to ecdysis) illustrating radial ridging. The tangential cut through the tubercle shows the parenchymatous cells (*p*) of the stratum laxum. Scale bar, 500  $\mu\text{m}$ . (B) Oblique view of experimentally fractured region of dorsal skin: loose connective tissue (*lct*) may be seen overlying the inner layer of the stratum compactum which has not ruptured. Scale bar, 500  $\mu\text{m}$ . (C) View of section through a small dorsal tubercle illustrating the partial disruption of the outer layer of stratum compactum (*ol*) by parenchymatous cells (*p*) of the tubercle core, and the separation of the inner (*il*) and outer layers of the stratum compactum by a zone of loose connective tissue. (D) Edge-on view of the fractured surface of the upper skin layer (epidermis + stratum laxum + outer layer of stratum compactum) showing interwoven mass of fibres of the stratum compactum following rupture and subsequent relaxation.



Fig. 11. (A) Transverse section through the original dorsal skin of *Ailuronyx seychellensis*. The epidermis (*e*) is thin in the hinge regions (*h*) between the tubercles (*t*). The integument is divided into two distinct regions, a thick composite outer region consisting of the epidermis, the stratum laxum of the dermis (*sld*) and the outer layer of the stratum compactum of the dermis (*olscd*), and a thin inner region consisting of the inner layer of the stratum compactum of the dermis (*ilscd*). The outer region is heterogeneous, with parenchymatous cells (*par*) interrupting the collagen fibres of the stratum laxum and, in the larger conical tubercles, the collagen fibres of the outer layer of the stratum compactum. The thin inner layer of the stratum compactum is homogeneous and continuous, and contains conspicuous pigment cells (*pc*). Loose connective tissue (*lct*) segregates the outer layer of the stratum compactum from the inner layer, and the latter from the body wall muscles (*bwm*). Scale bar, 0.5 mm. Masson's trichrome stain. (B) Longitudinal section through the original ventral skin of *Ailuronyx seychellensis*. Parenchymatous cells (*par*) occur only within the stratum laxum of the dermis (*sld*). The collagen fibres of the outer layer of the stratum compactum of the dermis (*olscd*) are uninterrupted, as are those of the inner layer (*ilscd*). Other abbreviations as in A. Scale bar, 0.25 mm. Mallory's azan trichrome stain. (C) Longitudinal section through a fresh wound on the dorsal skin of *Ailuronyx seychellensis*. Note the continuity of the thin inner layer of the stratum compactum of the dermis (*ilscd*) and the exposed ends of the collagen fibres of the outer layer of the stratum compactum of the dermis (*olscd*). Other abbreviations as in A. Scale bar, 0.25 mm. Mallory's azan trichrome stain. (D) Longitudinal section through a healed wound on the dorsal skin of *Ailuronyx seychellensis*. Note the continuity of the collagen fibres of the outer layer of the stratum compactum of the dermis (*olscd*), the lower height of the tubercles (*t*), and the poor differentiation of the parenchymatous (*par*) regions of the stratum laxum of the dermis (*sld*). Other abbreviations as in A. Scale bar, 0.2 mm. Mallory's azan trichrome stain.

acute apices and complex surface microarchitecture (Fig. 10A,B), while the smaller ones have a more rounded apex and lack the well-defined pattern of radiating ridges.

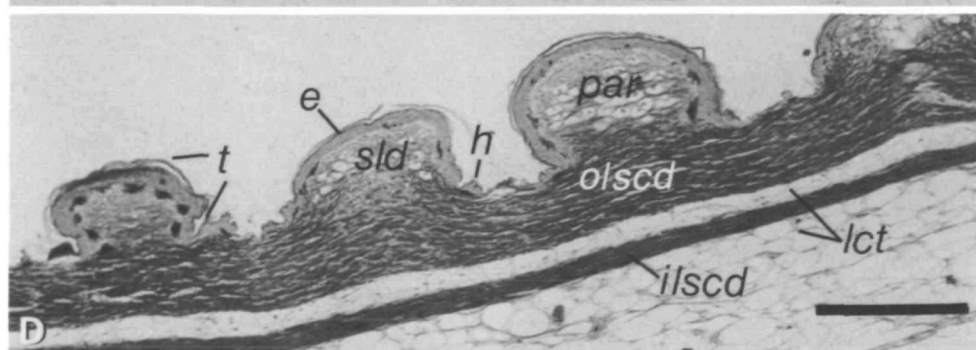
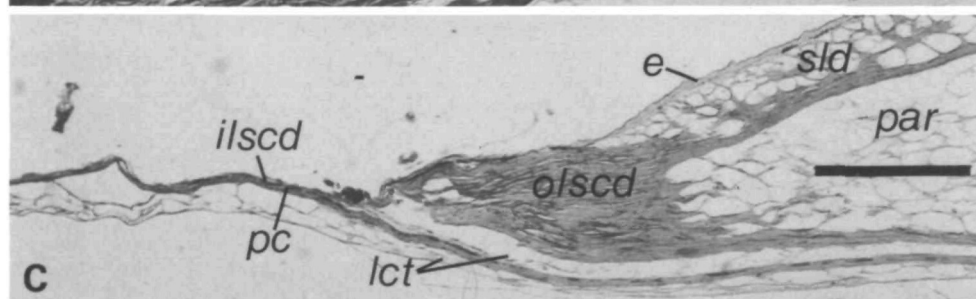
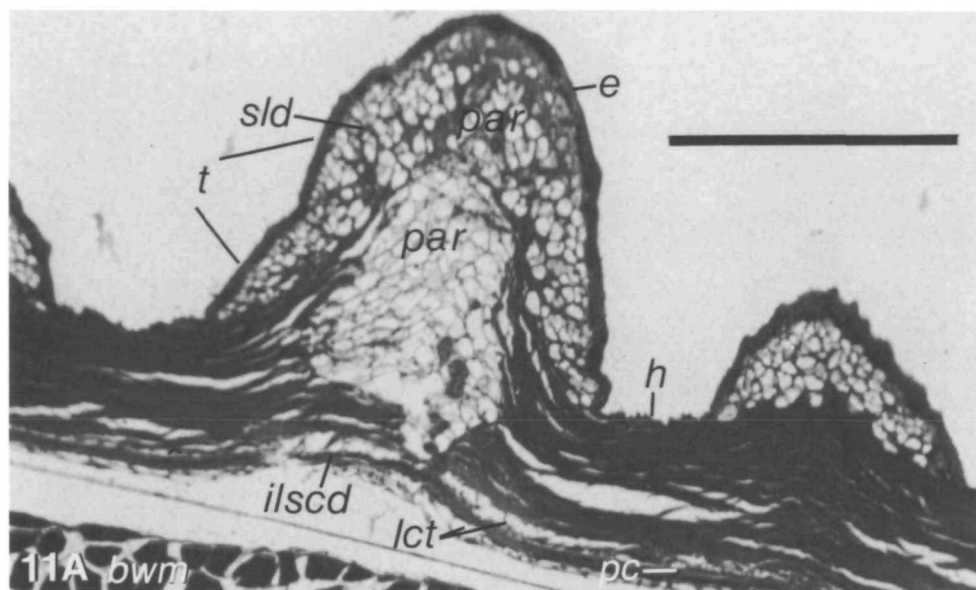
The ventral scales of *Ailuronyx seychellensis* are, on the whole, more similar in appearance to those of *Gekko gekko*.

Wounded areas of the dorsum appear smooth and shiny, and the underlying muscle is clearly visible through windows of the deeper layer of the pigmented stratum compactum (Fig. 9, arrowheads). Fresh wound edges appear to coincide with the grooved hinge regions mentioned above (Figs 9, 10B) and are somewhat irregular. Healed wounds are generally similar in appearance to original skin but may be distinguished by their smaller, more irregular tubercles, as well as on histological grounds (see below).

#### *Ailuronyx seychellensis*, histology of original skin

The epidermis of the dorsum is noticeably thinned in the hinge regions between tubercles (Fig. 11A), more so than in *Gekko gekko*. The stratum compactum consists of a thick outer zone and a much thinner, distinct inner zone (Figs 10C, 11A). The outer layer is much more heterogeneous than that of *G. gekko*. The outer region of the core of the conical tubercles and the majority of the content of





the smaller, dome-like tubercles consists of expanded parenchymatous cells of the stratum laxum, interrupted by thin and irregularly disposed collagen fibres (Figs 10C, 11A). The stratum compactum of the outer zone lacks the continuity of that of *G. gecko* and there is less crimping of the collagen fibres. Vertical fibres are not prominent in this zone. The collagen fibres of this zone are continuous or only partially interrupted beneath the smaller, dome-like tubercles and are continuous beneath the hinge regions (where a distinct stratum laxum is absent), but are significantly interrupted within the larger, conical tubercles. In the latter, collagen fibres are poorly represented and are divided around a central, collagen-free core of expanded parenchymatous cells that are encompassed entirely within the stratum compactum. Pigment cells are evident but scattered in all components of the outer layer.

The thin inner zone (6 % of integumentary thickness measured relative to the mean hinge region thickness) consists of collagen fibres and contains conspicuous pigment cells. The gap between the inner and outer dermal layers is more pronounced than in *G. gecko* and is occupied by loose connective tissue. A similar gap separates the inner layer from the body wall.

The ventral skin (Fig. 11B) is generally similar to that of the dorsum (see Fig. 11A). The core of the subimbricate scales is filled with expanded parenchymatous cells, but these are all derived from the stratum laxum. Although fibres of the stratum compactum intrude into the stratum laxum, there is no parenchymatous interruption within the stratum compactum itself. The collagen fibres of the inner layer of the stratum compactum are straighter than those of the outer layer and, unlike the inner layer of the dorsum, appear to contain no pigment cells.

#### *Ailuronyx seychellensis*, histology of freshly wounded skin

At the site of the wound only the inner layer of the stratum compactum remains intact (Fig. 11C). The wound is bounded by tubercles and rupture of the integument appears to have taken place at the junction of these scales with the thinner intervening hinge region, or perhaps at the regions underlying the larger tubercles. As a result of this, the collagen fibres of the outer zone of the stratum compactum have exposed free ends (Figs 10B,D, 11C).

#### *Ailuronyx seychellensis*, histology of healed wounded skin

In healed skin the inner zone of the stratum compactum retains its original appearance. The outer layer, however, regenerates without or almost without the conspicuous interruptions that characterize the subtubercular region of the undamaged integument (Fig. 11D). The tubercles themselves are lower in relief than those of intact skin and only weakly endowed with enlarged parenchymatous cells. In many respects these regenerated scales resemble more closely those of original ventral skin than they do original dorsal skin (Fig. 11A,B,D).

### Discussion

Vertebrate skin is typically involved in many functional roles, among them

support, and protection of the soft tissues, transport and storage of gases, metabolites and nutrients, locomotion, behavioural display, and sensory perception (Kresja, 1979). The observation that *Ailuronyx* and certain other geckos so readily part with the majority of the integument over large areas of the body begs the question of how and why such loss occurs without obvious detriment to the animal. Clearly, the independent acquisition of fragile skin by several gekkonid lineages suggests that under certain ecological conditions the ability to part with skin may be more valuable than keeping it. Indeed, observations of animals both in the wild and in captivity demonstrate that *Ailuronyx* does employ the facility of skin loss as an antipredator strategy against potential aggressors.

Understanding the evolution of regional integumentary loss requires an appreciation of the cutaneous mechanical properties that facilitate loss and their underlying morphological bases. The morphological specializations that appear to be correlated with skin loss in *Ailuronyx seychellensis* are limited to a number of features that are absent from, or only incipiently developed in, *Gekko gecko*.

One major feature which is present in *G. gecko*, and indeed most gekkonids (Schmidt, 1911, 1912, 1913; Lange, 1931), is the segregation of the stratum compactum of the dermis into physically distinct inner and outer layers. In most geckos these are relatively tightly bound together, while in *Ailuronyx* (see above) and *Geckolepis* (Schmidt, 1911, plate 25, fig. 18; Schubert & Christophers, 1985, figs 2, 3) these two layers are much less intimately interconnected. This loose connection provides a zone for slippage between the two layers of the dermis and, as a result, the outermost layers of the skin are mechanically independent of the deep layer of the dermis. In *Gekko gecko* the deep layer of the stratum compactum is only loosely bound to the underlying body wall muscles (Maderson *et al.* 1978a), while in *Ailuronyx* this association is much firmer. The more definitive subdivision of the integument into two units in *Ailuronyx* is reflected in the differing mechanical properties of each considered separately (see above) and in the emergent properties (O'Grady, 1984) of the whole skin (Fig. 4).

The inherent fragility of the outer integumentary complex is a result of interruption of the collagenous network of the stratum compactum by intervening cones of parenchymatous cells (Fig. 11A). The reduced number of collagenous fibres per unit area in these zones of weakness results in stress concentrations in the region of the large tubercles and failure occurs under relatively low tensile loading. Such zones of weakness are not uncommon in reptilian integuments, but are generally more restricted in their distribution. In particular, they are found in caudal autotomy planes (Schmidt, 1912; Woodland, 1920; Ali, 1950; Werner, 1967; Sheppard & Bellairs, 1972; Bellairs & Bryant, 1985) and in association with the exit points for defensive secretion in the tail-squirting geckos of the genus *Diplodactylus* (Rosenberg & Russell, 1980).

The relative strengths of the inner and outer integumentary units are a function not only of their gross morphological architecture, however, but also of the collagen fibre orientation and continuity. The thicker outer collagen fibres (40–60  $\mu\text{m}$  in diameter) are oriented at about 90° to the body long axis, with

thinner fibres being oriented at about  $0^\circ$ . If the thicker fibres were continuous they would reinforce the integument transversely. They are, however, interrupted within each of the large tubercles, thus providing only localized areas of significant bracing. Imposed loads result in failure at the zones of weakness and give rise to an integument that is both weak and fragile.

The criss-cross arrays exhibited by the inner layer (mean angle of  $55^\circ$  to the body long axis, Fig. 6) indicate that, as tested, considerable reorientation of fibres took place before they became aligned along the direction of applied loading, although this was not measured. The observed fibre angle of  $55^\circ$  in *Ailuronyx* approximates but does not match exactly the idealized fibre angle of  $60^\circ$  predicted by Alexander (1987), probably because the body cross-section is not circular. Fibre angles of  $45^\circ$ ,  $55^\circ$  and  $60^\circ$  occur frequently in animal integumentary collagens and the significance of these angles has been interpreted through a number of functional models. These, however, are primarily locomotory models (Clark & Cowey, 1958; Wainwright *et al.* 1976; Alexander, 1987) and are most applicable to aquatic animals that utilize the skin as a primary or secondary locomotory aid. The significance of specific fibre angles to function in *Ailuronyx* or other terrestrial vertebrates is probably more directly associated with skin extensibility or other non-locomotor functions.

In *Ailuronyx* the general properties of the integument associated with mechanical protection have been forsaken in favour of escape from potential predators. This has implications for the survival of the individual; while mechanical strength of the outer component of the skin is permanently reduced, upon loss the osmoregulatory properties of the integument (Maderson *et al.* 1978b; Landmann, 1985; Lillywhite & Maderson, 1982) are also temporarily compromised, at least until regeneration is complete. This impairment of function is due to the loss of the keratinized epidermis (Maderson *et al.* 1978b) and not to the reduction of the outer layer of the dermis (Licht & Bennett, 1972).

The mechanical properties of *Ailuronyx* skin represent one end of a continuum which also includes many species characterized by more 'typical' cutaneous attributes (Table 2). The 19 taxa examined in this study may be roughly segregated into two clusters, although absolute distinction between them is not possible. These clusters are demarcated on the basis of the mechanical properties of their skin, with group A representing forms with weak skin and group B forms with tougher skin (Table 2). Group A includes several species for which regional integumentary loss is well documented – *Ailuronyx seychellensis*, *Geckolepis typica* and *Teratoscincus scincus*. We believe that the mechanism of skin fracture is similar in all three taxa. The latter two species, however, differ from *Ailuronyx* in possessing large, flattened, imbricating scales. Anderson (1972) suggested that such scutellation might be easily cast off while retaining some underlying cutaneous tissue as a protective barrier. Schubert & Christophers (1985), however, claimed that all components of the integument were lost in the affected areas in *Geckolepis*. This interpretation is not consistent with the implications of the morphological (Schmidt, 1911) or behavioural (Meier, 1980) investigations of

earlier workers. Further, the loss of the entire integument over a broad area with no negative consequences is seemingly incompatible with the normal operation of the immune system, given the reasonably long period (2 months or more, McKeown & Miller, 1985) required for regeneration of the skin from the wound edges. Indeed, our interpretation of the light micrographs of Schubert & Christophers (1985) is that separation of the outer layers of skin occurs at the border of the lower layer of the stratum compactum with the overlying loose connective tissue, or perhaps within the lower zone itself.

Also included in group A are species such as *Aristelliger praesignis* and *Phelsuma madagascariensis* for which skin loss has been reported, and *Pachydactylus bibronii*, a closely related congener of a known fragile-skinned form. The remainder of the species in this group do not exhibit this antipredator defence (A. M. Bauer, personal observation), but in these forms the weakness of the skin is largely irrelevant in a functional context if the integument is a unitary structure, itself bound tightly to the underlying body wall.

For the most part, the geckos in group B, as would be predicted by the high tensile strength of their skin, do not exhibit fragile skin in life. Among the taxa included, only *Thecadactylus rapicauda* has been reported to display regional integumentary loss. However, this property is confined to certain insular forms (R. I. Crombie & T. J. Papenfuss, personal communication), and our specimen is from a mainland population (Rio Santiago, Amazonas, Peru). Two of the 19 taxa show strength and toughness values that are marginally incongruent, but these do not greatly disrupt the overall emergent pattern.

Relatively little is known about the biomechanical properties of reptilian skin, but what is known does not differ in any major way from the basic values obtained from the whole skin of *Gekko* or from the inner layer of *Ailuronyx* skin. In a comparative overview of the mechanics of snake skin, Jayne (1988) found that the typical stress-strain curve was J-shaped, the elastic modulus generally varied from 15 to 250 MPa and the tensile strength ranged from 5 to 80 MPa. Comparative data for gekkonid species that do not have fragile skins accord well with this general picture (Table 2).

The known details of the structure of reptile skin differ significantly in some respects from those of mammals. For example, elastin fibres play an important role in mammalian skin mechanics, but their distribution, relationships and functions are only poorly understood in reptiles (Lange, 1931; Pockrandt, 1937). In mammals, collagen forms a two-dimensional network of coiled fibres, often associated with elastin cores (Serafini-Fracassini *et al.* 1975), with elastin being the primary agent of recoil at low loads, while collagen provides high stiffness at larger extensions (Oxlund *et al.* 1988). The composite structure yields J-shaped stress-strain curves and tensile properties similar to those of reptiles. In the rat, the skin has a toughness of approximately  $15 \text{ kJ m}^{-2}$ , and an elastic modulus of about 10 MPa (Purslow, 1983). The tensile strength of cat skin is approximately 12 MPa (Wainwright *et al.* 1976).

Comparative study of gekkonid skin reveals two key innovations (the mechan-

ical independence of the outer region of the integument, and inclusion in that area of preformed zones of weakness) that are co-opted into exaptive systems (Gould & Vrba, 1982) and permit regional integumentary loss in *Ailuronyx* and perhaps other forms with fragile integuments. Thus, in *Ailuronyx* only the mechanical behaviour of outer components of the skin (epidermis, stratum laxum and the outer layer of the stratum compactum) is of significance in the context of naturally occurring predator-prey interactions. Likewise, measurements of whole skin mechanics of other species, perhaps including weak-skinned taxa from group A (Table 2) that do not lose the skin in nature, may be irrelevant in the context of the skin-loss defence strategy. Weak skin bound firmly to a strong and stiff backing, such as the body wall musculature, will not facilitate regional integumentary loss. Our data on gecko skin mechanics serve to highlight Wainwright's warning (1988) that mechanical 'properties must be seen in the context of natural history of the species being studied' if 'the properties are to relate structure and function to larger issues of ecology, behavior, and evolution'.

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