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Broeckhoven et al. Electronic Supplementary Material

On dangerous ground: the evolution of body armour in cordyline lizards

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Supplementary Methods 1. Calculation of predation risk.

A list was compiled of all South African snake species (with the exception of Typhlopidae, blind snakes), small to medium-sized carnivoran mammals, and actively hunting birds (birds-of-prey including owls, and corvids) (Table S1). Next, an extensive literature study [1-7] was conducted to compile a dataset of information on the four most important ecological traits that pertain to predation risk. These included diet, activity time, hunting method and habitat use of the predator. A score was assigned to each of these traits based on the risk it poses for cordyline lizards (Table S2).

Diet: Predators were scored based on the importance of lizards in their diet and classified in three dietary groups: (1) prey exclusively on lizards, (2) have a generalist diet including lizards and (3) do not prey on lizards. To illustrate, predators that specialise in lizards were assigned a score of 1 (= high risk), whereas those that do not prey on lizards were assigned a score of 0 (= no risk). Generalist species were assigned a score of 0.5 (= intermediate risk)

Activity time: A score was assigned based on the overlap in activity time between predators and cordyline lizards. Cathemeral species have random intervals of activity, approximately evenly distributed during both day and night, and pose an intermediate risk. Nocturnal and crepuscular species do not strictly adhere to given ecological definitions but are sporadically seen active during daytime and consequently still pose a small risk. Non-diurnal snakes were given a higher score because, unlike mammals and birds-of-prey, they have access to inactive lizards sheltering in their crevices.

Habitat use: A score was calculated based on the overlap in habitat use. Aquatic, fossorial and arboreal predators generally do not encounter cordyline lizards. However, sporadic movements to more terrestrial habitats might occur and therefore they still pose a small risk. Predators that occur across a variety of habitats have a much higher chance of encountering cordyline lizards. Exclusively terrestrial predators will pose the highest risk and were given the highest score.

Hunting strategy: A score was assigned based on the hunting strategy of the predator. In snakes, active foragers have a higher chance of locating prey compared to sit-and-wait foragers. In mammals, species that forage alone or in pairs will pose a similar predation risk, whereas those that forage in larger groups have an increased probability of finding prey. In predatory birds we discriminated between several hunting strategies. Scavengers feed on dead animals, posing little risk for living cordyline lizards. Birds that capture prey in flight, including swooping down and grabbing terrestrial prey in flight, pose less of a threat than birds that capture their prey solely on the ground. The latter therefore pose the highest risk. Birds that make use of both hunting methods will still pose a high risk, but not as high as birds that exclusively prey on the ground.

Table S1. List of predator species used to calculate predation risk/pressure

Snakes		Mammals		Birds	
Family	**Species**	**Family**	**Species**	**Family**	**Species**
Pythonidae	*Python natalensis*	Felidae	*Caracal caracal*	Pandioninae	*Pandion haliaetus*
Viperidae	*Bitis albanica*		*Felis silvestris lybica*	Accipitrinae	*Aviceda cuculoides*
	Bitis arietans		*Felis nigripes*		*Pernis apivorus*
	Bitis armata		*Leptailurus serval*		*Macheiramphus alcinus*
	Bitis atropos	Viverridae	*Civettictis civetta*		*Elanus caeruleus*
	Bitis caudalis		*Genetta genetta*		*Milvus migrans*
	Bitis cornuta		*Genetta tigrina*		*Haliaeetus vocifer*
	Bitis gabonica		*Genetta maculata*		*Gypohierax angolensis*
	Bitis inornata	Herpestidae	*Suricata suricatta*		*Gypaetus barbatus*
	Bitis rubida		*Paracynictis selousi*		*Neophron percnopterus*
	Bitis schneideri		*Cynictis penicillata*		*Necrosyrtes monachus*
	Bitis xeropaga		*Herpestes ichneumon*		*Gyps africanus*
	Causus defilippii		*Galerella sanguinea*		*Gyps coprotheres*
	Causus rhombeatus		*Galerella pulverulenta*		*Gyps rueppellii*
Lamprophiidae	*Amblyodipsas concolor*		*Rhynchogale melleri*		*Aegypius tracheliotus*
	Amblyodipsas microphthalma		*Ichneumia albicauda*		*Aegypius occipitalis*
	Amblyodipsas polylepis		*Atilax paludinosus*		*Circaetus pectoralis*
	Amplorhinus multimaculatus		*Mungos mungo*		*Circaetus cinereus*
	Aparallactus capensis		*Helogale parvula*		*Circaetus fasciolatus*
	Aparallactus lunatus lunatus	Canidae	*Otocyon megalotis*		*Terathopius ecaudatus*
	Atractaspis bibronii		*Vulpes chama*		*Polyboroides typus*
	Atractaspis duerdeni		*Canis adustus*		*Circus maurus*
	Boaedon capensis		*Canis mesomelas*		*Circus macrourus*
	Dipsina multimaculata	Mustelidae	*Mellivora capensis*		*Circus pygargus*
	Duberria lutrix lutrix		*Poecilogale albinucha*		*Circus ranivorus*
	Duberria variegata		*Ictonyx striatus*		*Circus aeruginosus*
	Gonionotophis capensis capensis	Felidae	*Caracal caracal*		*Micronisus gabar*
	Gonionotophis nyassae		*Felis silvestris lybica*		*Melierax metabates*
	Hemirhagerrhis nototaenia		*Felis nigripes*		*Melierax canorus*

Table S1 continued.

	Homoroselaps dorsalis		*Leptailurus serval*		*Accipiter tachiro*
	Homoroselaps lacteus				*Accipiter badius*
	Inyoka swazicus				*Accipiter minullus*
	Lamprophis aurora				*Accipiter ovampensis*
	Lamprophis fiskii				*Accipiter rufiventris*
	Lamprophis fuscus				*Accipiter melanoleucus*
	Lamprophis guttatus				*Kaupifalco monogrammicus*
	Lycodonomorphus inornatus				*Buteo buteo vulpinus*
	Lycodonomorphus laevissimus				*Buteo oreophilus*
	Lycodonomorphus obscuriventris				*Buteo rufinus*
	Lycodonomorphus rufulus				*Buteo rufofuscus*
	Lycophidion capense capense				*Aquila pomarina*
	Lycophidion pygmaeum				*Aquila rapax*
	Lycophidion variegatum				*Aquila nipalensis*
	Macrelaps microlepidotus				*Aquila wahlbergi*
	Montaspis gilvomaculata				*Aquila verreauxii*
	Prosymna bivittata				*Aquila spilogaster*
	Prosymna frontalis				*Hieraaetus pennatus*
	Prosymna janii				*Hieraaetus ayresii*
	Prosymna lineata				*Lophaetus occipitalis*
	Prosymna stuhlmannii				*Stephanoaetus coronatus*
	Prosymna sundevallii				*Polemaetus bellicosus*
	Psammophis angolensis			Sagittariidae	*Sagittarius serpentarius*
	Psammophis brevirostris			Falconidae	*Polihierax semitorquatus*
	Psammophis crucifer				*Falco naumanni*
	Psammophis jallae				*Falco tinnunculus*
	Psammophis leightoni				*Falco rupicoloides*
	Psammophis mossambicus				*Falco dickinsoni*
	Psammophis notostictus				*Falco chicquera*
	Psammophis subtaeniatus				*Falco vespertinus*
	Psammophis trigrammus				*Falco amurensis*
	Psammophylax rhombeatus				*Falco concolor*

Table S1 continued.

	Psammophylax tritaeniatus			*Falco eleonorae*
	Pseudaspis cana			*Falco subbuteo*
	Rhamphiophis rostratus			*Falco cuvierii*
	Xenocalamus bicolor			*Falco biarmicus*
	Xenocalamus sabiensis			*Falco peregrinus*
	Xenocalamus transvaalensis			*Falco fasciinucha*
Elapidae	*Aspidelaps lubricus lubricus*		Tytonidae	*Tyto alba*
	Aspidelaps scutatus			*Tyto capensis*
	Dendroaspis angusticeps		Strigidae	*Asio capensis*
	Dendroaspis polylepis			*Strix woodfordii*
	Elapsoidea boulengeri			*Glaucidium perlatum*
	Elapsoidea sundevallii			*Glaucidium capense*
	Hemachatus haemachatus			*Otus senegalensis*
	Hydrophis platurus			*Ptilopsis granti*
	Naja annulifera			*Bubo lacteus*
	Naja melanoleuca			*Bubo africanus*
	Naja mossambica			*Bubo capensis*
	Naja nigricincta woodi			*Scotopelia peli*
	Naja nivea		Corvidae	*Corvus capensis*
Colubridae	*Crotaphopeltis hotamboeia*			*Corvus albus*
	Dasypeltis inornata			*Corvus albicollis*
	Dasypeltis medici			*Corvus albicollis*
	Dasypeltis scabra			
	Dipsadoboa aulica			
	Dispholidus typus			
	Meizodon semiornatus			
	Philothamnus angolensis			
	Philothamnus hoplogaster			
	Philothamnus natalensis			
	Philothamnus semivariegatus			
	Telescopus beetzii			
	Telescopus semiannulatus			

Table S1 continued.

	Thelotornis capensis capensis		
Natricidae	*Natriciteres olivacea*		
	Natriciteres sylvatica		

Table S2. Summary of the four ecological traits pertaining to predation risk. Each trait is given a score based on the risk it poses for lizards. The scores were assigned to each of the three predator guilds separately. Shaded boxes indicate that these traits were not scored for the respective predator guild.

Ecological trait		**Snakes**	**Birds**	**Mammals**
Diet	No lizards	0	0	0
	Generalist	0.5	0.5	0.5
	Specialist	1	1	1
Activity time	Diurnal	1	1	1
	Nocturnal	0.5	0.25	0.25
	Crepuscular	0.5	0.25	0.25
	Cathemeral	0.75	0.50	0.50
Hunting strategy	Sit-and-wait forager	0.5		
	Active forager	1.0		
	Scavenger		0	
	Captures on ground		1	
	Captures in flight		0.5	
	Mixed		0.9	
	Solitary (pair) hunter			1
	Group hunter			1.5
Habitat use	Aquatic/near water	0.1	0.1	0.1
	Terrestrial	1	1	1
	Fossorial	0.1		
	Arboreal	0.1		
	Mixed	0.9		

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Supplementary Methods 2. Phylogenetic tree.

Partial gene fragments, representing 27 South African species of cordyline lizards, were obtained from three nuclear (PRLR, MYH2, KIF24) and three mitochondrial (12S, 16S, ND2) DNA gene regions [1]. Two platysaurids (i.e., *Platysaurus capensis* and *P. intermedius*), as well as three gerrhosaurids (i.e., *Cordylosaurus subtesselatus*, *Gerrhosaurus nigrolineatus*, and *Matobosaurus validus*) were included as outgroup taxa. Genbank was used to download all sequences, which were subsequently aligned and edited using MEGA v.6 [2]. A substitution model was calculated for each of the protein-coding gene fragments (ND2, PRLR, MYH2, KIF24) for each codon position, whereas a single substitution model was calculated for the each of the non-protein-coding gene fragments (12S and 16S). The Akaike information criterion with correction for sample size (AICc) was therefore implemented using JModeltest [3]. BEAST v. 2.1.3 [4] was used to attain an ultrametric tree with relative divergence times, and we used the models obtained from JModeltest for all six loci, as well as their parameters, to specify the site models in BEAUti. A relaxed lognormal clock model estimating around the clock rate of 1.0 was selected, because we were interested in relative, rather than absolute node ages. The birth-death model was selected as tree prior. A Markov Chain Monte Carlo (MCMC) was run for 20 million generations and the parameters were sampled every 2000 generations. Chain convergence was assessed using Tracer v. 1.6 [5], prior to discarding the first 10% as burn-in using TreeAnnotator v. 2.1.2 [4]. The remaining 9001 trees were summarized as a maximum clade credibility tree. Lastly, we used FigTree v. 1.4 [6] to visualize the resulting tree.

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Table S3. Summary of morphological variables of cordyline lizards used in the study.

Species	**BS**	**Osteoderm expression**			**Spinosity**					
		O_{VOL}	O_{SURF}	O_{THICK}	S_{EAR}	S_{NECK}	S_{TRUNK}	S_{FLEG}	S_{HLEG}	S_{TAIL}
Cordylus aridus	47.32	12.07	117.18	0.11	1.14	2.12	2.00	1.88	1.98	3.78
Cordylus minor	50.26	15.90	136.15	0.15	1.22	2.37	2.28	2.05	2.32	3.89
Cordylus imkeae	43.89	10.79	112.07	0.10	1.09	1.71	2.19	1.70	1.81	3.38
Cordylus mclachlani	50.68	13.79	125.72	0.13	1.28	2.22	2.52	2.42	2.40	4.23
Cordylus macropholis	53.67	22.07	148.20	0.25	1.49	2.19	3.47	1.89	2.05	3.82
Cordylus cordylus	55.13	14.97	110.84	0.16	1.18	2.49	2.88	2.30	2.47	4.90
Cordylus oelofseni	45.68	9.69	102.40	0.11	0.91	1.76	2.07	1.88	2.24	4.04
Cordylus niger	58.26	13.45	102.43	0.13	1.34	2.14	2.90	2.28	2.58	4.52
Cordylus jonesii	57.78	20.54	130.74	0.24	1.32	1.50	2.54	1.58	1.82	4.64
Cordylus vittifer	57.84	20.79	125.09	0.21	1.84	2.96	3.44	2.52	2.79	5.49
Namazonurus lawrenci	47.40	18.43	143.92	0.17	1.40	2.22	2.56	2.30	2.41	4.22
Namazonurus peersi	57.27	17.01	129.38	0.17	2.37	3.17	3.55	3.42	3.43	5.08
Hemicordylus capensis	68.85	3.15	37.19	0.10	1.45	0.00	0.23	1.96	2.20	3.76
Hemicordylus nebulosus	45.63	0.12	2.52	0.11	0.70	1.48	1.34	1.41	1.75	3.09
Ninurta coeruleopunctatus	52.35	1.41	20.56	0.10	1.02	1.50	1.67	1.30	1.81	2.77
Pseudocordylus langi	65.68	0.00	0.00	0.00	0.88	0.09	0.00	1.15	1.13	2.27
Pseudocordylus melanotus	87.07	0.00	0.00	0.00	1.77	0.00	0.00	1.79	2.17	4.32
Pseudocordylus transvaalensis	103.97	0.00	0.00	0.00	2.03	0.00	0.00	2.10	2.42	5.21
Pseudocordylus spinosus	57.24	0.50	7.44	0.11	1.38	0.00	1.08	1.37	1.63	3.53
Pseudocordylus subviridis	80.73	0.00	0.00	0.00	1.36	0.00	0.00	1.66	2.32	4.40
Pseudocordylus microlepidotus	97.08	0.00	0.00	0.00	2.59	0.00	0.00	2.28	2.31	5.47
Smaug breyeri	83.26	17.45	86.89	0.25	3.72	3.62	3.95	3.85	4.81	6.10
Smaug vandami	92.03	15.49	70.53	0.32	2.30	3.56	3.32	3.22	3.94	5.19
Smaug depressus	84.20	14.77	83.88	0.21	3.87	4.58	4.16	4.05	4.68	6.30
Smaug giganteus	129.40	52.91	120.92	0.63	5.10	7.86	5.94	6.47	6.54	11.81
Karusasaurus polyzonus	84.73	17.78	114.93	0.17	2.81	2.90	1.93	2.98	2.97	5.12
Ouroborus cataphractus	75.20	31.69	144.47	0.41	4.33	6.15	7.76	6.08	5.76	8.88

Abbreviations: BS = body size, O_{VOL} = osteoderm volume, O_{SURF} = osteoderm surface, O_{THICK} = osteoderm thickness, S_{EAR} = ear spine length, S_{NECK} = neck spine length, S_{TRUNK} = trunk spine length, S_{FLEG} = front leg spine length, S_{HLEG} = hind leg spine length, S_{TAIL} = tail spine length. All length and thickness measurements are given in mm, surface in mm^2 and volume in mm^3.

Table S4. Results of phylogenetic linear regression analyses showing the relationships of osteoderm morphometrics and spine lengths with body size in cordyline lizards.

Variable	Estimate	StdErr	*t*-value	*P*-value
O_{VOL}	-1.98	0.81	-2.43	0.02
O_{SURF}	-0.03	0.06	-0.53	0.6
O_{THICK}	-0.11	0.34	-0.32	0.75
S_{EAR}	1.22	0.26	4.75	<0.001
S_{NECK}	0.1	0.19	0.53	0.6
S_{TRUNK}	-0.7	0.3	-2.32	0.03
S_{FLEG}	0.59	0.12	4.74	<0.001
S_{HLEG}	0.83	0.17	4.82	<0.001
S_{TAIL}	0.78	0.13	5.9	<0.001

Table S5. Loading scores of a phylogenetic principal component analysis conducted on three osteoderm measurements. Values in bold represent loading scores greater than 0.70.

Variable	Loading score
O_{VOL}	**0.96**
O_{SURF} (residual)	**0.94**
O_{THICK}	**0.88**
Standard deviation	1.61
Proportion of variance	0.86

Table S6. Loading scores of a phylogenetic principal component analysis conducted on six spine measurements. Values in bold represent loading scores greater than 0.70.

Variable	Loading score
S_{EAR} (residual)	**0.82**
S_{NECK}	**0.84**
S_{TRUNK} (residual)	**0.89**
S_{FLEG} (residual)	**0.96**
S_{HLEG} (residual)	**0.92**
S_{TAIL} (residual)	**0.90**
Standard deviation	2.18
Proportion of variance	0.79

Table S7. Loading scores of a phylogenetic principal component analysis conducted on the climate/environmental variables. Values in bold represent loading scores with absolute values greater than 0.70.

Variable	pPC1	pPC2	pPC3	pPC4
1. Temperature				
1.1 Annual mean temperature	-0.47	**0.84**	-0.20	0.17
1.2 Temperature seasonality	-0.44	-0.59	-0.16	0.61
1.3 Max. temperature of warmest month	**-0.71**	0.44	-0.07	0.51
1.4 Min. temperature of the coldest month	-0.08	**0.92**	0.11	-0.24
1.5 Mean temperature of warmest quarter	-0.60	**0.70**	-0.18	0.34
1.6 Mean temperature of coldest quarter	-0.30	**0.94**	-0.09	-0.03
2. Precipitation				
2.1 Annual precipitation	**0.89**	0.08	-0.39	0.06
2.2 Precipitation of wettest month	0.67	0.15	**-0.70**	0.04
2.3 Precipitation of driest month	0.64	0.24	0.67	0.13
2.4 Precipitation seasonality	-0.15	0.11	**-0.94**	-0.10
2.5 Precipitation of wettest quarter	0.69	0.14	-0.68	0.02
2.6 Precipitation of driest quarter	0.67	0.19	0.67	0.16
3. Global surface vegetation cover	0.61	0.52	0.41	0.13
4. Cloud cover	**0.90**	0.00	-0.13	0.22
5. Global aridity index	**0.94**	-0.15	-0.27	-0.03
6. Solar radiation				
6.1 Direct normal irradiance	**-0.79**	-0.51	0.11	-0.13
6.2 Global horizontal irradiance	**-0.88**	-0.26	-0.17	-0.17
7. Elevation	0.21	-0.62	-0.05	0.40
Eigenvalue	2.73	2.15	1.82	1.08
Proportion of Variance	0.42	0.26	0.18	0.06
Cumulative Proportion	0.42	0.67	0.86	0.92

Table S8. Results of univariate phylogenetic linear regression analyses examining the effect of habitat use and all indices of predation risk/pressure on osteoderm thickness. Statistically significant results are indicated in bold.

Variable	Estimate	StdErr	*t*-value	*P*-value	*a*	σ^2
pPC_{ARID}	**-0.21**	**0.10**	**-2.15**	**0.04**	**-24.83**	**8.36**
pPC_{TEMP}	0.05	0.12	0.45	0.65	-31.46	14.60
Rel. terrestrial predation pressure (RTP_{PRES})	0.08	0.71	0.11	0.91	-31.71	14.94
Rel. terrestrial predation risk (RTP_{RISK})	0.26	0.53	0.49	0.63	-31.47	14.59
Rel. snake predation pressure	0.18	0.80	0.22	0.82	-31.45	14.68
Rel. snake predation risk	0.19	0.54	0.36	0.71	-31.98	15.10
Rel. mammal predation pressure	-0.12	0.81	-0.14	0.89	-31.69	14.92
Rel. mammal predation risk	0.18	0.62	0.30	0.77	-31.05	14.30
Rel. bird predation pressure	-0.08	0.71	-0.11	0.91	-31.71	14.94
Relative bird predation risk	-0.26	0.53	-0.49	0.63	-31.47	14.59
Total predation pressure	-0.12	0.52	-0.23	0.82	-32.46	15.62
Total predation risk	0.10	0.62	0.16	0.88	-31.57	14.80

Legend: *a*, model parameters of EB evolutionary model; σ^2, maximum likelihood estimate of the variance rate.

Table S9. Results of univariate phylogenetic linear regression analyses examining the effect of habitat use and all indices of predation risk/pressure on spinosity.

Variable	Estimate	StdErr	*t*-value	*P*-value	*a*	σ^2
pPC_{ARID}	-0.13	0.14	-0.88	0.39	-27.35	21.26
pPC_{TEMP}	0.05	0.16	0.32	0.76	-30.61	26.62
Rel. terrestrial predation pressure (RTP_{PRES})	0.18	0.98	0.18	0.86	-31.22	27.70
Rel. terrestrial predation risk (RTP_{RISK})	0.38	0.74	0.51	0.61	-30.99	27.07
Rel. snake predation pressure	0.03	1.10	0.03	0.98	-31.29	27.85
Rel. snake predation risk	0.26	0.75	0.34	0.74	-31.45	28.01
Rel. mammal predation pressure	0.36	1.12	0.32	0.75	-31.38	27.90
Rel. mammal predation risk	0.52	0.86	0.61	0.55	-29.94	25.28
Rel. bird predation pressure	-0.18	0.99	-0.18	0.86	-31.22	27.70
Relative bird predation risk	-0.38	0.74	-0.51	0.62	-30.99	27.07
Total predation pressure	-0.69	0.71	-0.98	0.34	-33.69	31.15
Total predation risk	0.32	0.86	0.37	0.71	-30.46	26.34

Legend: *a*, model parameters of EB evolutionary model; σ^2, maximum likelihood estimate of the variance rate.

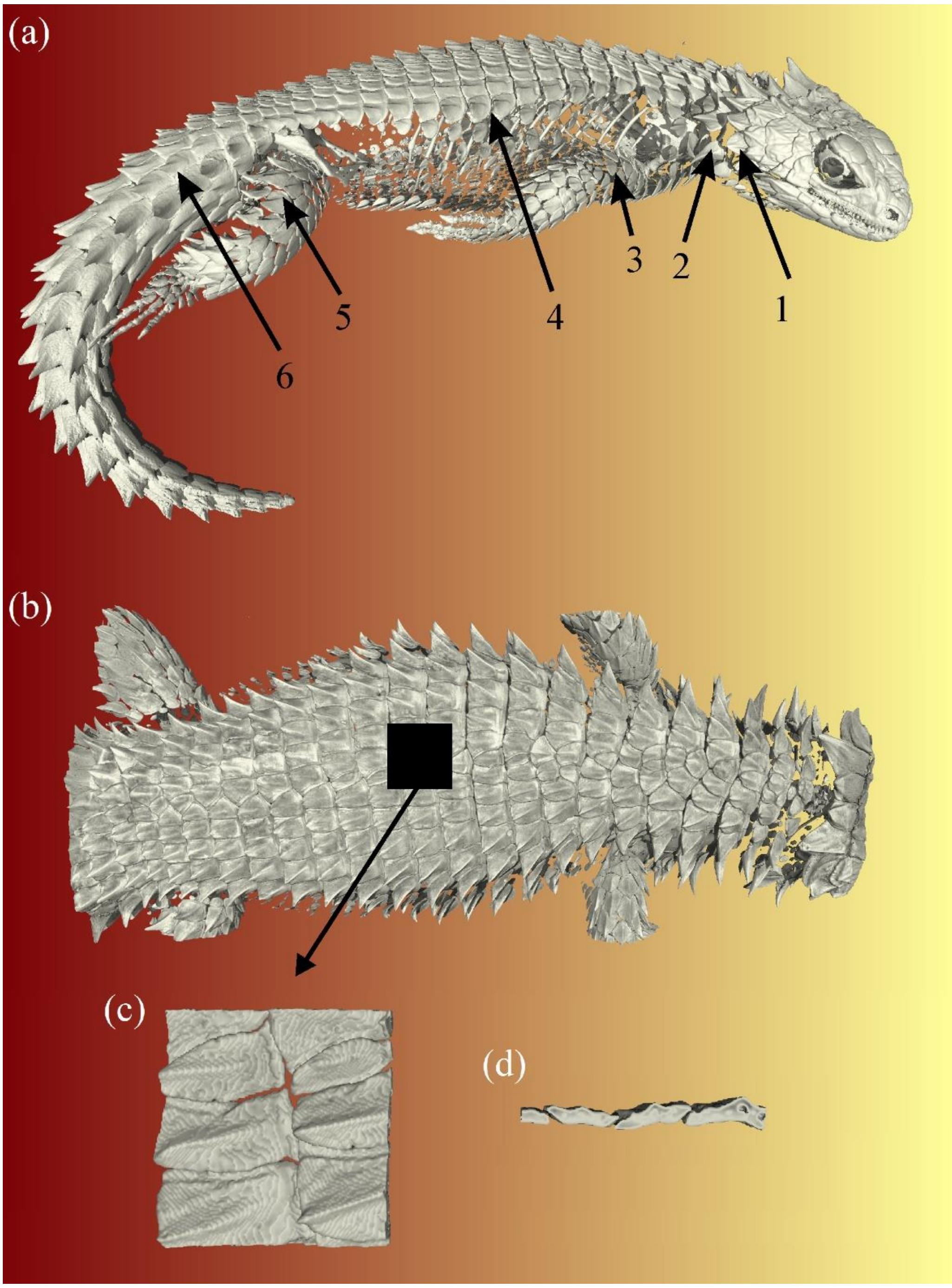

Figure S1. Graphical representation of the morphological characteristics used to describe body armour in cordyline lizards. Three-dimensional (3D) rendered micro-CT images of the full body (a) were used to calculate spine length. The region where the spine measurements were taken is indicated: (1) ear, (2) neck, (3) front leg, (4) trunk, (5) hind leg and (6) tail. 3D-rendered micro-CT images of the trunk region (b) were used to calculate osteoderm expression. The black square represents one of the region-of-interests (ROIs) used to calculate osteoderm characteristics. Osteoderm volume and surface were calculated directly from the extracted ROIs (c), whereas osteoderm thickness was measured using transversal sections (d).