Skin mechanics and morphology of two species of *Pachydactylus* (Reptilia: Gekkonidae)

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Received 17 November 1992; accepted 21 May 1993

The southern African species *Pachydactylus namaquensis* is one of only a few mainland species of geckos that exhibits the escape strategy of regional integumentary loss. The skin morphology and mechanics of this species were compared to the same parameters in the sympatric congener *P. bibronii*. The tensile strength and modulus of elasticity of the skin of both species fall in the middle range of values for geckos as a whole. Skin of *P. namaquensis*, however, has approximately half of the tensile strength of that of *P. bibronii*. As in other skin-losing forms, the morphological basis for weakness lies in the bilayering of the dermis and the presence of zones of weakness within the upper layer of the dermis. Field experience suggests that *P. namaquensis* does not lose the skin as easily as most geckos exhibiting regional integumentary loss. In this species this escape strategy has probably evolved in response to the prey subjugation mode employed by rock-dwelling lizard predators.

Pachydactylus namaquensis van suidelike Afrika is een van slegs 'n paar vasteland-geitjies wat die ontsnappingstrategie van regionale velverlies vertoon. Die morfologie en meganika van die vel van hierdie spesie is vergelyk met die van *P. bibronii*, 'n simpatriese lid van dieselfde genus. Die spansterkte en modulus van elastisiteit van die vel van albei spesies val in die middelgebied van waardes vir geitjies in geheel. Die vel van *P. namaquensis* het ongeveer die helfte van die spansterkte van dié van *P. bibronii*. Net soos in ander vorme wat die vel verloor, is die morfologiese basis vir swakheid gelee in die tweelagigheid van die dermis en die aanwesigheid van sones van swakheid in die boonste laag van die dermis. Ondervinding in die veld dui daarop dat *P. namaquensis* nie so maklik die vel verloor soos ander geitjies wat regionale velverlies toon nie. In hierdie spesies het hierdie ontsnappingstrategie waarskynlik ontwikkel in reaksie op prooi-onderwerpingsmetodes wat deur rotsbewonende akkedisvreters gebruik word.

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Regional integumentary loss is an escape strategy practised by a wide variety of gekkonine and sphaerodactyline geckos (Bauer, Russell & Shadwick 1989, 1992; Bauer & Russell 1992) and by at least some representatives of the family Scincidae (Mertens 1960; Greer 1986). Lizards utilizing this means of defence 'permit' the loss of portions of their skin to attackers in order to effect escape, in a manner somewhat analogous to the shedding of the tail in caudal autotomy. Skin loss is facilitated by the architecture of the dermis, which is characterized by a discontinuity of collagen fibers within the stratum compactum of the dermis and the presence of preformed zones of weakness within that portion of the dermis superficial to the discontinuity (Bauer *et al.* 1989, 1992). At least in some geckos, the main resting alignment of collagen fibers is perpendicular to the body long axis and further serves to weaken the skin with respect to tensile stresses applied longitudinally (Bauer *et al.* 1989). As a result of these properties, integumentary damage results in the loss of the skin external to the dermal discontinuity (all of the epidermis and approximately 90% of the dermis) at the wound site. A thin layer of the stratum compactum, which has a higher tensile strength than the overlying tissues, remains intact and apparently serves as a barrier to water loss, infection and solar radiation (Bauer *et al.* 1989).

The high incidence of healed wounds in wild-caught lizards indicates that this strategy is employed extensively in natural populations (Bauer *et al.* 1989). Skin loss may be the result of either predatory or intraspecific encounters (McKeown & Miller 1985), and appears to be dependent on the application of tensile or shear stress on the skin by external agents. Schubert & Christophers (1985) and Schubert, Steffen & Christophers (1990), however, have identified myofibroblasts in transmission electron micrographs of the dermis of the Madagascan gekkonine gecko *Geckolepis typica*, and have postulated that the mechanism of skin fracture involves an endogenously regulated rupture of the skin.

The phenomenon of regional integumentary loss has evolved a minimum of eight times among gekkonid lizards (Bauer & Russell 1992), although the precise number of independent derivations is uncertain, owing to poor resolution in the phylogeny of gekkonine geckos. Most of the originations of regional integumentary loss have occurred in lineages that are principally insular in their distribution. This has been related to the mode of prey subjugation employed by island *versus* mainland predators (Bauer & Russell 1992). Guilds of saurophagous predators on islands where skin-losing geckos occur are dominated by snakes (West Indies), primates (Madagascar) and non-raptorial birds (Seychelles, Micronesia). In comparison with carnivores and raptors, which usually deliver a killing bite or puncture to prey items during the subjugation phase of prey capture, these predators typically have extensive handling times during which the prey is pinned or held before being killed. Under such circumstances, regional integumentary loss may have a selective advantage (Bauer & Russell 1992). Similar selective pressures may exist in mainland habitats where lizards are preyed upon primarily by snakes or arthropods (Bauer *et al.* 1992; Bauer & Russell 1992).

In southern Africa, skin weakness has been reported anecdotally in only two species, both representatives of the genus *Pachydactylus*. *P. scutatus*, endemic to north-western Namibia and adjacent Angola, has large imbricating scales, and integumentary loss is probably the result of dermal zones of weakness occurring in the hinge regions at the base of the scales, as has been demonstrated in the Puerto Rican *Sphaerodactylus roosevelti* (Bauer *et al.* 1992). *P. namaquensis*, distributed from the Cape Fold Mountains north to southern Namibia, has been widely reported as a skin loser (FitzSimons 1943; Greene 1988; R.B. Huey, pers. comm.). However, this species lacks the scale morphologies typical of the other geckos capable of regional integumentary loss that have thus far been investigated. Furthermore, personal field experience with this species suggests that skin loss is not as easily or as often initiated as in many other skin-losing taxa. In this paper we examine the morphological basis for regional integumentary loss in this species and present biomechanical data on skin strength in *P. namaquensis* with respect to its sympatric and syntopic congener *P. bibronii*, and with respect to other species of fragile-skinned geckos.

Materials and Methods

Pachydactylus namaquensis and *P. bibronii* were collected in rocky habitat at Anysberg Nature Reserve, Cape Province, South Africa (33°44'S / 20°27'E) on 19 October 1991. These specimens have been deposited in the collection of the California Academy of Sciences, San Francisco. Four specimens of each species were euthanized by injection with pentobarbitol and their skin removed and placed in reptilian Ringer's solution (Rogers 1938). Width and length of each sample was measured with vernier calipers between the clamps of the tensometer. Mechanical testing was carried out on a Monsanto T10 tensometer and samples were stretched at a rate of 20 mm min^{-1}, giving strain rates of 0,02–0,04 s^{-1}. Force *versus* displacement was recorded on an x,y plotter and normalized into stress (σ = force per cross-sectional area) measured in pascals (1 Pa = 1 N m^{-2}) and strain (ϵ = the increment in length divided by the initial length), a unitless quantity. Loading was applied to samples of both dorsal and ventral skin in a longitudinal direction only. Bauer *et al.* (1989) demonstrated that strength in this direction was minimal and that it corresponded to naturally occurring wound orientations in another skin-losing species, *Ailuronyx seychellensis*. Samples were stretched to their break point and the values for failure strain (ϵ_f) and tensile strength (σ_m) were determined. The modulus of elasticity (E), a value representing the material stiffness, was determined as the tangent modulus of the linear portion of the stress–strain curve. Toughness (W) is the work necessary to break a unit volume of material and is expressed in J m^{-3} (joules per cubic meter), and is equal to the area under the stress–strain curve. Manual separation of the lower dermis of *P. namaquensis* from the more superficial dermis and epidermis was possible for one sample, and the inner dermis alone was subjected to mechanical testing.

Following mechanical testing, specimens were fixed in 10% neutral buffered formalin, decalcified, embedded in paraffin, and sectioned at 8–10 μm on a rotary microtome. In order to prevent distortion of the skin, sections included underlying body wall musculature. Sections were stained with haematoxylin and eosin, Mallory's and Mason's trichromes and Verhoeff's elastin stain (Humason 1979). Photomicrographs were taken on a Nikon Optiphot microscope. Measurements for skin thickness, necessary for the standardization of mechanical data, were obtained from these sections using ocular and stage micrometers. The mean skin thickness values reported (Table 1) are the average of measurements of 20 sections. Whole skin thicknesses were measured from the base of the dermis to the outer surface of the epidermis in the hinge region of dorsal body scales.

Figure 1 Freshly wounded *Pachydactylus namaquensis* from the Richtersveld National Park showing the extensive (but not exceptional) integumentary damage (arrows). The exposed areas remain covered by a thin portion of the lower dermis.

Results

Mechanical testing

The skin of both species of *Pachydactylus* was found to be weak, although that of *P. namaquensis* had only about one-third to one-half of the strength of that of *P. bibronii*. In all samples of the former species, failure occurred within the larger tubercles while in the latter fracture occurred at the periphery of enlarged tubercles. Force–length load curves for *P. bibronii* were characterized by a steadily increasing slope up to the point of failure, followed by a sudden drop in force to zero, or a more gradual drop in force over a length change equal to or slightly greater than that of initial extension. Similar force–length curves typified *P. namaquensis*, although in no instance was there an abrupt catastrophic failure of the skin as reflected by a sudden drop to

Table 1 Mechanical properties of the skin of *Pachydactylus namaquensis, P. bibronii* and representative weak- (*Ailuronyx, Sphaerodactylus*) and normal-skinned (*Gekko*) geckos (data for *Pachydactylus* spp. from this study, data for other taxa from Bauer *et al.* 1989, 1992)

Species	Skin thickness (mm)	Failure strain ϵ_f	Failure stress σ_m (MPa)	Modulus E (MPa)	Toughness W (MJ m^{-3})
Pachydactylus namaquensis					
dorsal skin (whole)					
n = 7	0,145	0,54	0,74	2,55	0,14
(SD)		(0,13)	(0,25)	(0,42)	(0,08)
dorsal skin (inner layer)					
n = 1	0,018	0,48	2,30	15,80	0,33
ventral skin (whole)					
n = 8	0,190	0,50	0,58	2,40	0,09
(SD)		(0,10)	(0,15)	(0,49)	(0,05)
Pachydactylus bibronii					
dorsal skin					
n = 4	0,200	0,60	1,27	5,24	0,44
(SD)		(0,33)	(0,37)	(3,70)	(0,26)
ventral skin					
n = 5	0,151	0,45	1,84	8,50	0,37
(SD)		(0,18)	(0,47)	(4,30)	(0,14)
Sphaerodactylus roosevelti					
whole skin					
n = 4	0,122	0,38	0,19	0,58	0,04
inner layer					
n = 1	0,005	0,61	4,82	20,30	-
outer layer					
n = 1	0,117	0,44	0,16	0,42	0,06
Ailuronyx seychellensis					
whole skin					
n = 8	0,36	0,31	1,28	7,20	0,27
inner layer					
n = 6	0,02	0,85	21,0	52	6,5
outer layer					
n = 6	0,30	0,29	0,9	4,6	0,13
Gekko gecko					
whole skin					
n = 10	0,22	0,57	11,5	42	2,4

force zero. The inner dermis of this species, tested alone, yielded a similar curve, with a gradual return to zero. When converted to stress–strain relationships the linear portion of the stress–strain curve for *P. bibronii* possesses a much higher slope (i.e. modulus of elasticity) than that of *P. namaquensis* (Figure 2), although the inner skin of the latter yields a modulus of elasticity that is much higher still. Failure strain (ϵ_f) for dorsal and ventral skin averaged 0,54 ± 0,042 and 0,50 ± 0,10, and 0,60 ± 0,33 and 0,45 ± 0,18 for *P. namaquensis* and *P. bibronii*, respectively. Tensile strength (σ_m) averaged 0,74 ± 0,25 MPa and 0,58 ± 0,15 MPa, and 1,27 ± 0,37 MPa and 1,84 ± 0,47 MPa for the whole skin samples. The modulus of elasticity (E) was also very low, with mean values of 2,55 ± 0,42 MPa and 2,40 ± 0,49 MPa for dorsal and ventral skin of *P. namaquensis* and 5,24 ± 3,7 MPa and 8,50 ± 4,3 MPa for comparable samples of *P. bibronii* (Table 1).

When considered separately, there was a drastic difference between the performance of inner dermis and the skin of *P. namaquensis* as a whole. The inner layer comprises approximately 12% of the total skin thickness (Table 1). Its failure strain was slightly lower than that of whole skin (0,48). Tensile strength, however, was 2,30 MPa, more than three times greater than that of the whole skin. The modulus of elasticity was 15,80 MPa, also considerably higher than that of the whole skin. Toughness of *P. namaquensis* dorsal and ventral whole skin averaged 0,14 ± 0,08 MJ m^{-3} and 0,09 ± 0,05 MJ m^{-3} and 0,33 MJ m^{-3} for the inner dermis alone. Values for *P. bibronii* were 0,44 ± 0,26 and 0,37 ± 0,14 MJ m^{-3}.

Histology

The morphological basis for skin fracture in *Pachydactylus namaquensis* lies within the vacuolated tissue in the enlarged tubercles of the dorsum (Figure 3C) and the imbricating plates of the ventrum (Figure 3B). The collagen fibres of the stratum compactum are discontinuous at points within the tubercles where extensions of the vacuolated tissue project toward the inner dermis (Figure 3D). In freshly wounded individuals, skin rupture can be seen to have occurred at such intra-tubercular discontinuities (Figure 3E). As in other skin-losing geckos examined to date, the deepest layer of the dermis is separated from the upper region (and the epidermis) by a gap filled with loose connective tissue. Another, more dense aggregation of connective tissue binds the deep dermis to the underlying somatic musculature.

Individual scales of *Pachydactylus namaquensis* are variable in size and consist of rounded, flattened tubercles interspersed among granular scales. The epidermal layer is quite thin. Most of the dermis is composed of collagen fibres oriented parallel to the body surface (as determined by histology rather than polarizing light analysis; Figure 3). Staining revealed the presence of only small amounts of elastin. Near the dermal–epidermal interface the fibre directions become less uniform and the dermis has a woven appearance. Total dermal thickness is minimal in the regions between scales, but these areas do not exhibit discontinuities in the outer dermal layer. Only a narrow gap filled with loose connective tissue separates the epidermis/outer dermis complex from a thin inner layer of parallel-fibred collagen that constitutes the 'inner dermis' (*sensu* Bauer *et al.*. 1989). This inner dermis is unbroken and unsegmented, even below the regions of outer dermal discontinuity.

The skin of *P. bibronii* likewise illustrates a dermal splitting into inner and outer zones. However, the large, pointed tubercles of this species contain largely solid masses of connective tissue that are firmly attached to the adjacent collagen fibres and there is no evidence of any preformed zones of weakness (Figure 3A). Comparable tubercular morphology has been demonstrated histologically in the Mediterranean gekkonine species, *Tarentola mauritanica* (Schmidt 1912).

Discussion

The strength of the entire skin of both species of *Pachydactylus* falls in the middle range of that of other geckos thus far tested (Table 1). Strength, stiffness, and for

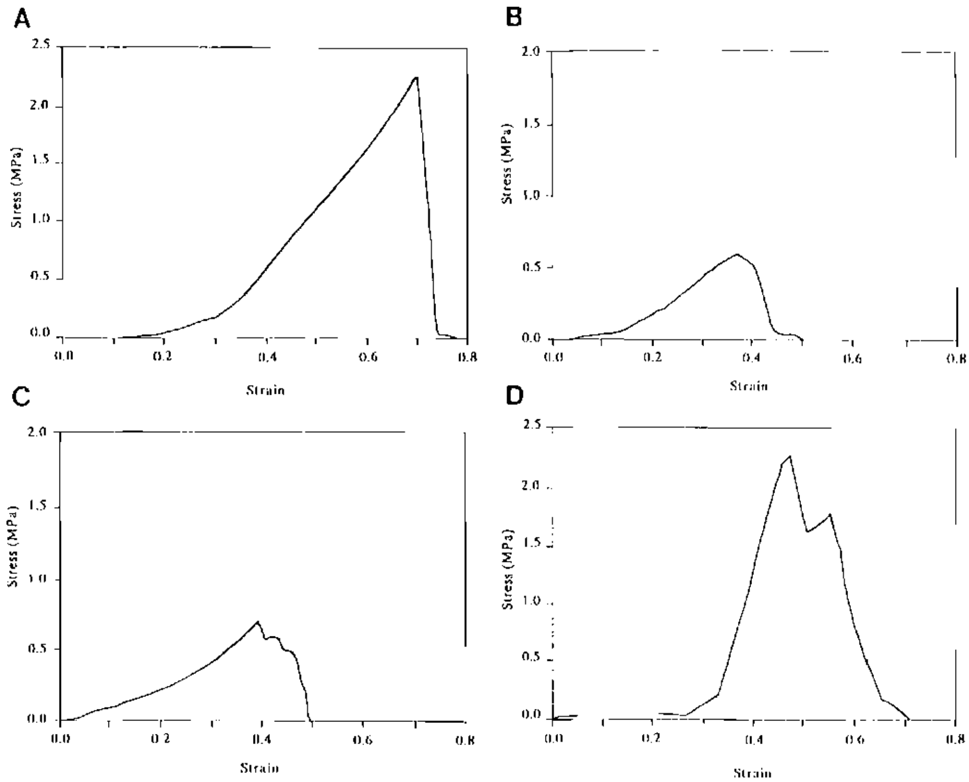

Figure 2 Representative stress–strain curves of (A) ventral whole skin of *Pachydactylus bibronii*, (B) ventral whole skin of *P. namaquensis*, (C) dorsal whole skin of *P. namaquensis* and (D) dorsal inner dermis of *P. namaquensis*.

P. bibronii, toughness, are significantly greater than for *Sphaerodactylus roosevelti* (Bauer *et al.* 1992). These parameters are significantly lower than those for *Gekko gecko* and other species regarded as non-fragile-skinned (Bauer *et al.* 1989). Dorsal skin of *P. bibronii* has similar tensile strength to that of *Ailuronyx seychellensis* (Bauer *et al.* 1989). However, the measurements of the latter were made on preserved skin rather than fresh tissue, and the significance of the use of fresh *versus* preserved gecko skin in material testing remains uncertain. Bauer *et al.* 1992) found that the fresh skin of the Puerto Rican species *Sphaerodactylus roosevelti* was considerably weaker than any of the formalin-fixed skins previously tested (Bauer *et al.* 1989). This result is predictable, but is confused by the findings that there were not appreciable mechanical differences between fresh and preserved skin of the tokay, *Gekko gecko* (Bauer *et al.* 1989). The similarity may be attributable to the planar arrangement of the collagen fibres in reptile skin (Lange 1931; Meyer, Bartels & Neurand 1989) and the paucity of elastin in geckos and other reptiles, as evidenced both empirically by histology and inferentially by the more nearly linear stress-strain curve of geckos in comparison with that of mammals (Veronda & Westmann 1970). The effect of fixation may be more pronounced in taxa with weak skin than in those (like *G. gecko*) with an integument of high tensile strength. That fixation is significant in this case is supported by the comparison of fresh *P. bibronii* skin with that of preserved material as reported by Bauer *et al.* 1989). In the preserved material tensile strength was recorded as 7,3 MPa and the modulus (E) as 23,7 MPa, or approximately six and 4,5 times the respective values for fresh material. On this basis it would appear that the skin of this species is moderately weak, but far stronger, stiffer and tougher than those species which are known to utilize regional integumentary loss as an escape strategy.

The relatively small difference between the strength and stiffness of the skin of *Pachydactylus namaquensis*, a skin-loser, and *P. bibronii*, which does not exhibit this strategy, is somewhat surprising. However, the mechanical parameters of the whole skin reflect the combination of those of its functional components, the inner dermis and the outer dermis plus epidermis. The strength of the inner dermis of *P. namaquensis*, and especially its stiffness, are high relative to those of *P. bibronii* whole skin, and the toughnesses of the two are comparable. Because of the relative thickness of the inner dermis in *P. namaquensis* (> 12% *vs* 4% in *Sphaerodactylus roosevelti* and 6% in *Ailuronyx seychellensis*) the contribution of this layer to whole skin values is especially significant. The biologically significant comparison is actually between the outer skin of the skin-losing species and the entire skin of the typical species, the respective mechanical units that are impinged upon by externally applied loads. Unfortunately the outer skin of *P. namaquensis* could not be isolated intact because of its absolute thinness and relative weakness. The high mechanical parameter values of the inner dermis are typical of all other skin-losing geckos studied thus far (Bauer *et al.* 1989, 1992).

The mechanisms of skin shedding seen in all geckos examined to date are dependent on the presence of a discontinuity within the stratum compactum and the existence of

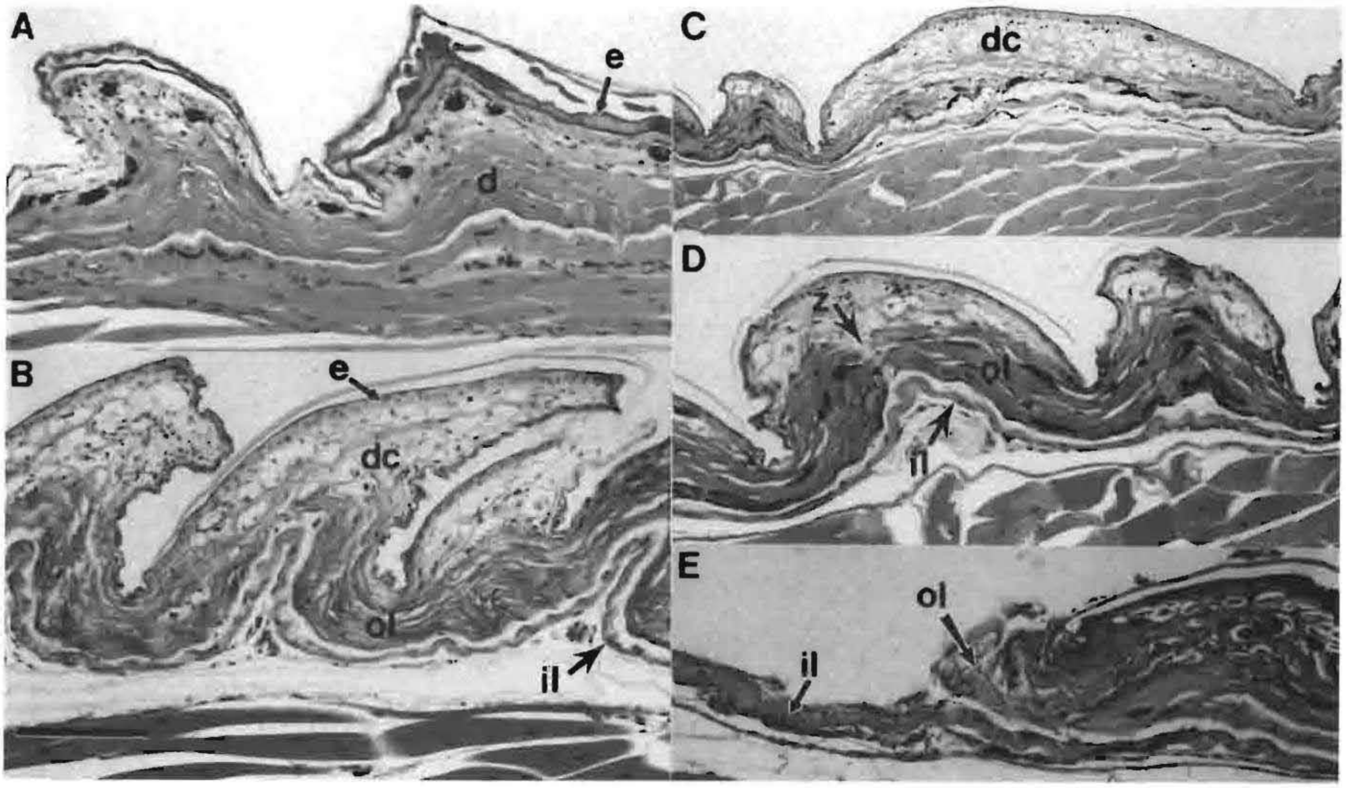

Figure 3 Histological sections through the skin of *Pachydactylus bibronii* and *P. namaquensis*. All sections stained with hematoxylin and eosin. (A) Dorsal skin of *P. bibronii* illustrating the compact core of tubercles. (B) Ventral and (C) dorsal skin of *P. namaquensis* illustrating the vacuolated tissue of tubercles and the bilayering of the stratum compactum. (D) Detail of a small dorsal tubercle of *P. namaquensis* showning the zone of weakness formed by the collagen discontinuity in the outer dermal layer. (E) Freshly fractured skin of *Pachydactylus namaquensis* illustrating the retention of the inner layer of dermis and the point at which mechanical failure has occurred. Abbreviations: d = dermis, dc = vacuolated dermal core of tubercle, e = epidermis, il = inner layer of stratum compactum of dermis, ol = outer layer of stratum compactum of dermis, z = zone of weakness in outer layer of stratum compactum. Scale bar (at lower left of B) = 125 μm (except for C, where the same unit = 250 μm).

preformed zones of weakness in the outer layer of the dermis. At least two different scale architectures produce the required breaks in the outer dermis. The imbricating dorsal scales of *Sphaerodactylus roosevelti*, and probably other geckos capable of regional integumentary loss (Bauer *et al.* 1992), exhibit zones of weakness or collagen discontinuities in the hinge regions of the scales. The zones of weakness in the skin of *Pachydactylus namaquensis* lie in the vacuolated tubercles of the dorsum and thickened ventral scales. This is similar to the condition seen in *Ailuronyx seychellensis*, although the tubercles of this species are much larger and more conspicuous than those of most *Pachydactylus*. In *P. bibronii* there are no discontinuities within the tubercles, which are filled with dense connective tissue. Rather, the thinnest point in the collagen matrix of the dermis lies at the edges of the tubercles, and it is there that fracture occurs under test conditions.

The essential differences between the morphological mechanisms of regional integumentary loss among geckos is a reflection of the independent origin of this strategy in several lineages. A review of the taxa known to utilize the strategy reveals a minimum of eight origins among gekkonine geckos (Bauer & Russell 1992). Even within *Pachydactylus*, two independent origins are implicated, one dependent on tubercular scale morphology in *P. namaquensis*, and another utilizing the hinge regions of imbricating scales in *P. scutatus* (Bauer & Russell 1992).

The evolution of regional integumentary loss in geckos in general has been related to the subjugation mode of the predators encountered. On the basis of the fact that most skin-losing lineages are island forms, Bauer & Russell (1992) have hypothesized that the strategy has evolved in response to features of prey subjugation that are most common in insular predators, the pinning or immobilization of prey prior to the delivery of a killing puncture. The hypothesis is difficult to assess on the basis of field data, but if it is correct, mainland geckos exhibiting regional integumentary loss require some special explanation. In the case of some very small geckos, such as the New World sphaerodactylines, in which mainland as well as insular forms have fragile skin (Hoogmoed 1973; Bauer *et al.* 1992), some of the most likely predators are arthropods (Bauer 1990). These would be expected to require fairly lengthy handling times when preying upon small vertebrates and would normally require immobilization of the prey by legs or mouthparts before a killing wound or injection could be delivered. In the case of *Pachydactylus namaquensis* no predators have been recorded in the literature. However, the typical retreat of these lizards in rock crevices suggests that snakes are likely predators. Many saurophagous colubrid snakes typically pin their prey with parts of their body before ingestion (Jones & Whitford 1989) and thus provide an opportunity for skin-losing lizards to escape. In comparison with some other geckos employing the mechanism, *P. namaquensis* does not part as readily with its integument (pers. obs., AMB). This may be due, in part, to the reliance on alternative modes of non-mutilatory defence, such as biting and vocalization, which are ably employed by this species. Alternatively, the relatively weak expression of regional integumentary loss in this gecko may be an exaptation, the fortuitous byproduct of unrelated selective pressures favouring the vacuolated tubercular morphology of the dermis.

Acknowledgements

We thank the Chief Directorate Nature and Environmental Conservation, Cape Province, for permission to collect the specimens used in this study. This project was completed while the senior author was supported by the John R. Ellerman Scholarship in Zoology at the University of Stellenbosch. Data collection was supported by Villanova University (AMB) and NSERC grant OGP0009745 (APR). S.F. Milone coordinated much of the laboratory work and W.R. Branch and M. Burger made the field work possible. P. le F. N. Mouton kindly prepared the Afrikaans abstract.

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