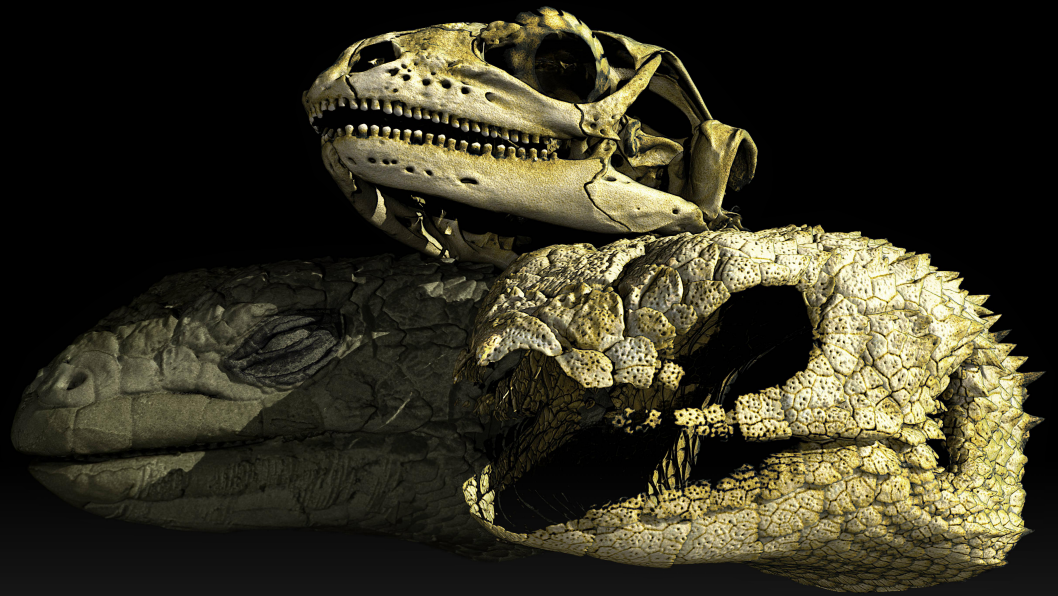


Supplementary Material



Microanatomy reveals functional roles of skin bones

Roy Ebel, Jane Melville, Eli Amson, Rocío Aguilar, Jay R. Black, and J. Scott Keogh

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Supplementary Note 1: The integumentary skeleton

Osteoderms belong to the integumentary skeleton, which has been proposed to date back ~475 million years, thus predating the first bony endoskeletons by ~50 million years (Erdtmann *et al.*, 2000; Sire, Donoghue, & Vickaryous, 2009). Osteoderms are perhaps most popularly known from the back plates of crocodylians and armoured dinosaurs (Romer, 1956; Francillon-Vieillot *et al.*, 1990; Scheyer & Sander, 2004; Vickaryous & Sire, 2009), and have been a recurrent motif of body armour evolution across tetrapods (Ebel, Melville, & Keogh, 2026). Among extant lineages, osteoderms occur in a few amphibians and a small number of mammals such as armadillos (Williams *et al.*, 2021). Humans can also grow skin bones, albeit pathologically (Hall, 2005). Osteoderms are common in non-avian reptiles, with their greatest diversity in non-serpent squamate reptiles (Vickaryous & Sire, 2009; Ebel *et al.*, 2025b).

Supplementary Note 2: Hypothesised functions of osteoderms

The selective forces underlying the acquisition of osteoderms remain elusive because our understanding of osteoderm functions is notably limited. But why is that? Natural body armour has inspired biomimetics for millennia (Yang *et al.*, 2012; Chintapalli *et al.*, 2014). Humans quickly recognised that mechanical reinforcement against the external environment provides protection from impacts and abrasion. It is therefore unsurprising that osteoderms are interpreted as bony skin armour (Broeckhoven, Diedericks, & Mouton, 2015; Frýdlová *et al.*, 2023). Yet this restrictive *a priori* assumption may be one reason why osteoderms are now among the least understood structures in the animal body. Functions beyond their role as body armour have largely remained contentious or merely anecdotal (Ebel *et al.*, 2025a).

Hypotheses encompass functions in lifestyle and locomotion, physiology, and visual contexts (Bellairs, 1970; Frey, 1988; Greer, 2007; Saitta, 2015; Dacke *et al.*, 2015; Clarac & Quilhac, 2019; Schucht *et al.*, 2020; Broeckhoven & du Plessis, 2022), with potential multi-functionality and trade-offs between different roles (Losos *et al.*, 2002; Broeckhoven, du Plessis, & Hui, 2017). In crocodylians, for instance, proposed functions include protection, heat collection, biomechanical support of the locomotor system, calcium storage, and blood-pH buffering (Frey, 1988; Jackson, Andrade, & Abe, 2003; Klein, Scheyer, & Tütken, 2009; Dacke *et al.*, 2015; Clarac & Quilhac, 2019).

Other possible lifestyle associations include a potential role in water retention, burrowing bio-mechanics, and possibly in arboreal climbing (Ebel *et al.*, 2025a, b). Reptilian scales and armour are thought to contribute to water retention in arid environments (Greer, 2007; Witzmann, 2009; Rutland, Cigler, & Kubale, 2019). Surface evaporation through the skin has been shown to account for up to 70%

of water loss in non-osteoderm-bearing lizards (Dawson, Shoemaker, & Licht, 1966). In contrast, owing to the large proportion of mineralised tissue (Khalil & Abdel-Messeih, 1962; Greer, 2007), the skin in osteoderm-bearing lizards is only half as hydrated (Khalil & Abdel-Messeih, 1962), resulting in comparatively low evaporative water loss (Dawson *et al.*, 1966). Adipose tissue in the osteodermal cavities may likewise contribute (Otto, 1909).

Regarding burrowing biomechanics, literature proposes contrasting associations with osteoderms. They may reinforce the skull in fossorial species (Westheide & Rieger, 2015), as cephalic osteoderms can distribute mechanical strain (Xue *et al.*, 2017; Marghoub *et al.*, 2023), which is a major factor during head-first burrowing (Navas *et al.*, 2004). On the other hand, osteoderms may be incompatible with a burrowing lifestyle as they are conspicuously reduced or absent in some highly specialised burrowing clades (Gadow, 1901; Camp, 1923; Smith, 1935; Bellairs, 1970; Bhullar & Bell, 2008), possibly due to an impairment of flexibility (Williams *et al.*, 2021).

Regarding arboreality, Chapple (2003) proposed an association between external scale morphology and lifestyle in *Egernia*-group lizards: lightly keeled taxa are often saxicolous or semi-arboreal, while smooth-scaled species generally live in burrows or crevices. As the cephalic osteoderms structurally reflect the organisation of the overlying scalation, osteoderms would capture such signals (Ebel *et al.*, 2025b; citing Estes, de Queiroz, & Gauthier, 1988; and Paparella & Caldwell, 2022). With this in mind, we may expect osteoderms to structurally reinforce body regions involved in climbing (Ebel *et al.*, 2025b). On the other hand, we consider it plausible that an overly elaborate osteoderm cover may be incompatible with the agility required for arboreal locomotion (Ebel *et al.*, 2025a).

A major obstacle to a better understanding of these functions is the lack of comparative analyses that systematically quantify how structural traits in the osteoderm cover of ecologically diverse groups align with different lifestyles and habitats. Prior μ CT-based work has characterised osteoderm distribution across body regions or the entire animal (Maisano *et al.*, 2002; Laver *et al.*, 2020); others have studied the microanatomy of individual osteoderms (Kirby, 2020; Iacoviello *et al.*, 2020), while Laver *et al.* (2020) determined the total osteoderm volume per specimen. In crocodylians, osteoderm vascularisation has been studied to draw inferences about thermoregulation, metabolic activity, and an amphibious lifestyle, all of which remain unresolved (Clarac *et al.*, 2018; Inacio Veenstra & Broeckhoven, 2022; Pochat-Cottilloux *et al.*, 2023).

Supplementary Note 3: Lifestyle correlates in bone microanatomy

Lifestyle correlates are well established in tetrapod bone microanatomy, including in trabecular networks (Georgiou *et al.*, 2019) and cross-sections of long bone diaphyses (Krilloff *et al.*, 2008; Canoville & Laurin, 2010), ribs (Amson *et al.*, 2014; Canoville, Buffrénil, & Laurin, 2016), and vertebrae (Dumont *et al.*, 2013; Hayashi *et al.*, 2013). The secondary acquisition of an aquatic lifestyle, for instance, correlates with an increase in bone compactness (osteosclerosis) and robustness (pachyostosis) (Ricqlès & Buffrénil, 2001; Houssaye, 2009; Buffrénil *et al.*, 2010). Limb-mediated burrowing, on the other hand, can show an association with limb-bone cortical thickness and trabecular anisotropy (Biknevicius, 1993; Botha, 2003; Amson *et al.*, 2017; Mielke *et al.*, 2018; Amson & Bibi, 2021). Despite the utility of bone microanatomy to explore past ecologies, a methodological gap existed in the reconstruction of a fossorial (i.e., burrowing) lifestyle in squamate reptiles (lizards and snakes). Here, post-cranial inference has little informative value because head-first burrowing ecomorphs evolved limb reduction repeatedly across multiple independent evolutionary lineages (Lee, 1998; Benesch & Withers, 2002; Wiens, Brandley, & Reeder, 2006).

Ebel *et al.* (2020) bridged this gap with the discovery of fossorial lifestyle correlates in squamate skull-roof microanatomy. They showed that squamates evolved thick and compact roofing bones in concert with a fossorial lifestyle, which is consistent with the mechanical strain exerted on the skull during head-first burrowing (Navas *et al.*, 2004). A number of studies have built upon their method (Kaffler *et al.*, 2023; Manning *et al.*, 2023; Fornari & Müller, 2025), which included structural quantification of skull-roof cross-sections extracted from micro-computed tomography (μ CT) scans.

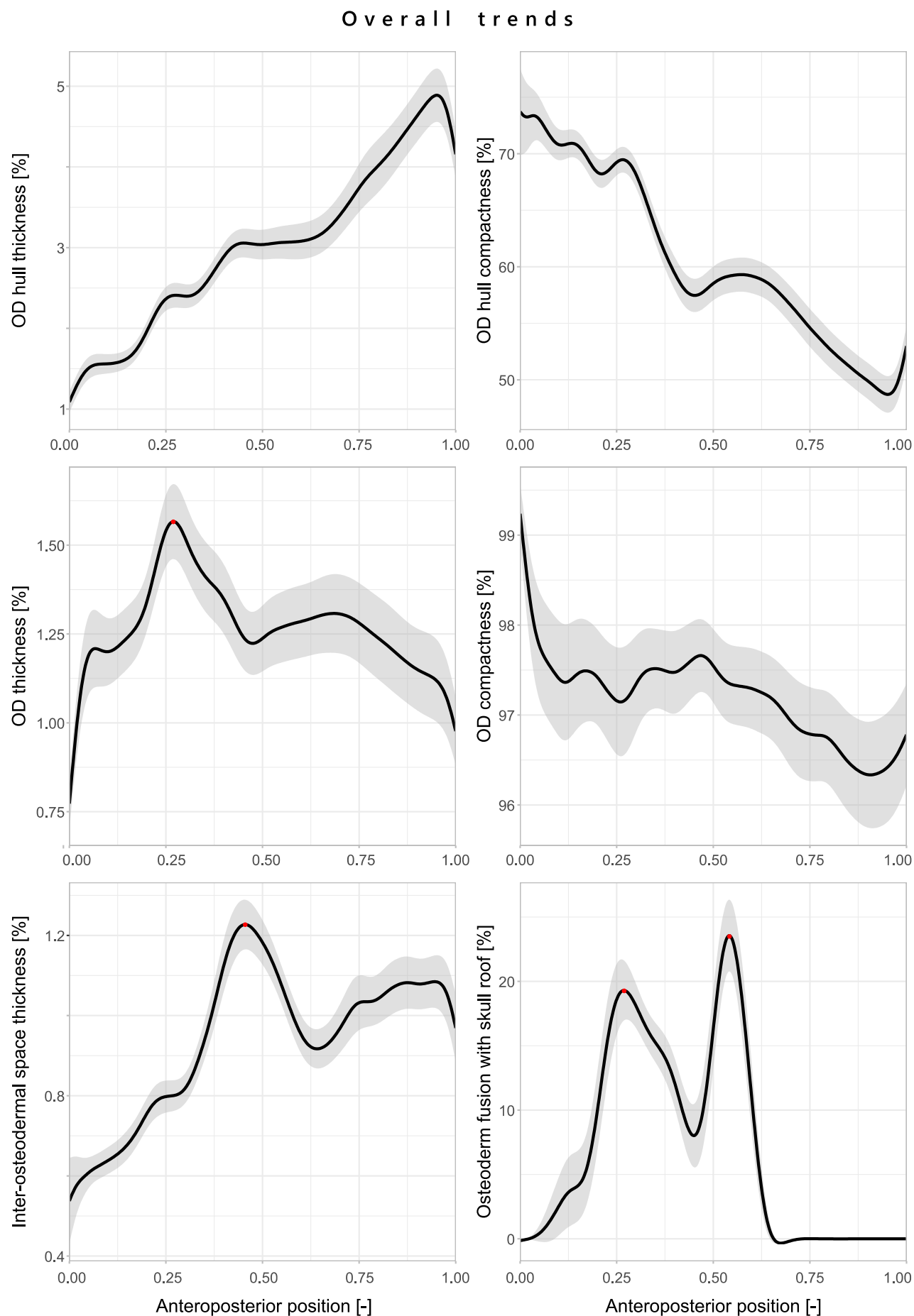
As a modern, non-destructive imaging technique, μ CT scanning allows the study of soft and hard-tissue structures in situ from ethanol-preserved specimens, commonly held in scientific collections of natural history museums (Broeckhoven & du Plessis, 2018; Keklikoglou *et al.*, 2019). The potential of skull-roof-based inference has recently been demonstrated in a lifestyle reconstruction of one of the earliest stem-serpents (in press with *Nature*). One limitation of the approach is that it does not quantify the osteoderm cover, which, for many squamate reptiles, effectively provides an additional composite bone layer around their head and body (Fig. 1). This illustrates just one of several compelling reasons to establish microanatomical lifestyle correlates in the osteoderm cover.

Supplementary Note 4: Biogeographic context of the *Egernia* group

The *Egernia* group serves as an ideal model system as it has been comprehensively studied in terms of its phylogeny, and its ecology is well-documented (Chapple, 2003; Brennan *et al.*, 2024). It comprises the Australian genera *Egernia*, *Liopholis*, *Bellatorias*, *Lissolepis*, *Tiliqua*, and *Cyclodomorphus*, as well as the genus *Corucia* from the Solomon Islands. *Egernia*-group lizards are best known for their pronounced sociality, but also for herbivory and large body size in various representatives (Hauschild *et al.*, 2000; Chapple, 2003). Presumed to be an ancestral condition, the *Egernia* group comprises numerous taxa that are skilled head-first burrowers (Greer, 1989; Chapple, 2003; Wu *et al.*, 2015). Others are incapable of active burrowing and rely on refuge beneath vegetation and litter, or they utilise burrows excavated by other animals (Hauschild *et al.*, 2000; Greer, 2007), and some taxa lead an arboreal lifestyle (Chapple, 2003; Greer, 2007). The biogeographic origins of the lineage have been traced to New Guinea with subsequent dispersal into Australia, with a humid habitat proposed as the ancestral state (Chapple, 2003). It is assumed that arid-adapted forms repeatedly evolved as habitats contracted and became increasingly fragmented (Horton, 1972; Heatwole & Taylor, 1987; Chapple, 2003; Chapple & Keogh, 2004). Their evolutionary history thereby mirrors the dynamic biogeographic history of the Australian continent, characterised by the contraction of rainforest through aridification over the past 25 million years (Adam, 1992; Sluiter *et al.*, 2022).

Supplementary Note 5: Directional heterogeneity

This section preserves the full descriptive results that support the directional trait-variability plots (Fig. 5 and Supplementary Figs. 1 and 21-26) and the discussion of posterior regionalisation in lifestyle signals. In an exploratory step, we inspected directional trait variability profiles. As a general anteroposterior trend in the *Egernia* group, we found that Th_{hull} increases while c_{hull} and Th_{OD} decrease in the posterior direction. Th_{OD} has a maximum at $\sim 27\%$, whereas Th_{matrix} peaks at $\sim 45\%$ (Supplementary Fig. 1). Th_{hull} and c_{hull} profiles show posterior separation between dry-tolerant vs. non-dry-tolerant taxa as well as fossorial vs. non-fossorial taxa. The latter also show separation in Th_{matrix} and possibly Th_{OD} profiles. Arboreality shows comparatively little separation in the anteroposterior profiles, with the possible exception of Th_{OD} . We note that these observations are purely exploratory and not supported by statistical tests.



Supplementary Fig. 1. Directional trait variability, general trends with maxima discussed in the text highlighted in red.

Supplementary Note 6: Background effects

We explored potential non-independence among predictors and found that a joint arboreal-fossorial state was absent in our dataset. We therefore compared discrete models in BayesTraits to test whether an independent evolutionary model could plausibly generate this pattern. Settings and results are provided in Supplementary Box 1. We then assessed potentially problematic collinearity among predictors using Variance Inflation Factors (*VIFs*) computed from an ordinary least-squares model that included *svl* and all three lifestyles. The *VIF* interpretation followed Belsley, Kuh, & Welsch (1980) and O'Brien (2007). Observed *VIFs* were $\in [1.12, 1.54]$, well below thresholds at which collinearity would be expected to bias coefficient estimates. We also explored the effect of body size and shared ancestry on the quantified traits in univariate analyses, the results of which are provided in Supplementary Tab. 1.

Supplementary Box 1. Settings and results for discrete model comparison in BayesTraits to test whether an independent evolutionary model could plausibly generate the observed joint-arboreal-fossorial-state absence in our dataset.

```
Analysis Type: MCMC
Iterations: 1100000
Sample Period: 1000
Steppingstone Iterations: 10000
Rate Dev: AutoTune
Prior Distribution: Uniform 0.00 100.00
Independent Log marginal likelihood #1: -48.081496, #2: -48.108923, #3: -48.120850
Dependent Log marginal likelihood #1: -45.949609, #2: -45.924806, #3: -45.964726

Model: Discrete: Dependent / Independent
Burn in: 100000
Steppingstone Stones: 100
Steppingstone Dist: Beta(0.400000,1.000000)
Seed: 1514818648
```

Supplementary Tab. 1. Results table for size-trait associations and phylogenetic signal in the quantified traits.

Trait	Size-trait associations			Blomberg's <i>K</i>			Pagel's λ		
	β_{std}	p_{raw}	p_{adj}	<i>K</i>	p_{raw}	p_{adj}	λ	p_{raw}	p_{adj}
<i>BS/TV_{hull}</i>	-0.915	$3.3 \cdot 10^{-13}$	$1.3 \cdot 10^{-12}$	0.59	0.041	0.055	0.78	0.0005	0.001
<i>Tb.N_{hull}</i>	-0.944	$3.3 \cdot 10^{-18}$	$2.7 \cdot 10^{-17}$	0.85	0.001	0.008	0.89	$2.2 \cdot 10^{-5}$	$1.7 \cdot 10^{-4}$
<i>Th_{hull}</i>	0.425	0.013	0.017	0.81	0.002	0.008	0.94	0.001	0.001
<i>C_{hull}</i>	0.526	0.003	0.005	0.50	0.167	0.167	0.71	0.049	0.061
<i>Th_{OD}</i>	0.478	0.003	0.005	0.89	0.011	0.029	0.92	$5.2 \cdot 10^{-5}$	$2.1 \cdot 10^{-4}$
<i>C_{OD}</i>	-0.560	0.001	0.003	0.65	0.027	0.043	0.79	0.006	0.009
<i>Th_{matrix}</i>	-0.018	0.92	0.92	0.60	0.061	0.070	0.52	0.053	0.061
<i>DA</i>	-0.201	0.31	0.35	0.67	0.023	0.043	0.79	0.062	0.062

Supplementary Note 7: Trait partitioning and lifestyle associations

We assessed lifestyle-related differentiation first in a multivariate analysis (Supplementary Box 2) and then across modules (Supplementary Tab. 2). Multivariate analyses narrowed potential trait-lifestyle associations to the thickness module (dry tolerance,

Supplementary Box 2. Testing lifestyle association across the multivariate dataset with phyloRRPP. Results with degrees of freedom (*Df*), sums of squares (*SS*), mean squares (*MS*), the coefficient of determination (*Trace-R²*), the *F*-statistic, the standardised effect size (*Z*), and permutation-based p-value (*Pr(>F)*).

```
Analysis of Variance, using Residual Randomization
Permutation procedure: Randomization of null model residuals
Number of permutations: 10000
Estimation method: Ordinary Least Squares
Sums of Squares and Cross-products: Type I
Effect sizes (Z) based on F distributions
```

	Df	SS	MS	Rsq	F	Z	Pr(>F)	
log_svl	1	118.61	118.611	0.35619	23.6512	5.0517	0.0001	***
dry_tolerant	1	25.81	25.809	0.07750	5.1463	2.9576	0.0016	**
fossorial	1	14.39	14.387	0.04320	2.8688	1.9474	0.0265	*
arboreal	1	8.70	8.696	0.02612	1.7341	1.1096	0.1340	
Residuals	33	165.50	5.015	0.49699				
Total	37	333.00						

fossoriality) and the structure module (dry tolerance, arboreality). The strongest trait-trait correlation in the structure module ($r = 0.78$) was between BS/TV_{hull} and $Tb.N_{hull}$. Conceptually, both index osteoderm hull structural complexity, and numerically, they showed a high degree of redundancy in PCA (Supplementary Box 3). We therefore collapsed them into the composite structural complexity index str_{hull} , on which the final affirmative tests for lifestyle signals were performed. All results are provided and visualised in Supplementary Tabs. 3 and 4, and Supplementary Fig. 4.

The phylomorphospace plots (Supplementary Figs. 2 and 3) reveal lifestyle-specific occupation patterns. Dry tolerance pro-

Supplementary Box 3. PCA statistics, basis for collapsing BS/TV_{hull} and $Tb.N_{hull}$ into a composite index str_{hull} .

```
> p_struct <- prcomp(
+ pc_dat[, c(
+ "hull_bs_tv",
+ "hull_tbn")],
+ center = TRUE,
+ scale. = TRUE)
> imp <- summary(p_struct)
+ )$importance
> for (i in 1:ncol(
+ imp)) {cat(sprintf(
+ "\n%s(%.2f%%)\n",
+ colnames(imp)[i],
+ imp[2, i] * 100))
+ print(round(
+ p_struct$rotation[,i],
+ 4))}

PC1(98.25%)
hull_bs_tv    hull_tbn
    0.7071    0.7071

PC2(1.75%)
hull_bs_tv    hull_tbn
   -0.7071    0.7071
```

Supplementary Tab. 2. Lifestyle-related differentiation across modules, with multivariate phyloRRPP in the thickness module, univariate phyloRRPP to $PC1$ & $PC2$ of residuals in the structure module, and univariate phyloRRPP directly to the fusion module, results summary.

Module	Predictor	p_{raw}	Z	$Trace-R^2$	p_{adjust}
Thickness	Dry tolerant	0.0061	2.46	0.0568	0.00915
	Fossorial	0.0057	2.47	0.0546	0.00915
	Arboreal	0.705	-0.544	0.00359	0.705
Structure	Arboreal ($PC1$)	0.0054	2.36	0.101	0.0162
	Arboreal ($PC2$)	0.0244	1.87	0.0701	0.0488
	Dry tolerant ($PC1$)	0.0023	2.56	0.122	0.0138
	Dry tolerant ($PC2$)	0.307	0.553	0.0157	0.307
	Fossorial ($PC1$)	0.0814	1.37	0.0419	0.122
	Fossorial ($PC2$)	0.282	0.635	0.0174	0.307
Fusion	Dry tolerant	0.0388	1.68	0.0472	0.116
	Fossorial	0.301	0.579	0.0116	0.452
	Arboreal	0.722	-0.617	0.00134	0.722

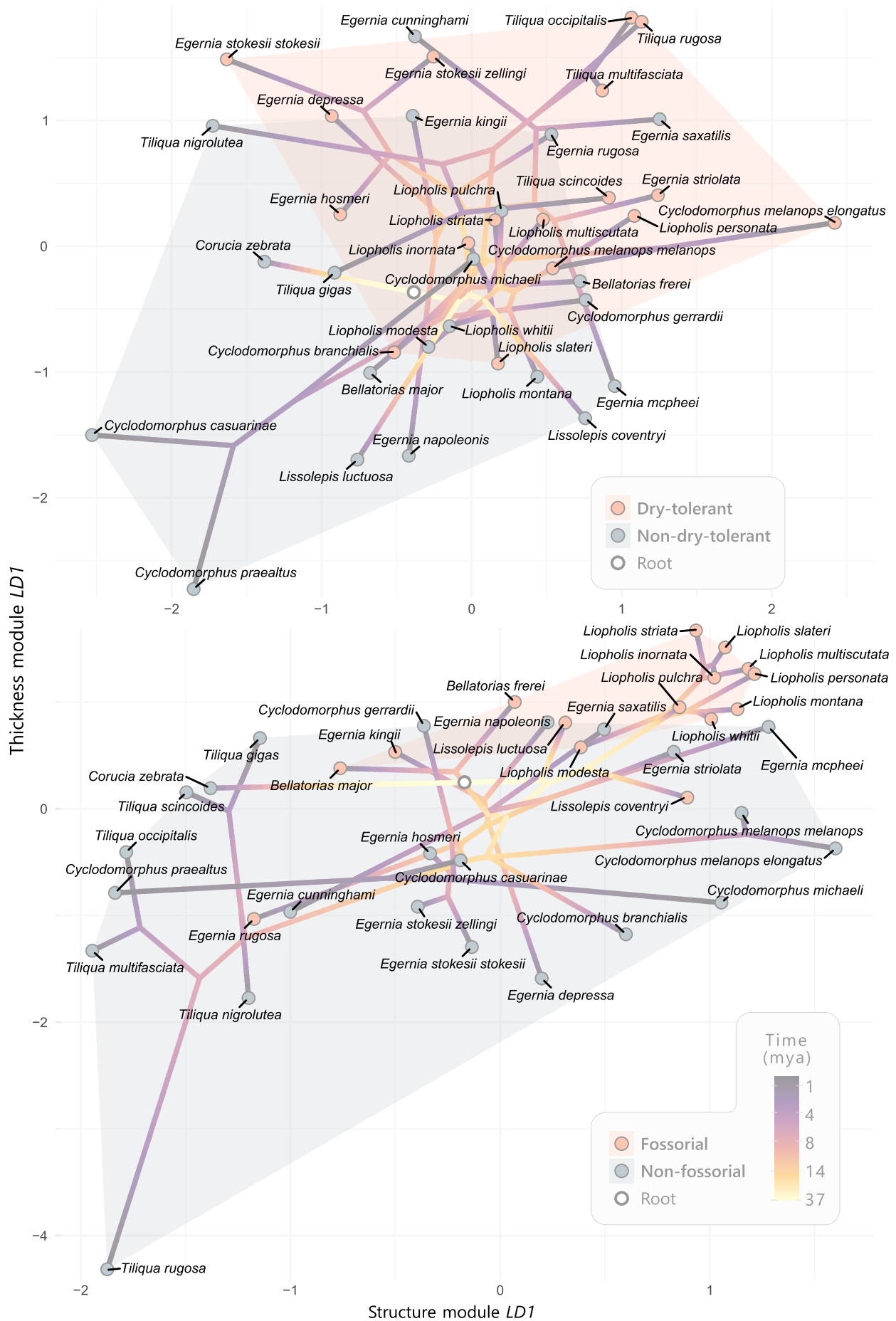
Supplementary Tab. 3. Results of the final affirmative tests for lifestyle signals across the remaining relevant trait-lifestyle combinations using phyloRRPP. Effect sizes reported as Cohen's d . P -values adjusted after Holm (1979).

Trait	Predictor	p_{raw}	d	p_{adjust}
str_{hull}	Arboreal	0.0001	-0.38	0.001
str_{hull}	Dry tolerant	0.004	0.03	0.040
DA	Dry tolerant	0.007	-0.78	0.073
DA	Fossorial	0.091	0.68	0.454
c_{hull}	Arboreal	0.586	0.14	1
c_{hull}	Dry tolerant	0.026	0.42	0.206
Th_{hull}	Dry tolerant	0.037	0.46	0.262
Th_{hull}	Fossorial	0.063	-0.84	0.379
Th_{matrix}	Dry tolerant	0.487	0.14	1
Th_{matrix}	Fossorial	0.002	-1.17	0.025
c_{od}	Arboreal	0.421	0.30	1
c_{od}	Dry tolerant	0.337	-0.06	1
Th_{od}	Dry tolerant	0.0003	0.62	0.004
Th_{od}	Fossorial	0.016	-0.98	0.144

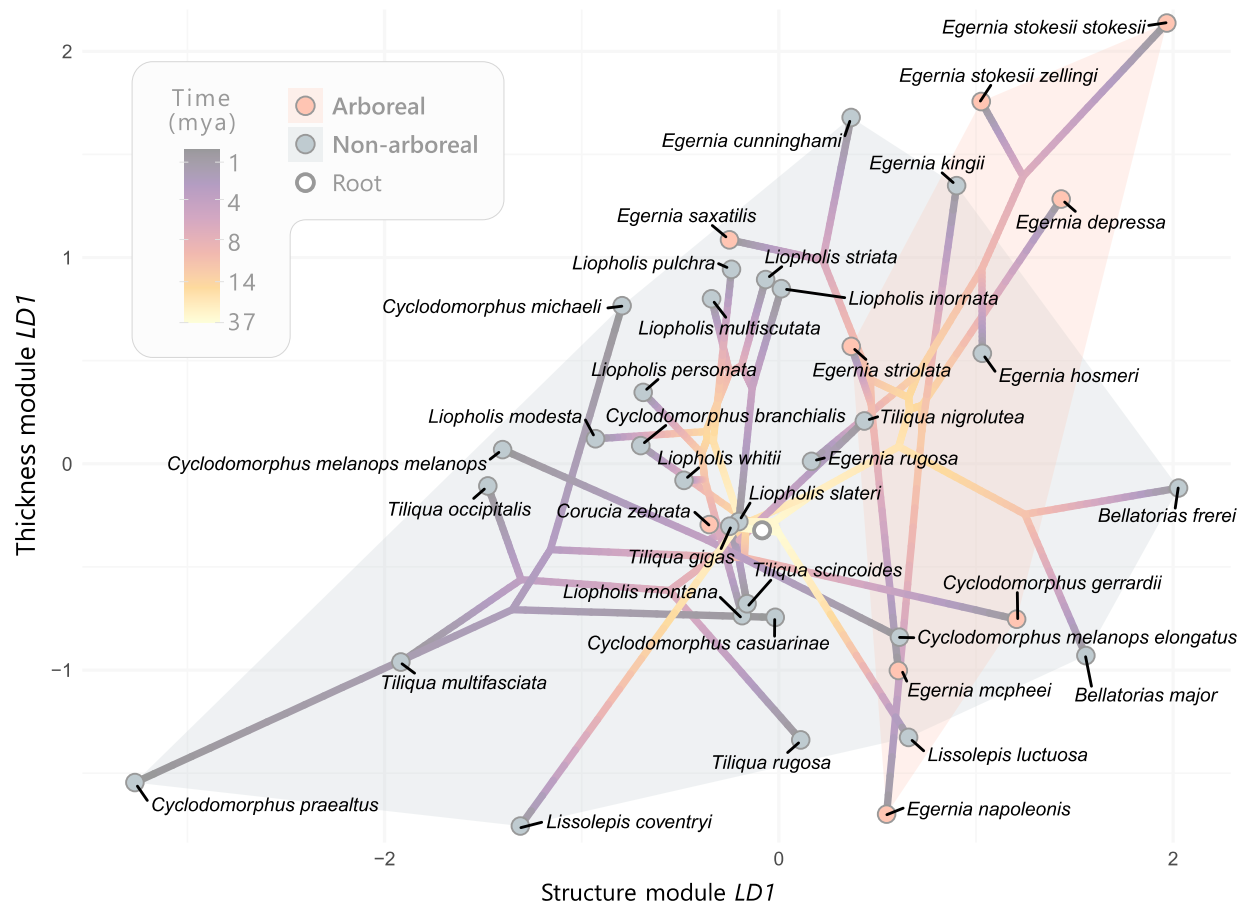
duced two roughly equally sized regions ($\Delta = 14\%$) overlapping in a central shared morphospace that contains the reconstructed common ancestor. From this shared region, lineages repeatedly enter exclusive lifestyle-specific areas at opposite ends of the space. The dry-tolerant morphospace is $\sim 57\%$ unique, with 7 lineages (59% of dry-tolerant tips) entering independently. The non-dry-tolerant morphospace is $\sim 67\%$ unique, with 10 lineages (48% of tips) entering independently. This pattern is consistent with both states forming opposing ends of an ecological spectrum repeatedly evolved from a generalised ancestor.

Supplementary Tab. 4. Quantified traits in the *Egernia*-group osteoderm cover, reported as lifestyle-group means and standard deviations (SD). Osteoderm cover thickness (Th_{hull}) and compactness (C_{hull}), individual osteoderm thickness (Th_{OD}) and compactness (C_{OD}), thickness of inter-osteodermal spaces (Th_{matrix}), degree of anisotropy (DA), fusion with the skull roof (fus), osteoderm surface per osteoderm cover volume (BS/TV_{hull}), osteoderm number per osteoderm cover volume ($Tb.N_{hull}$), and, as a composite derived from the latter two, osteoderm cover structural complexity (str_{hull}). For a visualisation of these results, see Supplementary Fig. 4.

	Trait	Mean $\pm$ SD		Trait	Mean $\pm$ SD
Dry-tolerant	Th_{hull} [%]	3.89 ± 1.22	Non-fossorial	Th_{hull} [%]	3.95 ± 1.09
	C_{hull} [%]	56.5 ± 5.4		C_{hull} [%]	55.7 ± 6.6
	Th_{OD} [%]	1.35 ± 0.5		Th_{OD} [%]	1.36 ± 0.42
	C_{OD} [%]	97.2 ± 1.6		C_{OD} [%]	97.0 ± 1.7
	Th_{matrix} [%]	1.04 ± 0.22		Th_{matrix} [%]	1.10 ± 0.18
	DA [-]	0.276 ± 0.035		DA [-]	0.281 ± 0.041
	fus [%]	4.52 ± 2.62		fus [%]	5.19 ± 2.59
	BS/TV_{hull} [mm $^{-1}$]	19.78 ± 10.27		BS/TV_{hull} [mm $^{-1}$]	17.73 ± 11.61
	$Tb.N_{hull}$ [*mm $^{-1}$]	5.40 ± 2.62		$Tb.N_{hull}$ [*mm $^{-1}$]	4.66 ± 2.54
	str_{hull} [-]	0.026 ± 1.41		str_{hull} [-]	-0.320 ± 1.465
Non-dry-tolerant	Th_{hull} [%]	3.41 ± 0.87	Arboreal	Th_{hull} [%]	3.73 ± 1.49
	C_{hull} [%]	54.3 ± 5.3		C_{hull} [%]	55.9 ± 3.4
	Th_{OD} [%]	1.11 ± 0.28		Th_{OD} [%]	1.21 ± 0.25
	C_{OD} [%]	97.3 ± 1.4		C_{OD} [%]	97.6 ± 1.3
	Th_{matrix} [%]	1.01 ± 0.15		Th_{matrix} [%]	1.02 ± 0.18
	DA [-]	0.303 ± 0.036		DA [-]	0.281 ± 0.056
	fus [%]	5.63 ± 2.05		fus [%]	5.39 ± 2.82
	BS/TV_{hull} [mm $^{-1}$]	20.00 ± 11.37		BS/TV_{hull} [mm $^{-1}$]	16.53 ± 5.89
	$Tb.N_{hull}$ [*mm $^{-1}$]	5.18 ± 2.47		$Tb.N_{hull}$ [*mm $^{-1}$]	4.62 ± 1.69
	str_{hull} [-]	-0.021 ± 1.43		str_{hull} [-]	-0.410 ± 0.861
Fossorial	Th_{hull} [%]	3.13 ± 0.81	Non-arboreal	Th_{hull} [%]	3.60 ± 0.92
	C_{hull} [%]	54.7 ± 3		C_{hull} [%]	55.1 ± 5.9
	Th_{OD} [%]	1.00 ± 0.25		Th_{OD} [%]	1.22 ± 0.44
	C_{OD} [%]	97.7 ± 1		C_{OD} [%]	97.2 ± 1.5
	Th_{matrix} [%]	0.91 ± 0.1		Th_{matrix} [%]	1.02 ± 0.18
	DA [-]	0.306 ± 0.026		DA [-]	0.294 ± 0.03
	fus [%]	5.05 ± 2.04		fus [%]	5.05 ± 2.25
	BS/TV_{hull} [mm $^{-1}$]	23.23 ± 8.6		BS/TV_{hull} [mm $^{-1}$]	20.95 ± 11.75
	$Tb.N_{hull}$ [*mm $^{-1}$]	6.25 ± 2.19		$Tb.N_{hull}$ [*mm $^{-1}$]	5.49 ± 2.7
	str_{hull} [-]	0.491 ± 1.181		str_{hull} [-]	0.127 ± 1.521



Supplementary Fig. 2. LD1-LD1 phylomorphospace plots, full-sized with tip labels, for dry tolerance (top) and fossoriality (bottom).

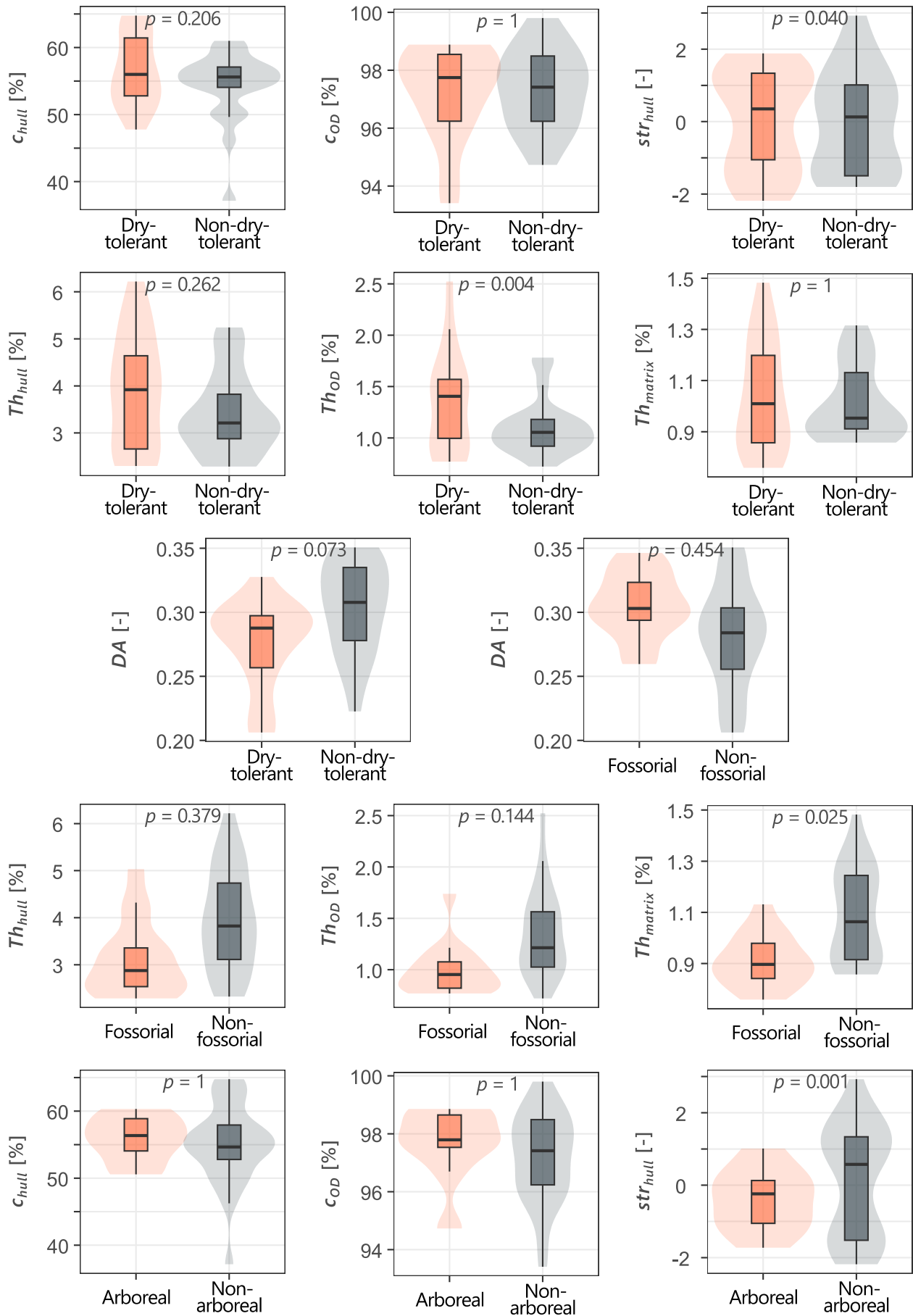


Supplementary Fig. 3. LD1-LD1 phylomorphospace plots, full-sized with tip labels, for arboreality.

Fossoriality shows a strongly asymmetric pattern. The ancestral condition lies in the non-fossorial morphospace, which occupies a broad region that is ~97% unique. Fossorial taxa occupy a much smaller region ($\Delta = -69\%$) that is 68% unique. Four lineages (67% of fossorial tips) independently enter this exclusively fossorial space, and no lineages move in the opposite direction. Arboreality shows a more complex pattern. The ancestral condition lies centrally within the extensive non-arboreal morphospace (~79% unique). The arboreal morphospace is smaller ($\Delta = -44\%$) and ~32% unique, largely embedded within the non-arboreal region but extending into two small unique areas. Three lineages (44% of arboreal tips) independently enter arboreal-unique space, and four lineages (14% of non-arboreal tips) enter non-arboreal-unique space. Spatial separation alone is not very informative, but differences in disparity can still carry signal (Foote, 1997).

Supplementary Note 8: Osteoderm fusion patterns

Fusion-area profiles showed a bimodal distribution, with maxima located at ~27% over the frontal bones and ~54% over the parietal bones (Supplementary Fig. 5). *Tiliqua* exhibits a third maximum in the region of the nasal bones. *Corucia*, in contrast, lacks the parietal fusion area entirely. Mean fusion area asymmetry across specimens was ~0.24%, with the 95% CI ($\in [0.017\%, 0.462\%]$) not overlapping the midline. A one-sample t-test against zero supported this pattern ($p = 0.035$, Supplementary Box 4), which suggests right-sided bias. In the modular analysis, no lifestyle association was detected for the fusion module ($p \in [0.12, 0.72]$; Supplementary Tab. 2), and fusion was therefore excluded from downstream analyses. Beyond this shared pattern, lineage-specific deviations occur. *Tiliqua* show additional fusion over the nasal bones, whereas the *Corucia* specimens in our dataset lacked parietal fusion

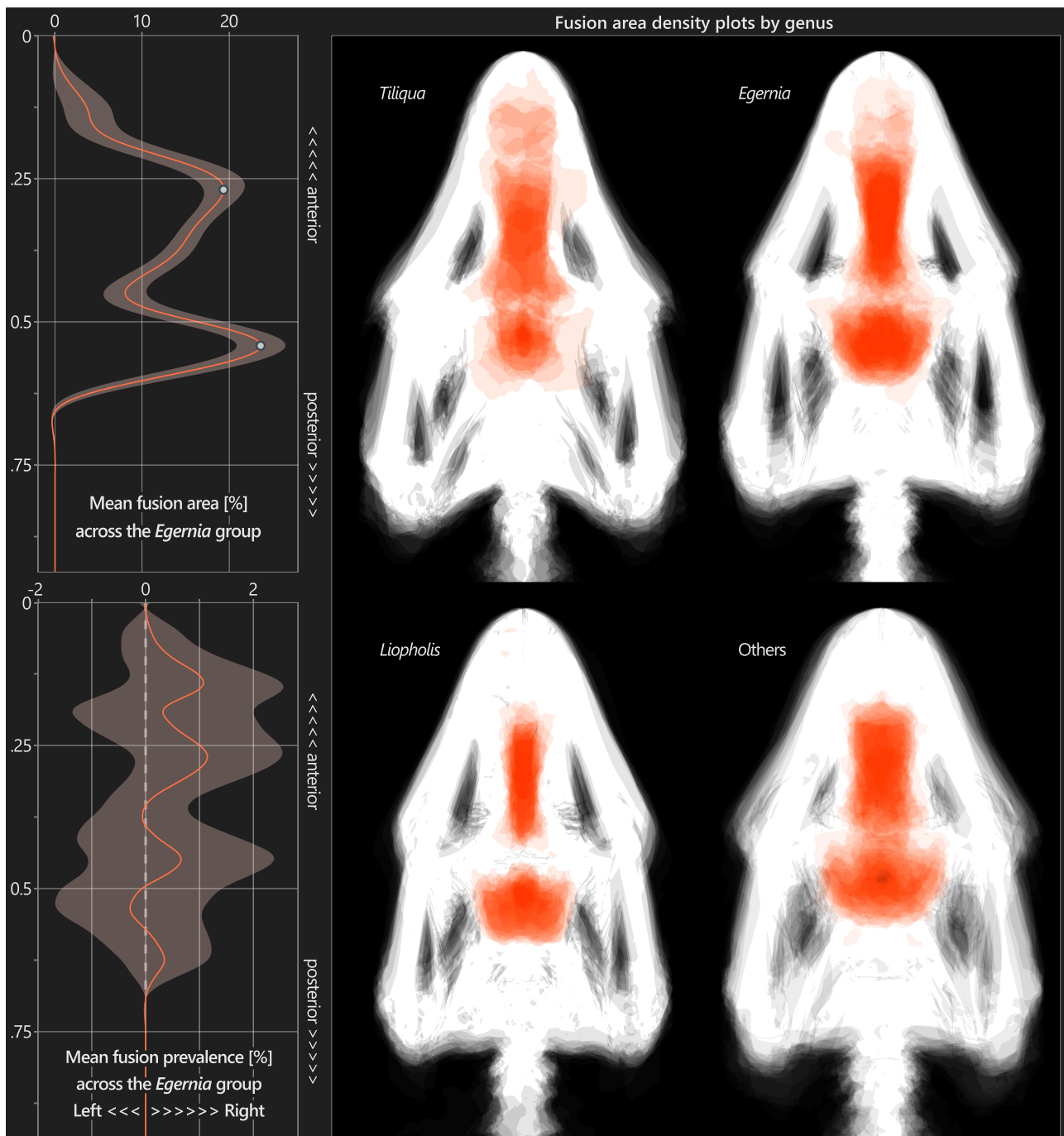


Supplementary Fig. 4. Trait distribution between lifestyle groups for the combinations analysed in affirmative lifestyle signal testing: osteoderm cover thickness (Th_{hull}) and compactness (c_{hull}), individual osteoderm thickness (Th_{OD}) and compactness (c_{OD}), thickness of inter-osteodermal spaces (Th_{matrix}), degree of anisotropy (DA), and osteoderm cover structural complexity (str_{hull}). P -values adjusted after Holm.

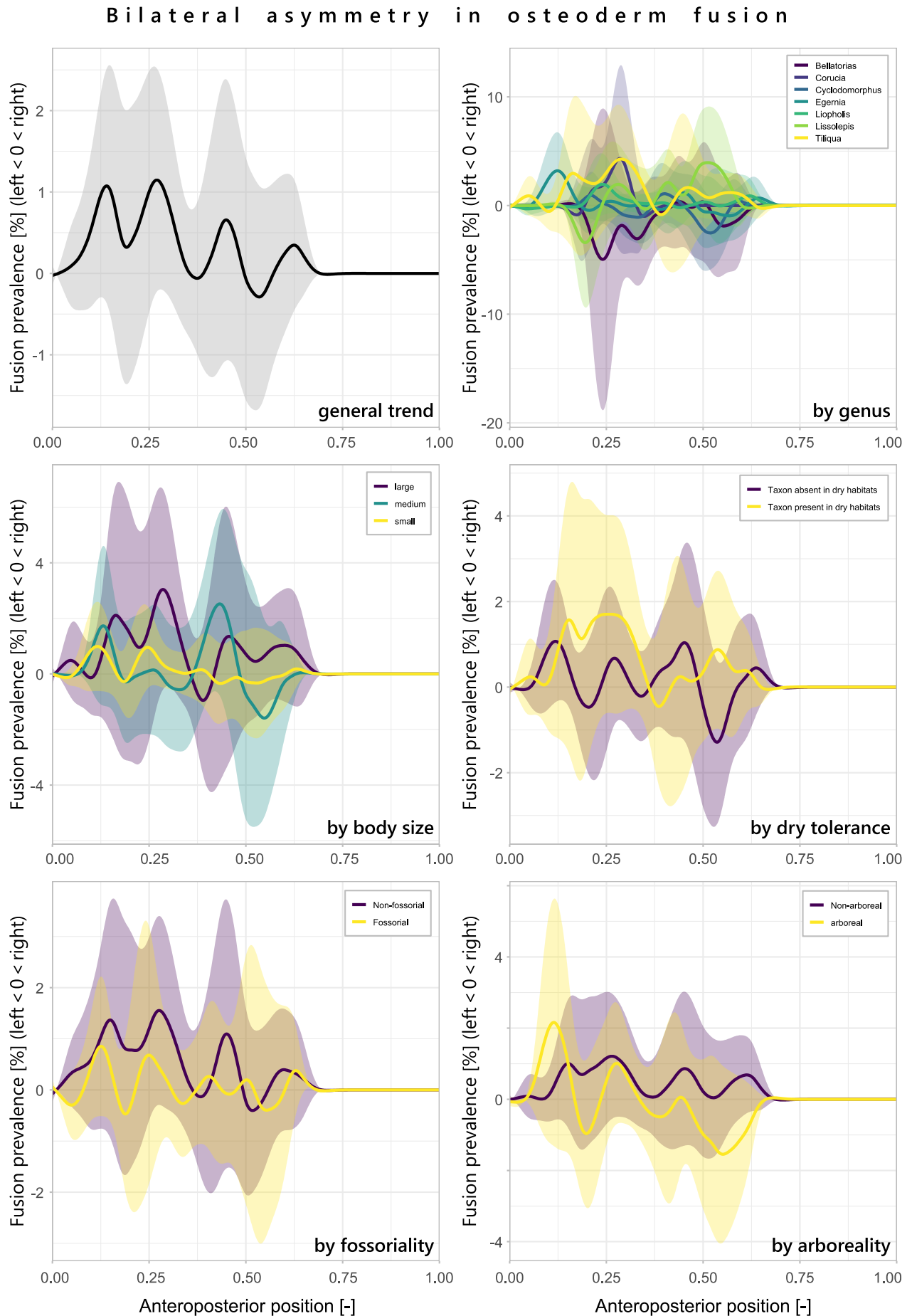
entirely. Broader sampling will be required to determine whether this is diagnostic for *Corucia*. We observed that fusion areas rarely matched the dimensions of the skull-roof bones or osteoderms they interconnected. Individual fusion zones often linked a single osteoderm to multiple roofing bones or connected several osteoderms to the same bone. As osteoderms interact with the skull to distribute strain (Xue *et al.*, 2017; Marghoub *et al.*, 2023), we propose

Supplementary Box 4. Fusion area asymmetry one-sample t-test against zero.

```
> print(asym_t_test)
One Sample t-test
data: asym_means$mean_asym
t = 2.142, df = 79, p-value = 0.03527
alternative hypothesis: true mean is not equal to 0
95 percent confidence interval: 0.01693717 0.46184688
sample estimates: mean of x 0.239392
```



Supplementary Fig. 5. Directional trait variability for fusion area of skull roof osteoderms and asymmetry thereof (left), and top-view-projection density plots of fusion area by genus (right), with red colour value indicating local fusion prevalence.



Supplementary Fig. 6. Directional trait variability in bilateral asymmetry of osteoderm fusion with the skull roof.

that this structural incongruence may confer mechanical advantages. The arrangement parallels other composite protective systems, such as the turtle shell (Zangerl, 1969; J. Gauthier, pers. comm., 23 March 2025). This bilateral asymmetry suggests that fusion does not follow a fixed anatomical template. The right-sided bias (mean $\sim 0.24\%$; $p = 0.035$) may reflect osteoderm detachment under asymmetric mechanical stress, complementing known mechanisms in which biomechanical strain contributes to the formation and patterning of reptile scales and osteoderms (Milinkovitch *et al.*, 2013; Cooper, Jahanbakhsh, & Milinkovitch, 2025; Dubansky *et al.*, 2025). If mechanically induced detachment plays a role, this asymmetry may represent a morphological correlate of lateralised behaviour (Rogers & Andrew, 2002), a phenomenon with deep evolutionary roots in reptiles (Reisz *et al.*, 2020).

This argument, however, raises a more general functional question. We observed that osteoderms and the skull roof associate across a spectrum from true fusion to a (more or less) tight apposition. These regions could allow osteoderms to function as a sacrificial protective layer. Once strain distribution between osteoderms and the skull roof exceeds a critical value, osteoderms may fracture away and absorb energy. In line with this, our dataset included specimens with defective or missing osteoderms but otherwise intact skull roof.

As a technical limitation, we note we could not always reliably distinguish true fusion from tight apposition based on our μ CT scans. Intimate association was more apparent in larger specimens, raising the possibility that minute gaps in smaller individuals remained undetected. Future research should therefore employ instrumented mechanical testing in addition to finite element analysis to evaluate this hypothesis experimentally.

Supplementary Note 9: On the evolution of dry tolerance

The genus *Liopholis* deviates from the expected association between dry tolerance and osteoderm thickness (Fig. 6 of the main text). This may reflect regulatory behaviour that constrains evolution, known as the Bogert effect (Huey, Hertz, & Sinervo, 2003; Muñoz, 2022). These lizards communally retreat into their burrows during the hottest parts of the day, where temperature and humidity remain comparatively stable (Henzell, 1972; Webber, 1978, 1979; Chapple, 2003). Fossoriality, possibly combined with sociality, may therefore buffer the selective pressure for thicker osteoderms. On a more general note, our reconstructions recovered no statistical support for the 'humid-ancestor' hypothesis proposed in earlier literature (Horton, 1972; Heatwole & Taylor, 1987; Chapple, 2003).

The ancestral state for dry tolerance remained unresolved (Fig. 6). This reflects the conceptual limitation of inferring deep evolutionary history from extant tip states. A similar pattern emerges from the LD1 phylomorphospace (Fig. 2 of the main text), which places dry-tolerant and non-dry-tolerant taxa at opposing ends, implying repeated divergences from a generalist ancestor. However, we caution against an overly strict interpretation: the LD1 metric inherently introduces circularity, and there is little biological reason to expect that the absence of dry tolerance would drive a specific morphotype.

Notably, the time-calibrated phylogeny underlying our analysis (Brennan *et al.*, 2024) challenges the hypothesis that the *Egernia* group entered Australia from New Guinea during the Pliocene (5.3–2.6 mya). Divergence estimates instead place the Australian crown group at ~ 25.6 mya and the split from *Proegernia* at ~ 36.5 mya. These dates support a much earlier arrival, potentially in the late Eocene when humid tropical forests dominated the continent. Thus, while the timeline shifts, the ecological conclusion remains unchanged: a humid habitat was ancestral, followed by repeated independent evolution of arid-adapted forms, often in concert with thicker osteoderms, as ancestral habitats became increasingly fragmented.

Supplementary Note 10: Extended assessment of the arboreality signal

Arboreal *Egernia*-group lizards showed lower structural complexity than non-arboreal taxa. In contrast to the strong signal recovered for fossoriality, the effect size was comparatively small ($d = -0.383$) and not detectable in multivariate analysis ($p = 0.13$). Likewise, arboreality shows a low degree of aggregation on the phylogeny, characterised by a low RI (0.25) and numerous reconstructed reversions. In our box-and-whisker plots, arboreal taxa cluster near the centre of the str_{hull} spectrum, whereas non-arboreal taxa span both extremes in a bimodal distribution (Fig. 3 of the main text). This suggests that, while arboreal taxa avoid extreme structural complexity, they do not converge on a specific morphotype. The lack of a strong functional signal likely reflects the different evolutionary demands of these lifestyles. Fossoriality involves extensive morphological specialisation such as limb reduction and cranial consolidation (Gans, 1974, 1978).

By contrast, the functional-morphological solution space for an arboreal lifestyle is much more diffusely defined (Kulyomina, Moen, & Irschick, 2019). Examples include neuroanatomy and skull morphology (Allemand *et al.*, 2017; Watanabe *et al.*, 2019; Macrì *et al.*, 2019; Pandelis, Grundler, & Rabosky, 2023). We therefore propose that it is comparatively easy to adopt arboreality when ecological space opens. Owing to ancestral habitat contraction and fragmentation, many species now occupy habitats with little or no tree cover. Therefore, the strongest predictor for arboreality may simply be the presence of trees, with morphological adaptations playing a subordinate role. Arboreality was reconstructed as likely non-ancestral to the Australian clade, with three independent acquisitions, including a major cluster originating in the shared ancestor of *Egernia*, followed by four reversions. Thus, seven of nine arboreal taxa likely inherited the trait from this ancestor. The evolution of str_{hull} showed only limited apparent correspondence with arboreality, especially in *Tiliqua*, which exhibit low structural complexity despite being non-arboreal. We note that trait mapping did not account for effects through allometry and non-focal lifestyles.

Supplementary Note 11: Context, allometry, and phylogenetic signal

Although we validated the functional predictions for dry tolerance (H1) and fossoriality (H2), we found no single raw trait to be strictly diagnostic. Neither suffices to reliably predict lifestyle without context, and no reconstructed trait-lifestyle history matches the phylogeny cleanly. This suggests a complex network of interactions rather than a linear cause-and-effect association. Except for the arboreal-fossorial combination, the lifestyles considered here are not mutually exclusive. Competing effects of non-focal lifestyles can therefore dampen the focal signal, either through direct association or trait-trait correlation. While overall trait integration was moderate ($r = 0.32$) and lacked sharply defined biological modules, local correlations influenced our models. For instance, Th_{OD} and Th_{matrix} are positively correlated ($r = 0.56$) but carry opposite lifestyle signals for dry tolerance ($d = 0.62$) and fossoriality ($d = -1.17$). Consequently, our models predict that a dry-tolerant taxon would exhibit a slightly smaller Th_{OD} if it were also fossorial, even though fossoriality does not have a detectable effect on Th_{OD} in isolation.

Body size accounted for ~36% of the total multivariate variance. For traits showing lifestyle associations, the strongest size effects occurred in str_{hull} ($|\beta_{std}| \geq 0.92$), followed by Th_{OD} ($\beta_{std} = 0.48$). Prior literature discusses size-related constraints in bone microanatomy, suggesting that small animals may lack the space for complex inclusions (Ebel *et al.*, 2020). Our dataset did not indicate such a 'lower limit' constraint. Instead, we observed that larger taxa had a disproportionately thicker, more compact, and less structurally complex osteoderm cover ($|\beta_{std}| \in [0.43, 0.94]$). This suggests positive allometry, where support structures scale disproportionately faster than body size to maintain performance (Clemente & Dick, 2023). We propose that this biomechanical scaling extends to the integumentary skeleton. Regarding shared ancestry, str_{hull} and Th_{OD} showed comparatively strong phylogenetic signal ($K \in [0.59, 0.89]$, $\lambda \in [0.78, 0.92]$), whereas phylogenetic signal in Th_{matrix} was borderline non-significant ($p \in [0.053,$

0.061]). Phylogenetic signal can obscure functional signals when traits track shared ancestry, which is why the phylogenetic context is essential for the correct interpretation of trait variation.

Taken together, these findings suggest that the *Egernia*-group osteoderm cover is a system that evolved under phylogenetically structured patterns, modified by complex functional associations. Notably, the intensity of the lifestyle signal roughly parallels the degree of functional-morphological specialisation that we would expect to arise from the respective lifestyles: fossoriality > dry tolerance > arboreality. However, these aspects are traditionally only studied and recognised in the endoskeleton or soft tissue. As the integumentary system has received comparatively little attention in this regard, we encourage future research to expand the study of lifestyle-trait associations in the osteoderm cover, but also to validate our findings experimentally. This could help to further resolve the still poorly understood functional adaptations and exaptations of the osteoderm cover across tetrapods.

A natural next step is to replicate the framework developed here in clades with structurally distinct osteoderm architectures, which would test the generality of the lifestyle signals we identified in *Egernia*-group skinks. Varanid lizards are a strong candidate. They span a wide size range and diverse lifestyles, and recent work reconstructs multiple independent late-Miocene osteoderm acquisitions in Australopapuan varanids that coincide with continental aridification (Ebel *et al.*, 2026). Whether the dry-tolerance signal we report replicates in this independent morphological and phylogenetic context would help distinguish clade-specific from general functional patterns.

Supplementary Note 12: Scan acquisition

We performed μ CT scans on 80 ethanol-preserved specimens representing 38 *Egernia*-group taxa (Supplementary Tab. 5). Juveniles and visibly damaged specimens were excluded. Whenever possible, each species was represented by at least two specimens of both sexes, and where applicable, two specimens per subspecies to capture morphological disparity even when the phylogeny did not resolve taxa at that level. Scans were acquired on a Phoenix Nanotom M (Waygate Technologies, Huerth, Germany) with a 10-minute scan time, collecting 1199 projections with 500 msec timing, a diamond-coated tungsten target, no filter, with 300 mA tube current, and a tube voltage of 65 kV for smaller specimens or 120 kV for larger specimens. We kept the setup and workflow as constant as possible across scans.

Snout-vent length (svl) was recorded before scanning (159 ± 81 mm), and linear head size (22.1 ± 11.2 mm) was measured digitally following Ebel *et al.* (2020). Across the dataset, voxel size averaged 20.6 ± 9.6 μ m, yielding a stable voxel-to-head-size ratio of $(9.5 \pm 0.8) \cdot 10^{-4}$. Scan volumes were reconstructed using the Phoenix Datos|x (RRID:SCR_017996) reconstruction software, applying an in-line median filter and ROI-CT filter. Volumes were manually registered along morphological axes of the respective specimens, and pruned to exclude all structures posterior to cervical vertebra C2. Unless noted otherwise, segmentation, quantification, and 3D visualisation were performed with VGSTUDIO MAX 2025.4 (RRID:SCR_017997).

Supplementary Tab. 5. Metadata, scan settings, and volume thresholding. Constant settings across dataset include a 10-minute scan time, collecting 1199 projections with 500 msec timing, a diamond-coated tungsten target, no filter, and 300 mA tube current. Abbreviations: snout-vent length (svl), head diameter (dia_{head}) Australia (AU), Queensland (QLD), South Australia (SA), Victoria (VIC), Western Australia (WA).

Specimen	Sex	Locality	svl [mm]	dia_{head} [mm]	Voltage [kV]	Voxel size [μ m]	Isovalue threshold
<i>Bellatorias frerei</i> MV D14417		n/a	186	20.5	120	22.5	31776
<i>Bellatorias frerei</i> MV R1617		n/a	189	23.4	120	25	35405
<i>Bellatorias major</i> MV D8588	♀	-9.08, 141.25	304	32.8	120	37.5	36044
<i>Bellatorias major</i> MV D8617	♀	n/a	288	30.8	120	35	19097
<i>Corucia zebrata</i> MV D5951		-6.57, 155.35	239	35.7	120	32.5	36526

Specimen	Sex	Locality	svl [mm]	dia _{head} [mm]	Voltage [kV]	Voxel size [μm]	Isovalue threshold
<i>Corucia zebrata</i> MV D65062	♂	Solomon Islands	269	34.0	120	35	27015
<i>Cyclodomorphus branchialis</i> MV D4605		-32.75, 115.87	84	7.7	65	10.5	16381
<i>Cyclodomorphus branchialis</i> MV D65874	♀	-31.33, 123.6	70	6.6	65	9	16369
<i>Cyclodomorphus casuarinae</i> MV D56347		-42.95, 147.25	143	11.2	65	16	14931
<i>Cyclodomorphus casuarinae</i> MV D5733		-42.22, 146.48	173	13.8	65	17	28142
<i>Cyclodomorphus gerrardii</i> MV D3463		-29.68, 152.93	247	26.7	120	32.5	23517
<i>Cyclodomorphus gerrardii</i> MV D56631	♂	-31.47, 152.6	166	19.0	120	25	27969
<i>Cyclodomorphus melanops elongatus</i> MV D63713	♂	-32.57, 136.75	100	7.9	65	11	26946
<i>Cyclodomorphus melanops elongatus</i> MV D63714	♀	-32.57, 136.75	107	7.7	65	11	23832
<i>Cyclodomorphus melanops melanops</i> MV D42000		n/a	92	8.3	65	11	4343
<i>Cyclodomorphus melanops melanops</i> MV D42002		n/a	93	7.8	65	10	21957
<i>Cyclodomorphus michaeli</i> MV D33722		-37.35, 149.48	92	7.0	65	9	25694
<i>Cyclodomorphus michaeli</i> MV D39196		-37.35, 149.48	92	7.7	65	10.5	22856
<i>Cyclodomorphus praealtus</i> MV D70896		-36.38, 148.42	80	7.2	65	10.5	24338
<i>Cyclodomorphus praealtus</i> MV D77601		-35.87, 148.5	94	7.7	65	10.5	26327
<i>Egemia cunninghami</i> MV D16461		-36.75, 145.66	205	25.7	120	30	34565
<i>Egemia cunninghami</i> MV D52969	♂	-36.75, 145.66	225	27.2	120	30	34600
<i>Egemia depressa</i> MV D2877		AU, SA	79	12.2	65	13.5	16844
<i>Egemia depressa</i> MV D3443		AU, WA	93	13.3	65	13	34091
<i>Egemia hosmeri</i> MV D4985	♂	-19.65, 134.18	147	19.2	120	19	34120
<i>Egemia kingii</i> MV D706		n/a	182	20.5	120	25	28109
<i>Egemia kingii</i> MV R927		n/a	231	25.2	120	30	33240
<i>Egemia mcphreei</i> MV D15423		-31.32, 148.98	96	10.4	65	13.5	31645
<i>Egemia mcphreei</i> MV D54283		-31.32, 148.98	96	11.5	65	14.5	30290
<i>Egemia napoleonis</i> MV D8252		-34.33, 123	141	16.1	65	18	17080
<i>Egemia rugosa</i> MV D52428	♀	AU, QLD, Cleokee Stn.	246	26.8	120	30	35168
<i>Egemia rugosa</i> MV D8943	♂	n/a	217	24.6	120	27.5	36921
<i>Egemia saxatilis intermedia</i> MV D69680	♂	AU, VIC, Grampians	104	12.2	65	15	27916
<i>Egemia saxatilis intermedia</i> MV D75648	♀	-36.91, 148.13	109	11.9	65	14.5	29641
<i>Egemia saxatilis saxatilis</i> MV D39320		n/a	111	13.8	65	16	29345
<i>Egemia saxatilis saxatilis</i> MV D39322	♀	-37.20, 142.47	114	13.4	65	15	30475
<i>Egemia stokesii stokesii</i> MV R931		n/a	150	18.0	65	18	28439
<i>Egemia stokesii stokesii</i> MV R932		n/a	149	16.8	65	17.5	30175
<i>Egemia stokesii zellingi</i> MV D16268	♀	-31.97, 141.45	144	17.2	120	20	36073
<i>Egemia stokesii zellingi</i> MV D56346	♂	-31.97, 141.45	132	17.9	120	17.5	36160
<i>Egemia striolata</i> MV D50641	♂	-29.78, 146.07	100	12.4	65	15	29473
<i>Egemia striolata</i> MV D77705	♀	-35.73, 143.91	101	11.5	65	15	29123
<i>Liopholis inornata</i> MV D51748	♀	AU, QLD, Birdsville	77	11.1	65	11.5	28601

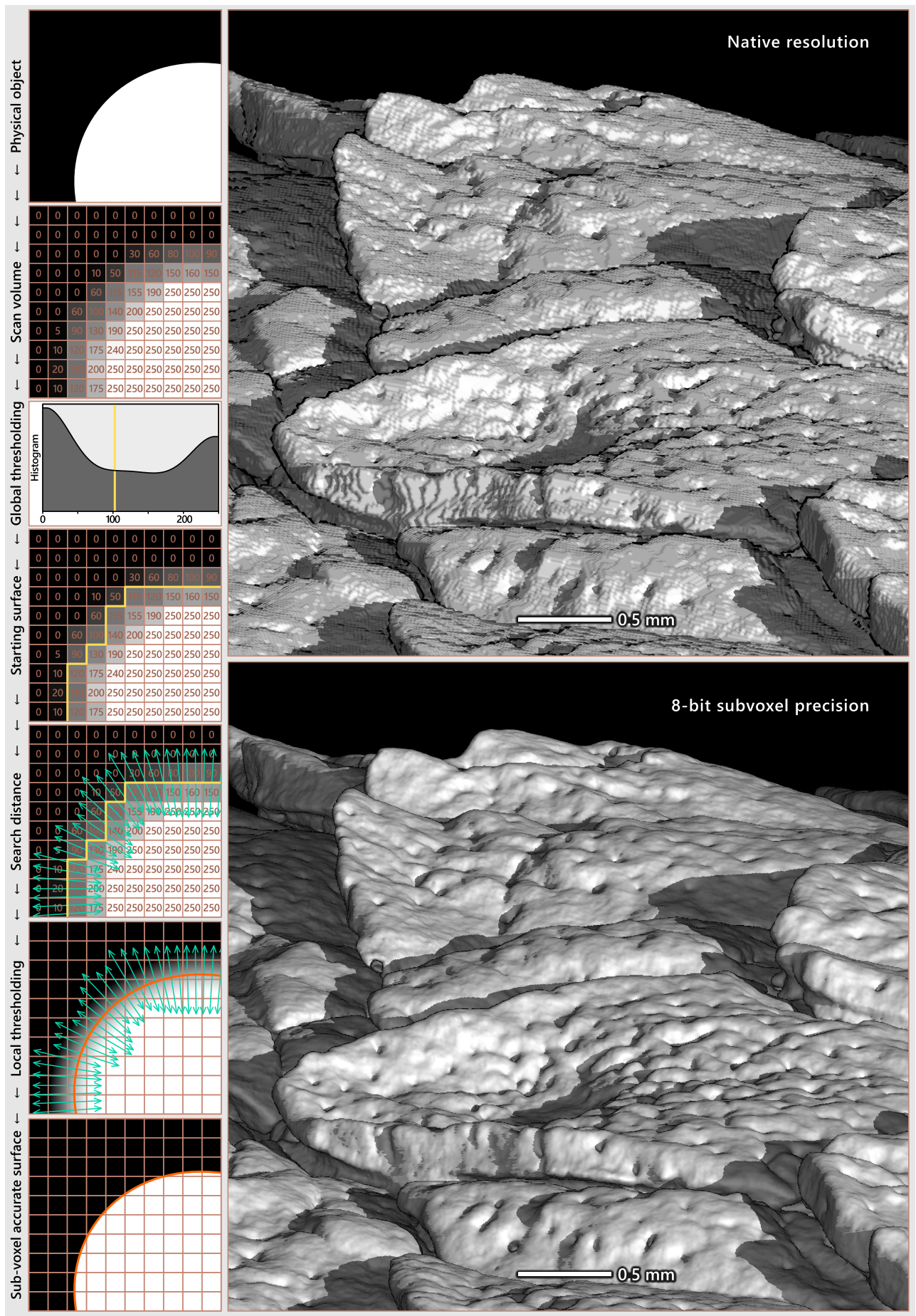
Specimen	Sex	Locality	svl [mm]	dia _{head} [mm]	Voltage [kV]	Voxel size [μm]	Isovalue threshold
<i>Liopholis inornata</i> MV D61201	♂	-34.90, 140.52	78	11.3	65	12.5	27898
<i>Liopholis margaretae personata</i> MV D56333		-31.20, 138.47	95	10.9	65	13.5	27024
<i>Liopholis margaretae personata</i> MV D56334		-31.32, 148.98	87	10.6	65	12.5	24352
<i>Liopholis modesta</i> MV D38507		-29.05, 151.60	103	11.6	65	14	25144
<i>Liopholis modesta</i> MV D38508		-29.05, 151.60	106	12.9	65	15.5	29060
<i>Liopholis montana</i> MV D2022		-35.53, 148.77	90	11.0	65	14	24227
<i>Liopholis montana</i> MV D75706		-36.95, 147.13	96	10.5	65	13.5	28054
<i>Liopholis multiscutata</i> MV D54086		-35.83, 137.25	88	11.0	65	12.5	6369
<i>Liopholis multiscutata</i> MV D54425	♂	-35.83, 137.25	80	11.1	65	12	25739
<i>Liopholis pulchra</i> MV D5677		n/a	97	11.5	65	14	22233
<i>Liopholis pulchra</i> MV D71559		n/a	96	12.3	65	14	25064
<i>Liopholis slateri slateri</i> MV D476	♂	-24.30, 132.68	84	11.5	65	12	19598
<i>Liopholis slateri slateri</i> MV D92	♀	-27.55, 135.45	92	12.3	65	13.5	18849
<i>Liopholis striata</i> MV D4953	♀	-21.53, 133.88	90	12.2	65	14	25800
<i>Liopholis striata</i> MV D4982	♂	-21.53, 133.88	97	13.0	65	14.5	27535
<i>Liopholis whitii</i> MV D34037	♂	-31.60, 148.95	82	10.8	65	13	26931
<i>Liopholis whitii</i> MV D75028	♀	n/a	77	9.5	65	11	24940
<i>Lissolepis coventryi</i> MV D55626	♂	n/a	85	9.4	65	12.5	29135
<i>Lissolepis coventryi</i> MV D75390	♀	-37.06, 142.47	78	8.3	65	10.5	25989
<i>Lissolepis luctuosa</i> MV D1226		AU, WA	104	11.5	65	14.5	14563
<i>Lissolepis luctuosa</i> MV D903		-33.63, 150.28	135	15.6	65	18	31095
<i>Tiliqua gigas</i> MV D14411	♀	-8.67, 142.92	277	32.3	120	35	32077
<i>Tiliqua gigas</i> MV D5926		n/a	232	28.8	120	32.5	29418
<i>Tiliqua multifasciata</i> MV D1087	♂	n/a	238	29.2	120	30	30575
<i>Tiliqua multifasciata</i> MV R1615	♀	n/a	228	29.2	120	30	30143
<i>Tiliqua nigrolutea</i> MV D39107	♂	-36.00, 148.78	293	30.6	120	32.5	34672
<i>Tiliqua nigrolutea</i> MV D41716		-36.33, 150.08	312	33.8	120	35	36629
<i>Tiliqua occipitalis</i> MV D39228	♀	-34.73, 135.87	241	27.6	120	30	33239
<i>Tiliqua occipitalis</i> MV D9524	♂	-33.85, 135.23	258	27.0	120	37.5	33890
<i>Tiliqua rugosa aspera</i> MV D71306	♂	-37.19, 142.34	296	34.2	120	37.5	37631
<i>Tiliqua rugosa aspera</i> MV D76315	♀	-36.07, 141.33	334	36.5	120	37.5	34680
<i>Tiliqua rugosa rugosa</i> MV D40045		n/a	276	33.3	120	35	35452
<i>Tiliqua rugosa rugosa</i> MV D8005		n/a	275	37.3	120	37.5	34552
<i>Tiliqua scincoides intermedia</i> MV D11976		n/a	331	33.5	120	37.5	33760
<i>Tiliqua scincoides intermedia</i> MV D72665	♂	-16.68, 132.06	318	35.1	120	32.5	33701
<i>Tiliqua scincoides scincoides</i> MV D33288	♀	n/a	283	29.8	120	32.5	32870
<i>Tiliqua scincoides scincoides</i> MV D48672	♂	-37.63, 149.46	264	28.8	120	32.5	33206

Supplementary Note 13: Segmentation

As an x-ray-based visualisation method, computed tomography translates the radiodensity of a physical object into grey values in a digital volume. Thresholding these grey values is a critical step in processing. It isolates voxels (“3D-pixels”) above a defined grey value and converts them into a unified Region of Interest (ROI) for downstream analyses. In vertebrate morphology, this is commonly used to extract the comparatively radiodense endoskeleton from the surrounding scan volume. It can also be used to isolate the entire specimen from its environment, which is useful for volume-rendered whole-specimen visualisations (see Fig. 1). This works because μ CT scans of unstained ethanol-preserved specimens typically show three discrete maxima in their grey-value histogram. In order of increasing radiodensity, these correspond to air, soft tissue, and hard tissue. Although the absolute positions of these maxima vary across scans, their order is consistent and their relative spacing is comparatively stable (albeit in a non-linear fashion). An intuitive and replicable threshold between these maxima is their interpeak midpoint. It is the standard preset in VGSTUDIO MAX and aligns with the behaviour of the IsoData and Default thresholding methods in FIJI (Landini *et al.*, 2025). Unlike prior work (Ebel *et al.*, 2020; Kaffler *et al.*, 2023; Fornari & Müller, 2025), we apply thresholding volumetrically rather than slice by slice, which should improve coherency.

A major problem in digitising morphological structures via μ CT is the partial-volume effect (Mano *et al.*, 2021). No biological surface follows the stepped outline of a digital volume when its representation is constrained by voxel size. A voxel that is partially intersected by a surface therefore holds a grey value that reflects a mixture of the two structures it separates. The decision to include or exclude such a voxel in the ROI is consequently arbitrary and sensitive to small changes in scan acquisition or thresholding strategy. This can introduce systematic error in microanatomical quantification (Bouxsein *et al.*, 2010). We address the issue by means of sub-voxel-accurate computation, an approach widely used in industrial and engineering metrology (e.g., Stopp, Christoph, & Weise, 2020; Xue & Li, 2025). In VGSTUDIO MAX, this is implemented through the Advanced Surface Determination function, which applies local thresholding to fit a surface in 3D space that maximises grey-value separation within a defined search distance from a starting contour (which itself may be based on a global grey-value threshold). It refines the fitted surface at an 8-bit sub-voxel level ($2^8 = 256$ increments per voxel along each axis), which effectively increases the precision to 1/10 of a voxel (Supplementary Fig. 7, Läßle, 2009). This enables much finer localisation of object outlines and thus approximates structural detail lost during digitisation.

After performing an advanced surface determination to isolate all hard tissue from the rest of the scan volume, we cleaned and removed all endoskeletal elements by manual segmentation. We then constructed a continuous ROI that included the individual osteoderms and the spaces that interconnect between them. We bridged these spaces using the close function in the erode/dilate dialog, first in an exploratory pass with the box mode to exclude undetected extra-osteodermal particles, and then with the computationally more demanding sphere mode at a search distance of 32 voxels to obtain a topologically continuous surface. To interconnect osteoderm islands separated by more than 32 voxels, we added a linear sequence of accessory points before re-running the algorithm. This bridged all physiological gaps in the osteoderm cover, excluding the ear openings, eye openings, and mouth opening. We note that we did not apply this procedure to pathological openings caused by osteoderm damage or loss. As a final step, we subtracted voxels intersecting the endoskeleton to counteract artificial inflation introduced by over-smoothing across concave internal surfaces. The result is a “shrink-wrapped” ROI representing the osteoderm cover (or osteoderm hull), used in all downstream quantification that treats the osteoderm cover as a functional unit (rather than as a set of individual osteoderm elements).



Supplementary Fig. 7. Example workflow for sub-voxel accurate surface computation, modified from Hiller & Hornberger (2016; left) with corresponding oblique lateral view on the skull roof osteoderms of *Egernia depressa* MV 3443 in native resolution (13 μ m, top right) and at 8-bit sub-voxel precision (bottom right), isosurface-rendered with VGSTUDIO MAX.

Supplementary Note 14: Microanatomical quantification

We first dilated the osteoderm-hull ROI spherically by 1 voxel and extracted four new volumes from it. Into each of these, we pasted the non-dilated osteoderm-hull ROI. This procedure prevents the pruning of voxels that intersect ROI boundaries during extraction, while preserving the sub-voxel-accurate ROI for downstream analysis. We also pasted the ROI defining the individual osteoderms (that we used earlier to construct the osteoderm-hull ROI).

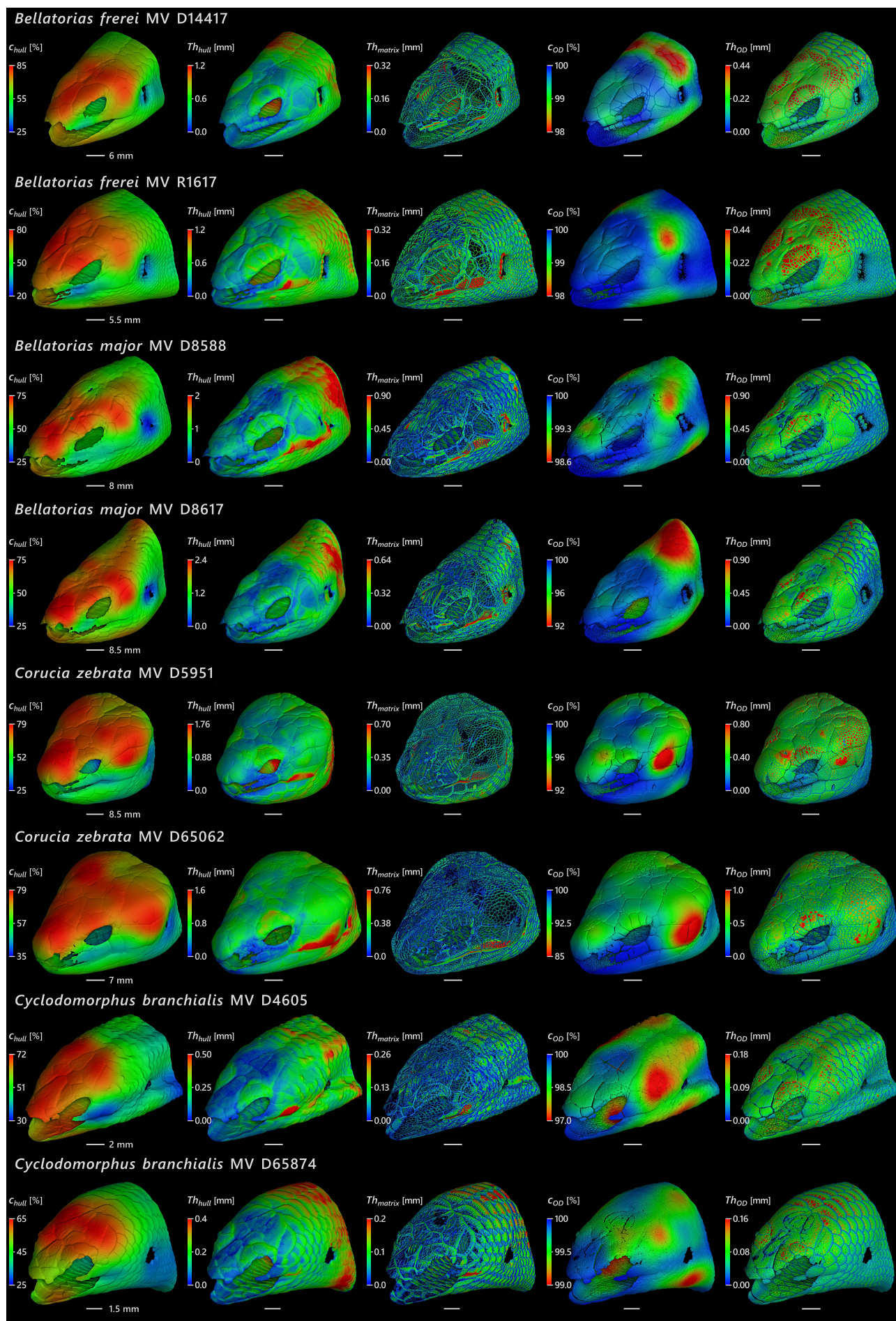
In the first volume, we performed an advanced surface determination (search distance 4 voxels, no filtering, no void removal) between the hard- and soft-tissue maxima to define the individual osteoderms. We note that the procedure does not evaluate voxels outside the extracted volume, regardless of the specified search distance. The extraction step therefore ensured that the resulting surface remained within the predefined osteoderm-hull limits while still permitting sufficient search distance to differentiate structures within those limits. From the osteoderm-hull ROI properties (morphometrics tab), we reported *BV/TV*, *BS/BV*, *Tb.Th*, *Tb.N*, *Tb.Sp*, and *DA*. These traits are typically interpreted for the microanatomical quantification of trabecular bone. Their interpretation in our framework is detailed in the manuscript subsection Quantified traits.

In the second volume, we defined the surface as predetermined through the osteoderm-hull ROI. We then performed an inclusion analysis with the osteoderm ROI as indication ROI (smoothing window 100 voxels, directional variability = [0,1,0]) to compute osteoderm cover compactness (as defined in the Quantified traits section). We recorded the mean value and exported directional trait variability as a csv file. We then performed a wall thickness analysis with the sphere method (analysis: material, create closed surface, tick components, Supplementary Figs. 8-17), which computes thickness by determining the diameter of the largest sphere that can fit inside a surface at any given point. We recorded the mean value, and exported directional trait variability as a red-white gradient image stack in 500 increments.

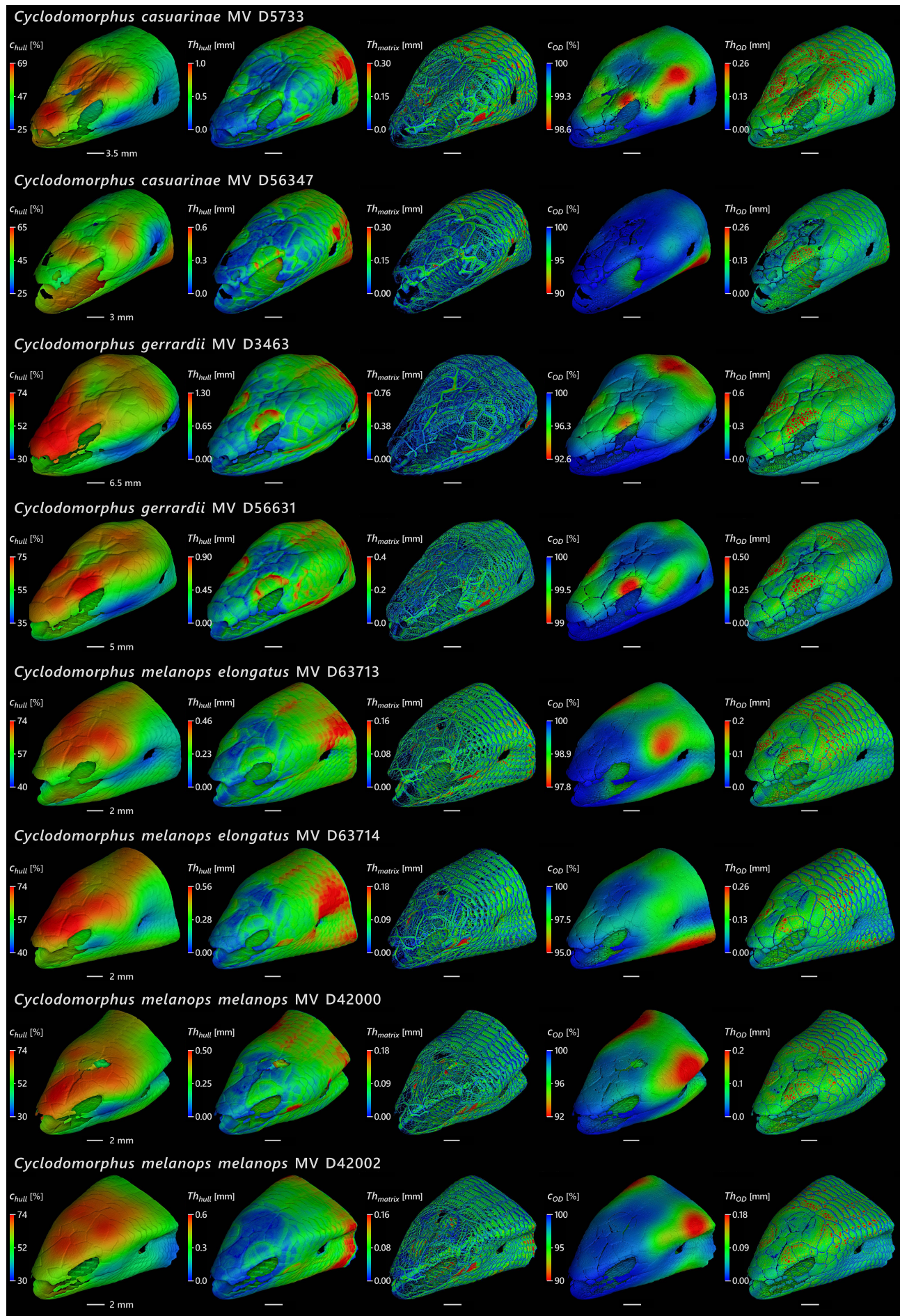
In the third volume, we performed another advanced surface determination halfway between the hard- and soft-tissue maxima (search distance 4 voxels, filter particles < 100 voxels, filter all voids), this time targeting the individual osteoderm elements. On the resulting ROI, we performed a porosity analysis with VG EasyPore under default settings, recorded the mean value, and exported directional trait variability as a csv file. For downstream analysis, we converted porosity [%] into compactness [%] by subtracting each value from 100. We then performed a wall-thickness analysis with the sphere method (Supplementary Figs. 8-17), recorded the mean value, and exported directional trait variability as a red-white gradient image stack in 500 increments (Supplementary Fig. 18).

In the fourth volume, we pasted the osteoderm ROI from the third volume and subtracted it from the osteoderm-hull ROI (preexisting from the initial extraction). The resulting ROI represented the inter-osteodermal spaces (or matrix). We defined the surface as predetermined through this matrix ROI and quantified local matrix thickness with the sphere method (Supplementary Figs. 8-17). We recorded the mean value and exported directional trait variability as a red-white gradient image stack in 500 increments (Supplementary Fig. 18). The spacing ensured that increments remained safely above voxel size while providing much higher sampling resolution than exporting individual cross-sections (e.g., Ebel *et al.*, 2020).

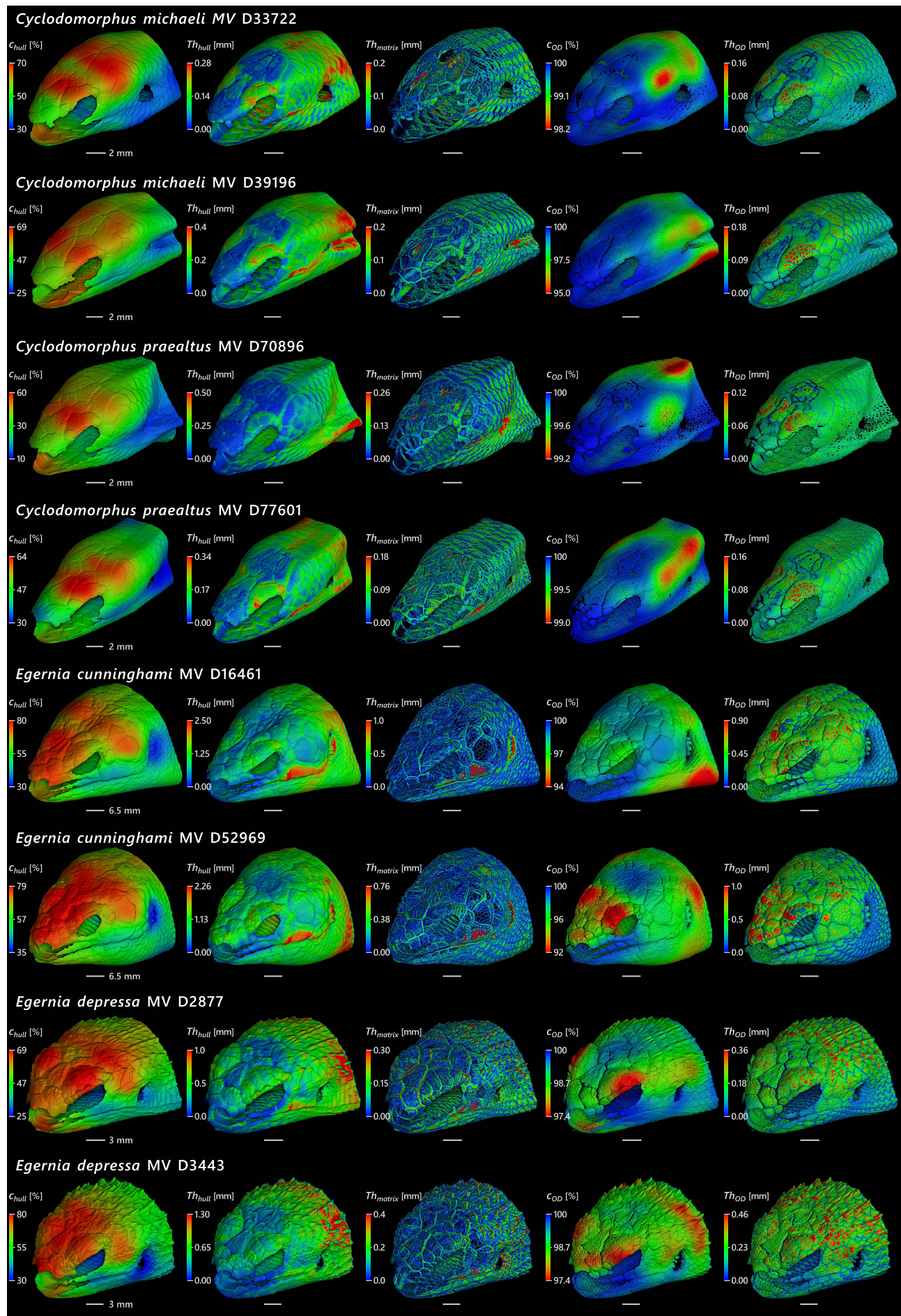
All quantification was computed volumetrically and at sub-voxel accuracy. Prior microanatomical work on structures of comparable geometry (dermal bones of the skull roof) relied on per-slice grey-value analyses in cross-sectional series (Ebel *et al.*, 2020; Kaffler *et al.*, 2023; Manning *et al.*, 2023; Fornari & Müller, 2025). Our protocol refines these approaches, as it quantifies structure volumetrically in 3D-space with 8-bit sub-voxel processing. A technical consequence is that compactness values are not strictly comparable between methods. In 2D cross-sections, canals and voids that open to the exterior can be misinterpreted as internal cavities, inflating porosity estimates by design. We therefore expect comparatively low osteoderm compactness values with our protocol. Osteoderm cover compactness, however, is unaffected by whether a space communicates with the exterior, as it is based on an inclusion analysis later translated into compactness (compactness = 1 - proportion of inclusions).



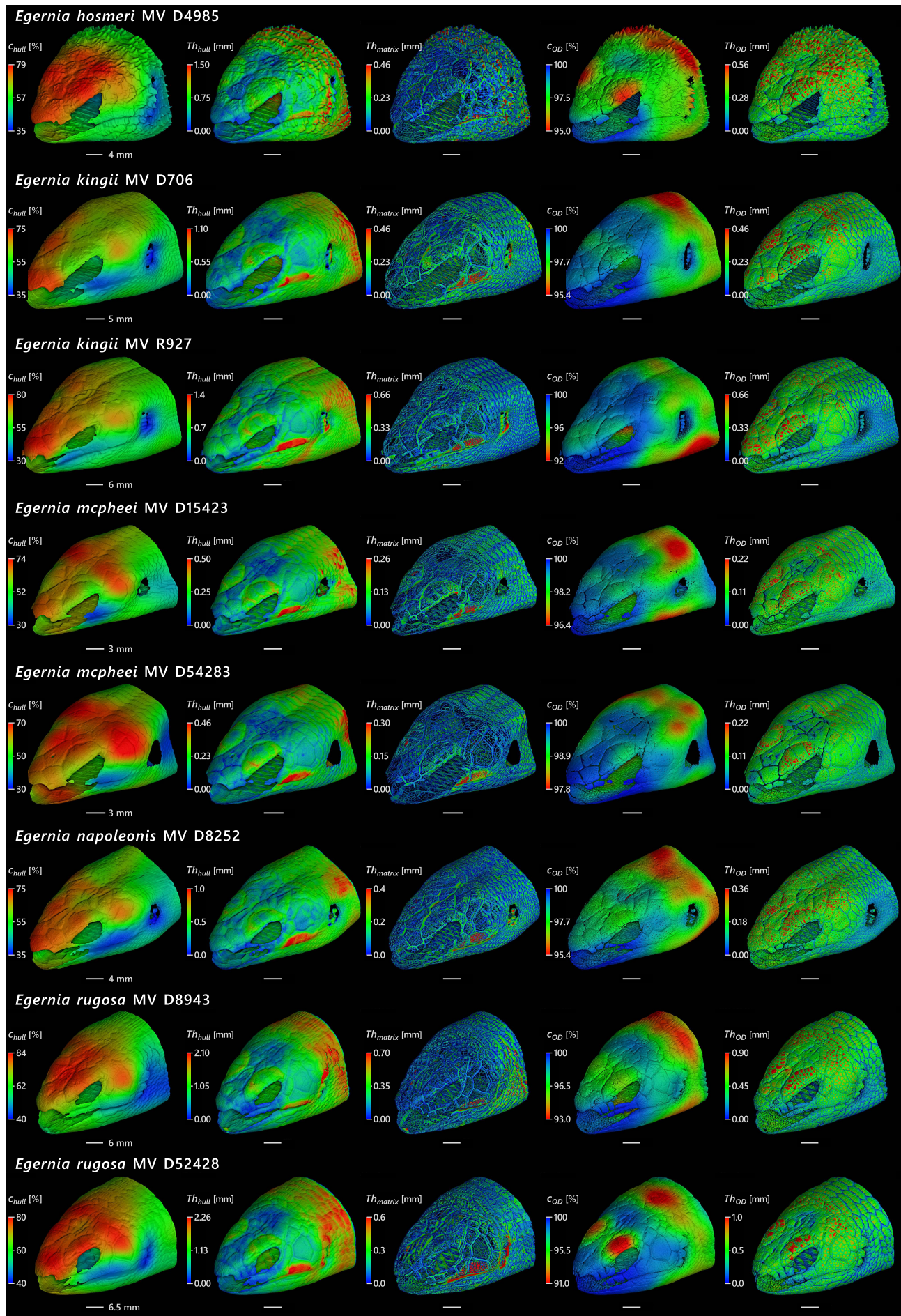
Supplementary Fig. 8. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



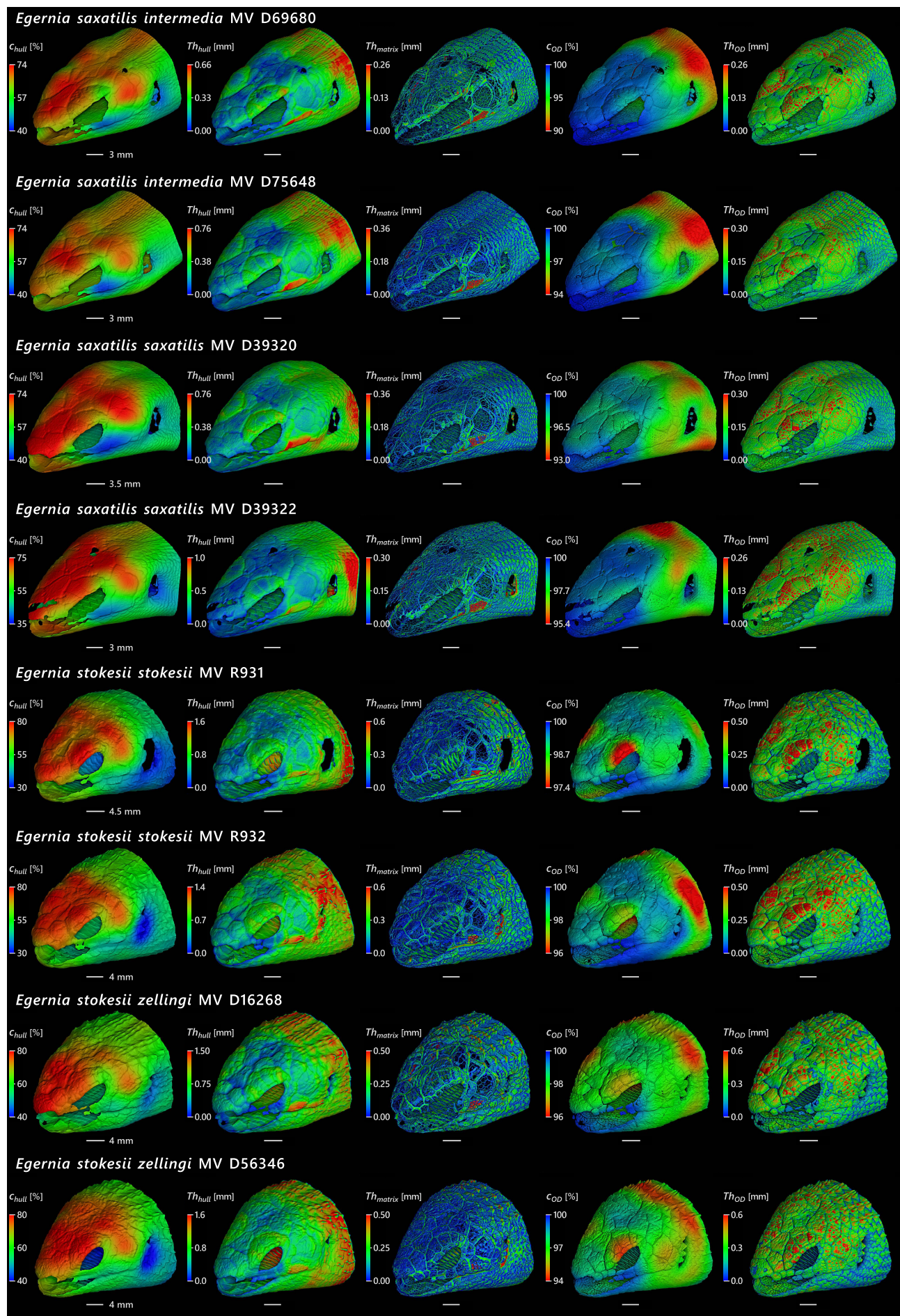
Supplementary Fig. 9. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



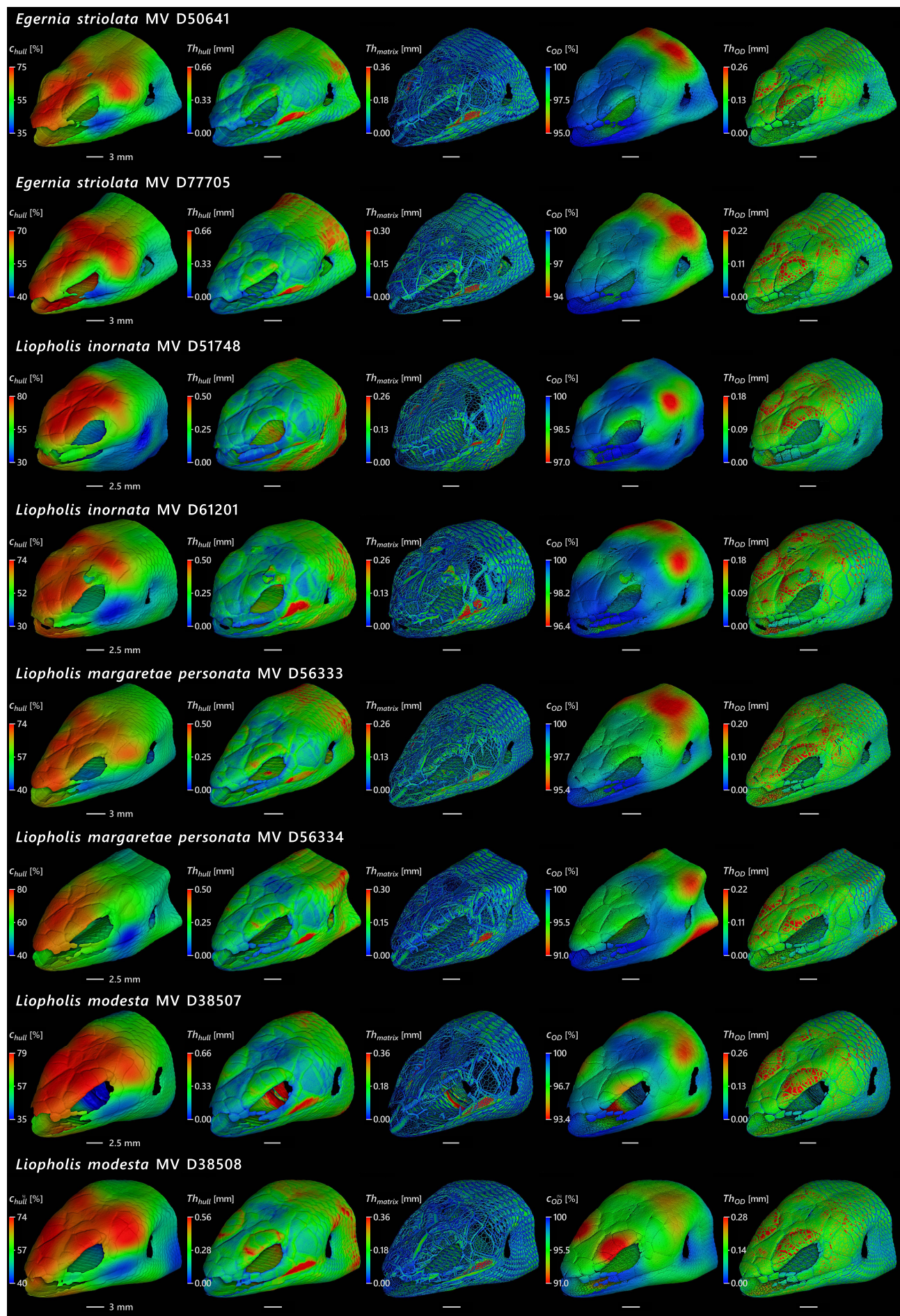
Supplementary Fig. 10. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



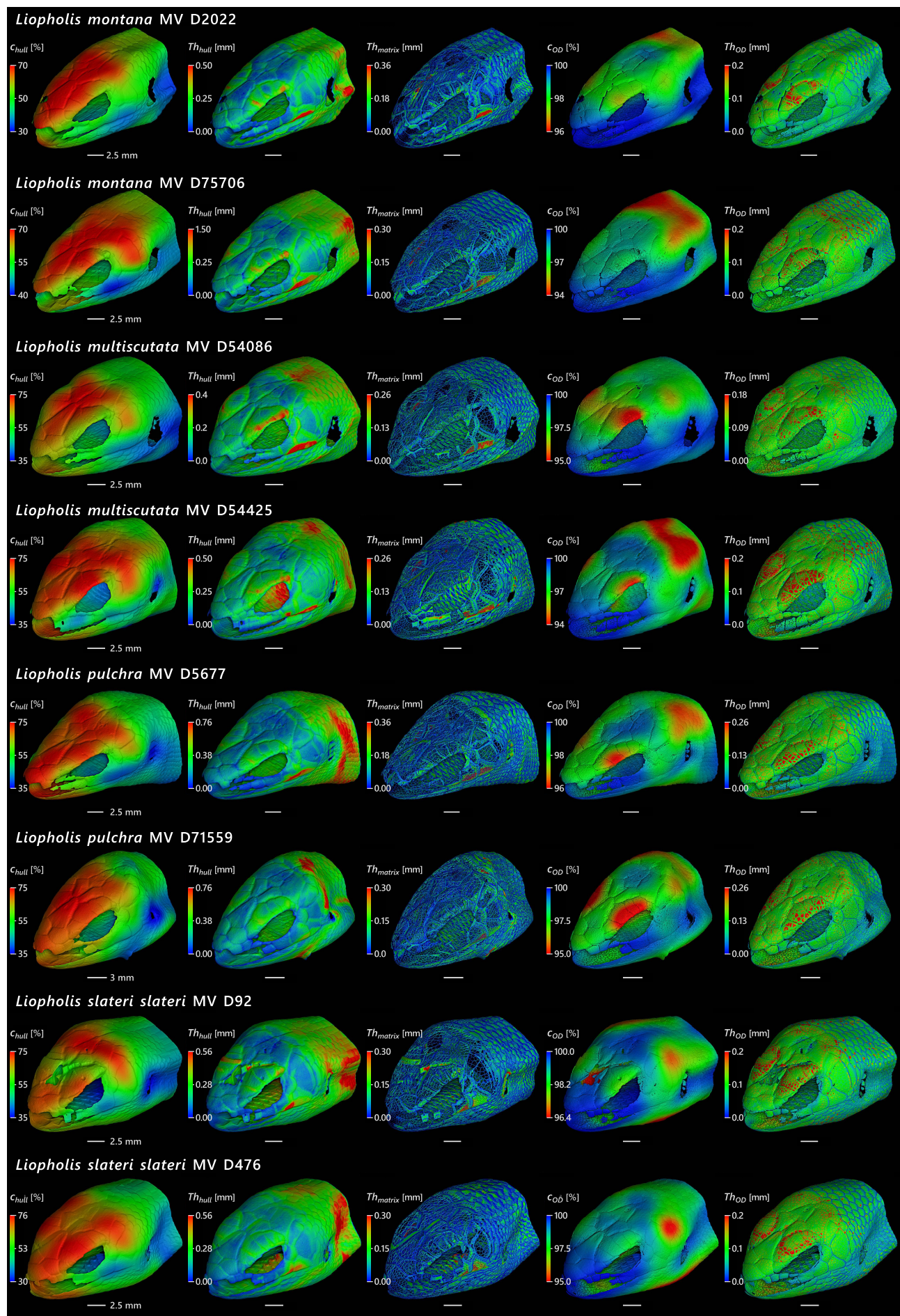
Supplementary Fig. 11. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



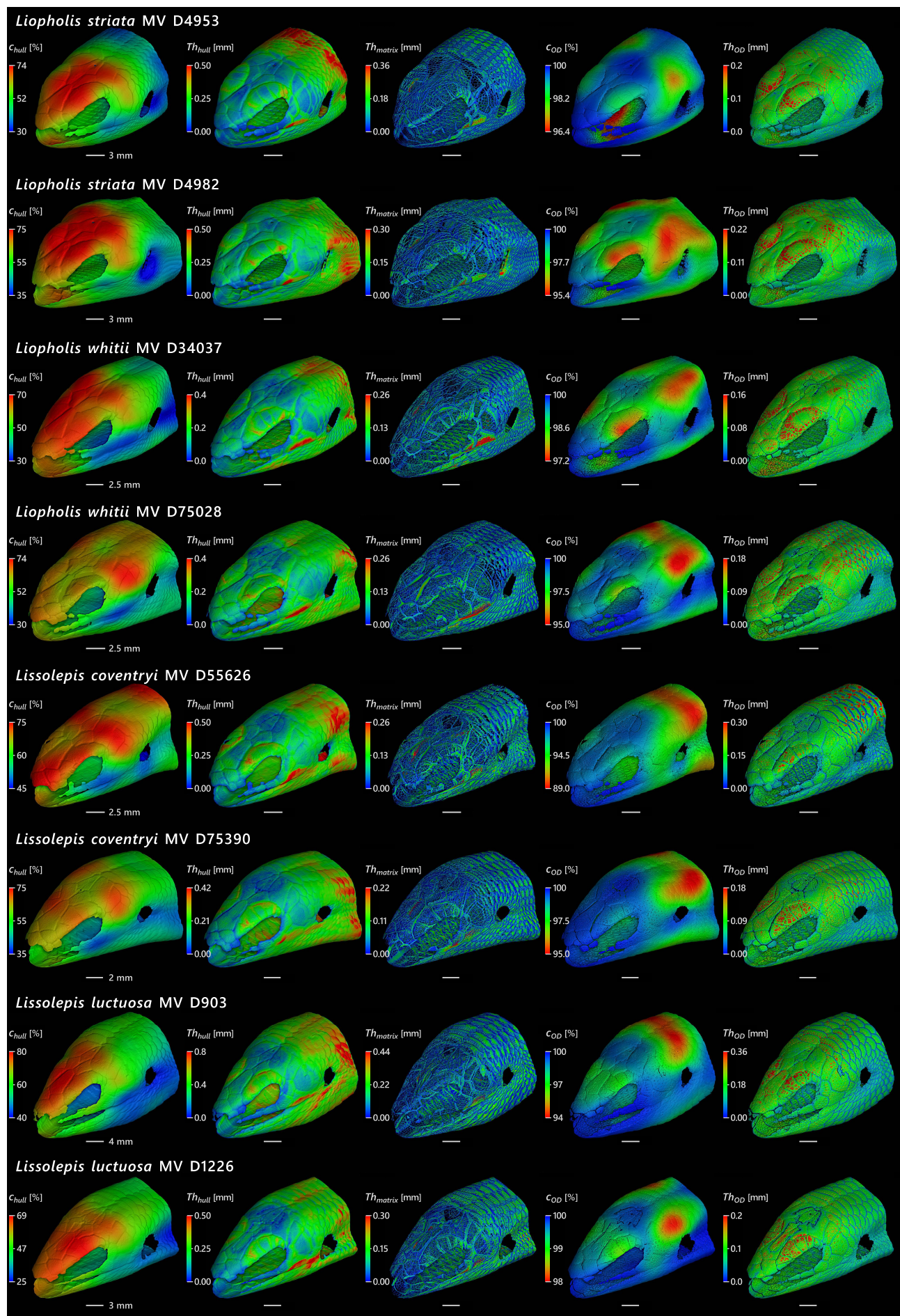
Supplementary Fig. 12. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



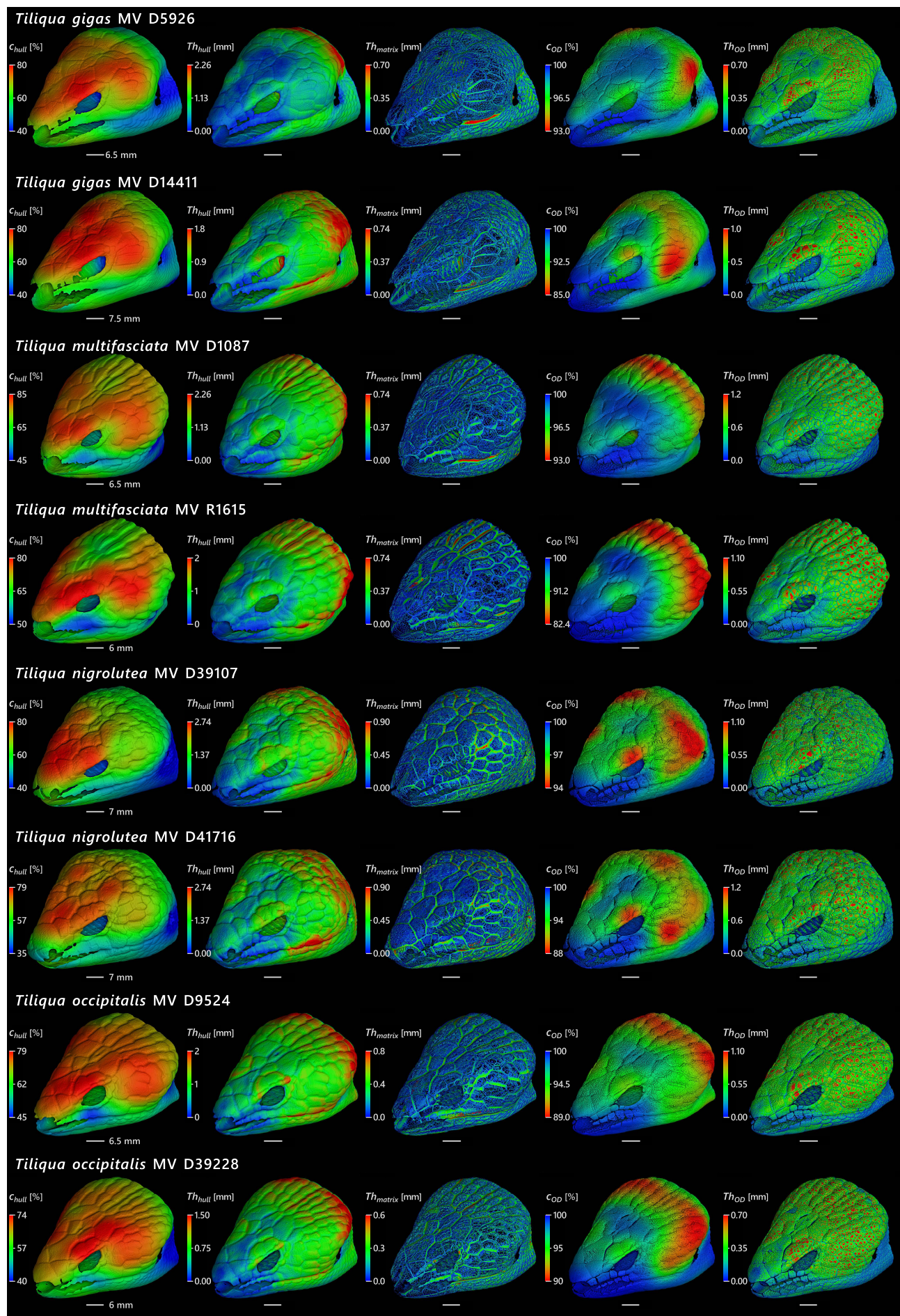
Supplementary Fig. 13. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



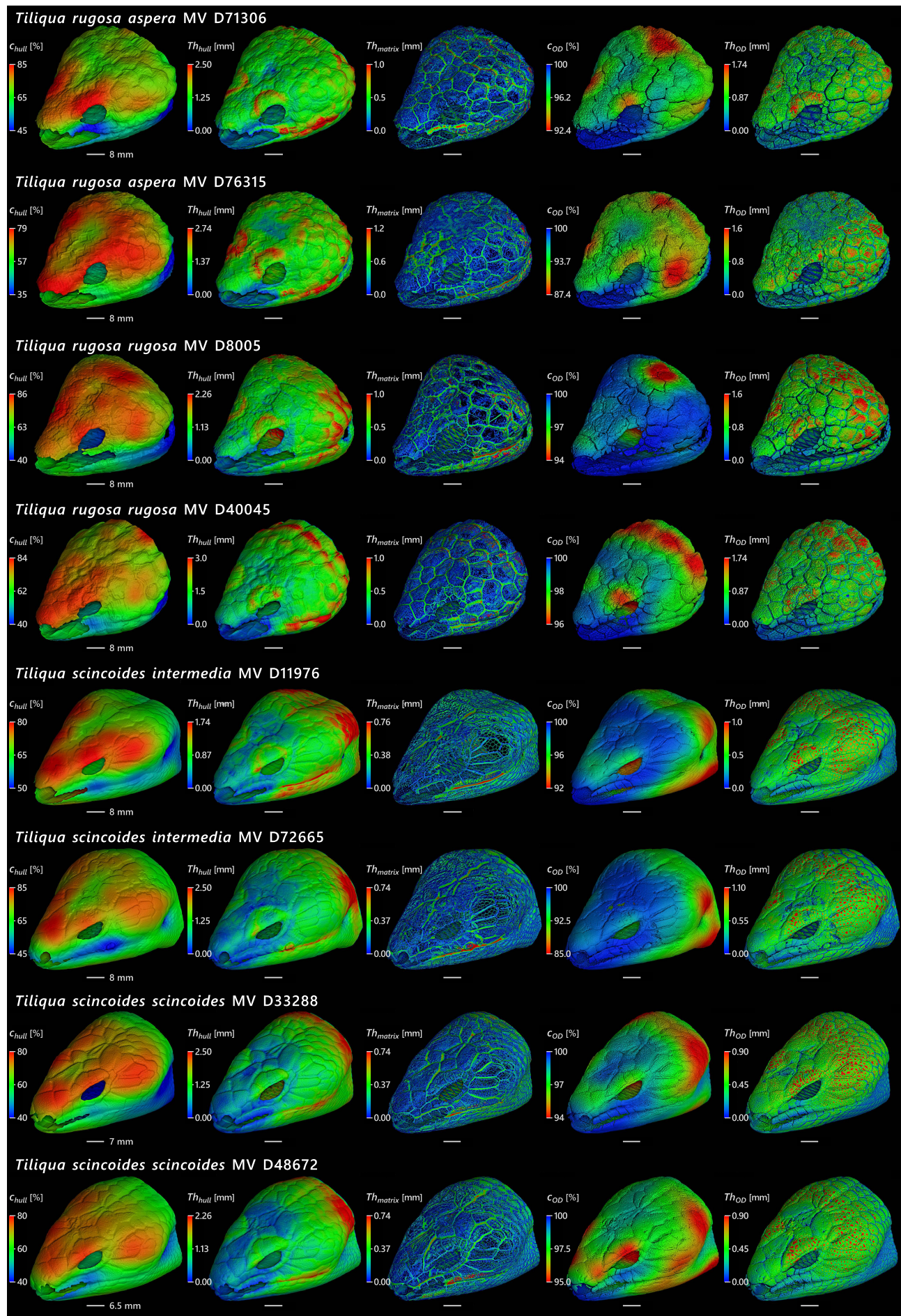
Supplementary Fig. 14. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



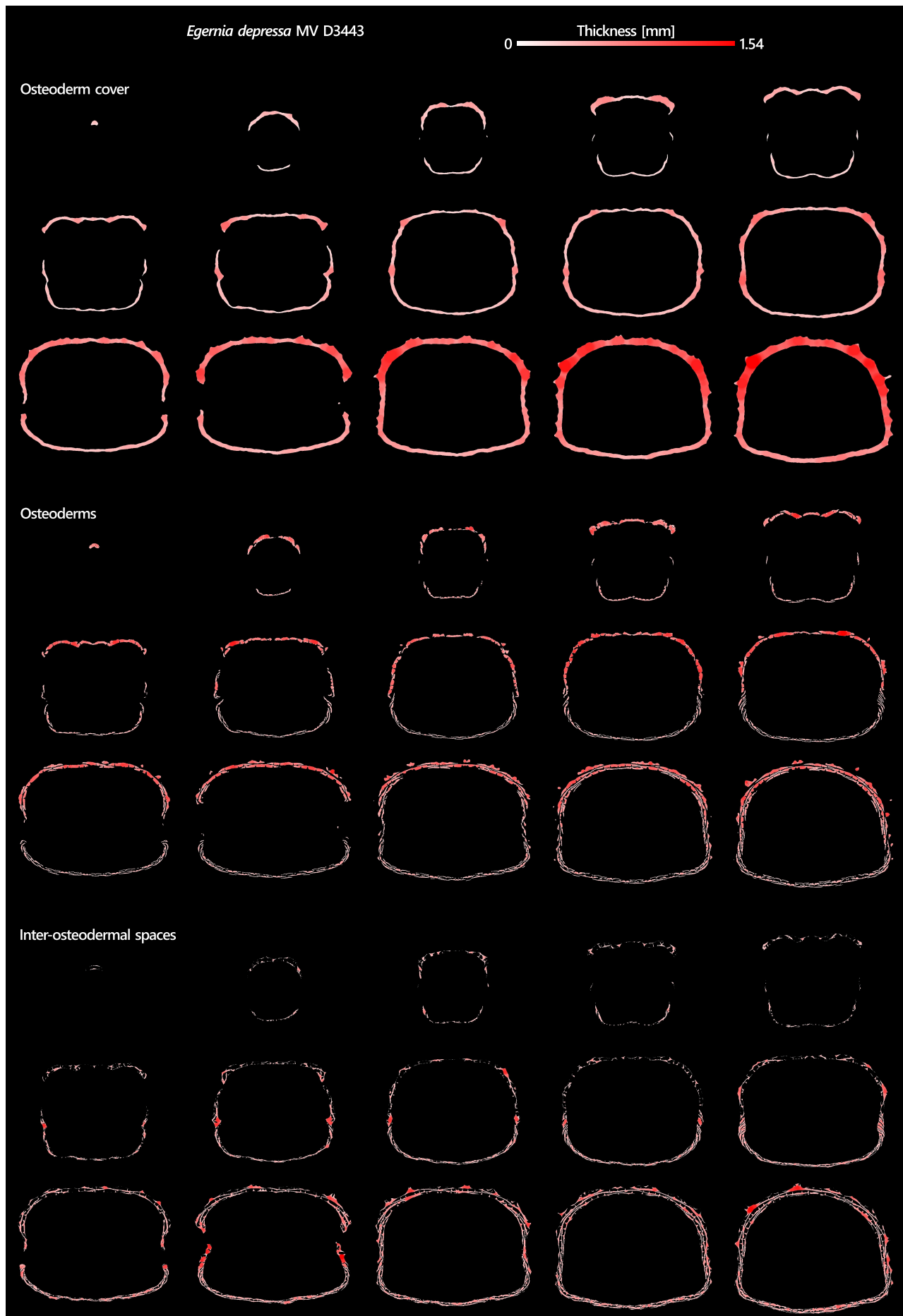
Supplementary Fig. 15. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



Supplementary Fig. 16. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



Supplementary Fig. 17. 3D specimen overview: hull compactness & thickness, matrix thickness, osteoderm compactness & thickness (from left).



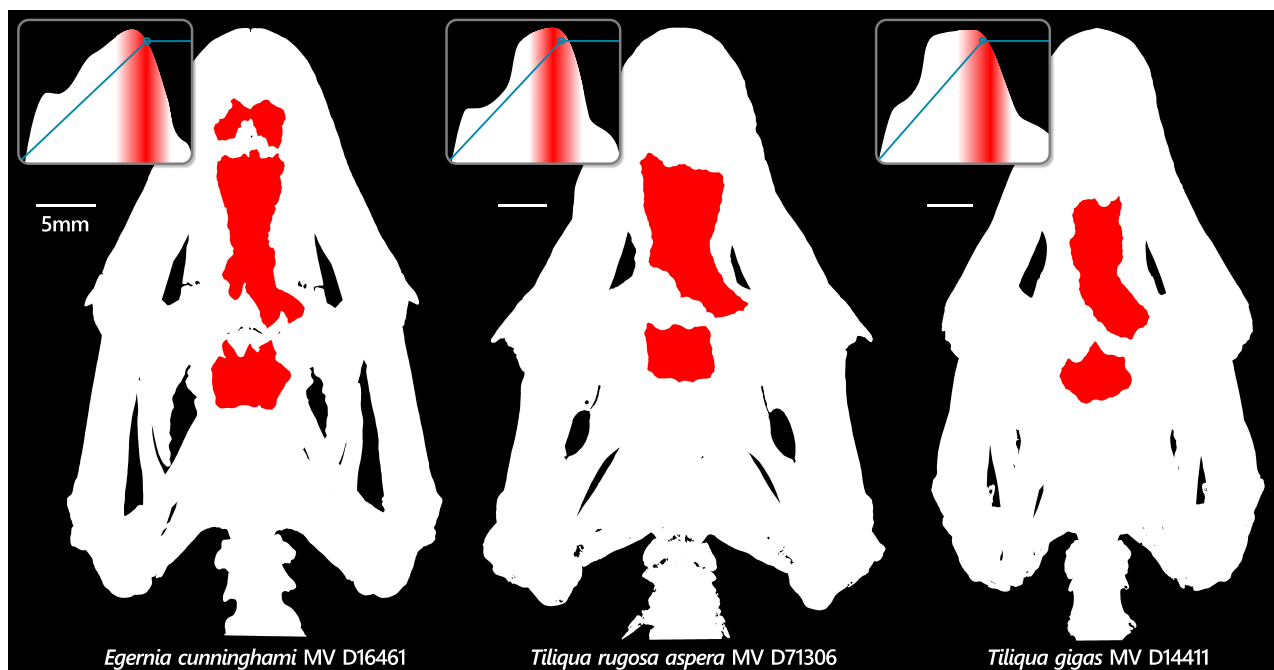
Supplementary Fig. 18. Subset of the exported directional trait variability image stacks, with red-white gradient coding for local thickness, at the example of *Egernia depressa* MV D3443.

Supplementary Note 15: Quantification of fusion with the skull roof

As a final step, we quantified fusion between the skull roof and cephalic osteoderms. To this end, we exported a Phong volume render of the cranium in top-view parallel projection (3000×5000 px Tiff). Before export, we colour-coded the histogram to render fused regions in red, with intensity reflecting penetration depth into the bone surface. To this end, opacity was set to increase linearly from 0% at the lower histogram end to 100% at the hard tissue maximum. We isolated the fusion area in GIMP 2.10 (RRID:SCR_003182) using Color Select, removed artefacts manually, and connected fusion islands up to 50 px by grow-shrink operations before filling them with monochromatic red (#FF0000). We thresholded unfused bone and background to black (#000000) and white (#FFFFFF), flattened the image, and exported it again, including left- and right-half versions. We embedded scale (px/mm) in FIJI 2.16 (RRID:SCR_002285) based on the VGSTUDIO MAX scale bar. We then quantified fusion area and total bone area in this projection, and we report relative fusion [%] as their ratio. Examples of thresholded top-view parallel fusion projections are provided in Supplementary Fig. 19.

To extract directional gradients, we used the imager package (Barthelme *et al.*, 2025) in R. Here, we computed the proportion of fusion pixels (red) and total pixels (red + white) at each position along the anteroposterior axis for the whole image, and we report this as directional trait variability in fusion area [%]. We repeated this for the left and right halves and report overall fusion asymmetry as the ratio of total fused area between sides [%], and directional asymmetry as the difference at each position along the anteroposterior axis [%].

We then used the imager package to extract slice-wise values from the image stacks exported with VGSTUDIO MAX, in which local thickness was encoded as a red-white gradient. We converted these values to millimetres and normalised anteroposterior trait-mapping positions to align compactness and fusion with the thickness data. The resulting data frame reports, for each specimen, compactness and thickness of the osteoderm cover, individual osteoderms, and inter-osteodermal spaces, as well as relative fusion and its bilateral asymmetry, in 500 increments along the anteroposterior axis. This provides the basis for exploring directional trends and potential locally confined lifestyle signals in downstream analyses. Other R packages utilised in our analysis include: ape (Paradis, Claude, & Strimmer, 2004), car (Fox & Weisberg, 2019), geomorph (Adams & Otárola-Castillo, 2013), ggplot2 (Wickham, 2016), nlme (Pinheiro *et al.*, 2024), phangorn (Schliep, 2011), phytools (Revell, 2012), RRPP package (Collyer & Adams, 2018), sf (Pebesma, 2018), and strap (Bell & Lloyd, 2015).



Supplementary Fig. 19. Select thresholded top-view parallel fusion projections, with fusion area between the skull roof and the osteoderm cover highlighted in red. Note that these comparatively large specimens show pronounced bilateral asymmetry in their fusion area. Histogram settings underlying the original (non-thresholded) renders are shown in the respective top left corners, teal line representing opacity.

Supplementary Note 16: Quantified traits – specimen and taxon levels

Supplementary Tab. 6. Quantified traits in the *Egernia*-group osteoderm cover, reported for individual specimens. Osteoderm cover thickness (Th_{hull}) and compactness (c_{hull}), individual osteoderm thickness (Th_{OD}) and compactness (c_{OD}), thickness of inter-osteodermal spaces (Th_{matrix}), degree of anisotropy (DA), fusion with the skull roof (fus), osteoderm surface per osteoderm cover volume (BS/TV_{hull}), and osteoderm number per osteoderm cover volume ($Tb.N_{hull}$).

Specimen	Th_{hull} [%]	c_{hull} [%]	Th_{OD} [%]	c_{OD} [%]	Th_{matrix} [%]	DA [-]	fus [%]	BS/TV_{hull} [mm ³]	$Tb.N_{hull}$ [*mm ³]
<i>Bellatorias frerei</i> MV D14417	3.60	58.9	1.17	99.3	0.93	0.320	3.63	13.27	3.91
<i>Bellatorias frerei</i> MV R1617	2.99	56.1	0.94	99.6	0.81	0.296	1.51	13.55	3.74
<i>Bellatorias major</i> MV D8588	3.99	53.0	1.10	99.6	1.00	0.338	5.42	8.42	2.24
<i>Bellatorias major</i> MV D8617	4.19	58.6	1.27	95.9	1.01	0.295	3.92	7.69	2.26
<i>Corucia zebrata</i> MV D5951	3.58	51.2	1.06	96.8	1.09	0.275	0.00	7.74	1.99
<i>Corucia zebrata</i> MV D65062	2.70	61.5	1.29	92.7	0.85	0.334	0.00	7.05	2.17
<i>Cyclodomorphus branchialis</i> MV D4605	3.34	52.7	1.03	98.1	1.21	0.296	9.74	31.09	8.21
<i>Cyclodomorphus branchialis</i> MV D65874	4.29	42.8	1.02	99.6	1.43	0.272	8.00	39.63	8.50
<i>Cyclodomorphus casuarinae</i> MV D56347	3.66	48.4	1.05	94.9	1.22	0.312	6.72	22.69	5.50
<i>Cyclodomorphus casuarinae</i> MV D5733	3.89	44.1	0.92	99.4	1.21	0.313	2.92	23.16	5.12
<i>Cyclodomorphus gerrardii</i> MV D3463	2.23	59.6	1.01	96.4	0.83	0.350	4.44	9.84	2.94
<i>Cyclodomorphus gerrardii</i> MV D56631	2.63	59.1	1.14	99.7	0.89	0.308	4.48	12.88	3.81
<i>Cyclodomorphus melanops elongatus</i> MV D63713	3.36	61.1	1.41	99.2	0.97	0.309	2.12	25.66	7.85
<i>Cyclodomorphus melanops elongatus</i> MV D63714	4.51	61.7	1.70	97.9	1.05	0.290	5.93	22.82	7.05
<i>Cyclodomorphus melanops melanops</i> MV D42000	3.64	56.8	1.21	95.9	1.09	0.316	6.77	26.67	7.59
<i>Cyclodomorphus melanops melanops</i> MV D42002	4.19	55.2	1.15	96.2	1.02	0.259	7.43	32.16	8.89
<i>Cyclodomorphus michaeli</i> MV D33722	2.72	46.9	0.85	99.4	1.32	0.226	7.90	39.39	9.24
<i>Cyclodomorphus michaeli</i> MV D39196	2.78	52.5	0.99	97.9	1.12	0.330	4.25	33.28	8.74
<i>Cyclodomorphus praealtus</i> MV D70896	3.37	29.8	0.67	99.9	1.59	0.331	6.46	53.55	7.98
<i>Cyclodomorphus praealtus</i> MV D77601	2.48	44.6	0.77	99.7	1.05	0.359	7.41	44.13	9.84
<i>Egernia cunninghami</i> MV D16461	4.73	56.3	1.50	97.4	1.26	0.220	5.62	8.93	2.52
<i>Egernia cunninghami</i> MV D52969	4.93	59.5	1.52	95.1	1.05	0.225	9.77	8.42	2.51
<i>Egernia depressa</i> MV D2877	5.04	48.2	1.31	99.0	1.32	0.234	9.35	21.13	5.10
<i>Egernia depressa</i> MV D3443	5.55	54.3	1.73	98.7	1.30	0.217	7.75	16.09	4.37
<i>Egernia hosmeri</i> MV D4985	5.34	54.2	1.40	97.4	1.14	0.257	3.68	12.91	3.51
<i>Egernia kingii</i> MV D706	3.24	54.3	1.04	98.2	0.96	0.232	4.70	13.10	3.56
<i>Egernia kingii</i> MV R927	3.18	58.2	1.16	96.3	0.87	0.296	3.60	10.06	2.93
<i>Egernia mcphreei</i> MV D15423	2.50	57.9	1.00	98.6	0.90	0.335	7.10	25.75	7.47
<i>Egernia mcphreei</i> MV D54283	2.15	53.3	0.83	99.1	0.92	0.345	10.12	27.12	7.23
<i>Egernia napoleonis</i> MV D8252	3.15	54.1	1.03	97.6	0.93	0.351	5.63	18.95	5.13
<i>Egernia rugosa</i> MV D52428	5.02	61.2	1.71	96.2	1.14	0.270	8.21	7.60	2.33
<i>Egernia rugosa</i> MV D8943	5.05	60.8	1.77	96.3	1.12	0.250	5.19	8.07	2.46
<i>Egernia saxatilis intermedia</i> MV D69680	2.90	61.4	1.15	94.7	0.85	0.292	6.44	18.90	5.81
<i>Egernia saxatilis intermedia</i> MV D75648	3.19	63.3	1.33	97.2	0.91	0.278	7.32	18.40	5.83
<i>Egernia saxatilis saxatilis</i> MV D39320	2.82	59.0	1.02	96.7	0.79	0.264	9.80	20.03	5.92
<i>Egernia saxatilis saxatilis</i> MV D39322	3.41	57.5	1.02	98.1	0.89	0.259	4.11	20.35	5.86
<i>Egernia stokesii stokesii</i> MV R931	5.45	48.9	1.33	99.2	1.29	0.210	3.77	13.12	3.21

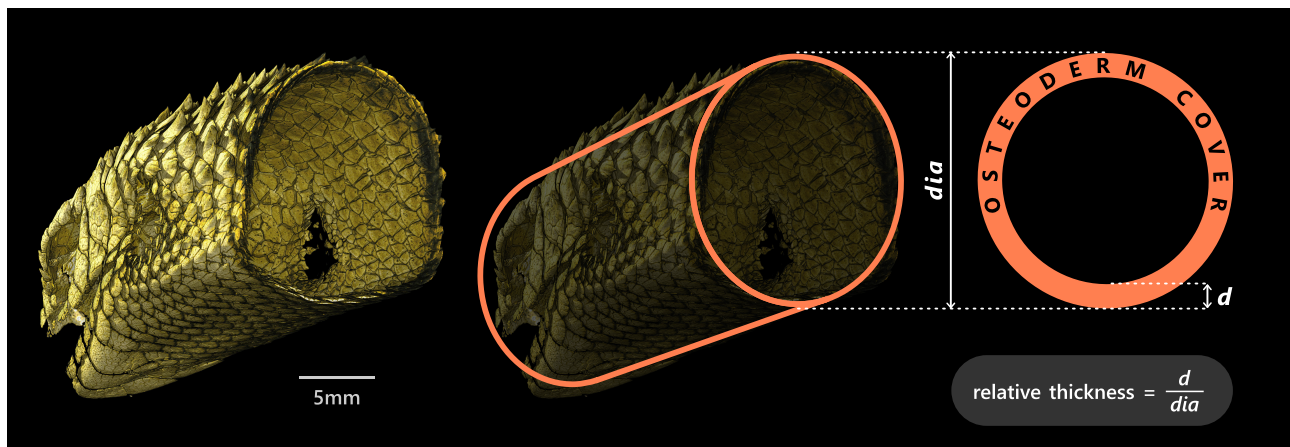
Specimen	Th_{hull} [%]	C_{hull} [%]	Th_{OD} [%]	C_{OD} [%]	Th_{matrix} [%]	DA [-]	fus [%]	BS/TV_{hull} [mm ⁻¹]	$Tb.N_{hull}$ [*mm ⁻¹]
<i>Egernia stokesii stokesii</i> MV R932	5.37	52.3	1.53	98.2	1.26	0.203	3.38	13.77	3.60
<i>Egernia stokesii zellingi</i> MV D16268	5.86	57.8	1.67	97.8	1.24	0.219	3.71	11.13	3.22
<i>Egernia stokesii zellingi</i> MV D56346	6.57	55.0	1.57	97.3	1.16	0.198	3.14	12.93	3.56
<i>Egernia striolata</i> MV D50641	2.32	58.5	0.99	98.3	0.91	0.292	7.46	21.39	6.26
<i>Egernia striolata</i> MV D77705	2.75	59.3	1.05	97.3	0.92	0.292	7.25	20.91	6.21
<i>Liopholis inornata</i> MV D51748	2.86	48.3	0.75	99.2	0.88	0.310	1.75	33.24	8.03
<i>Liopholis inornata</i> MV D61201	2.46	53.3	0.85	98.6	0.83	0.279	4.48	29.56	7.88
<i>Liopholis margaretae personata</i> MV D56333	2.75	57.0	0.95	98.0	0.77	0.297	2.92	28.28	8.06
<i>Liopholis margaretae personata</i> MV D56334	2.58	58.9	1.04	95.6	0.81	0.309	7.38	24.99	7.36
<i>Liopholis modesta</i> MV D38507	5.99	51.0	0.96	97.1	1.23	0.258	6.69	25.60	6.54
<i>Liopholis modesta</i> MV D38508	2.65	58.3	1.01	95.0	0.83	0.328	5.30	21.75	6.35
<i>Liopholis montana</i> MV D2022	2.23	51.6	0.78	98.6	0.89	0.334	5.49	29.63	7.66
<i>Liopholis montana</i> MV D75706	2.59	56.6	0.96	97.3	0.91	0.336	5.70	27.48	7.78
<i>Liopholis multiscutata</i> MV D54086	1.98	54.6	0.77	98.2	0.76	0.293	6.19	29.90	8.16
<i>Liopholis multiscutata</i> MV D54425	2.86	54.0	0.89	97.3	0.87	0.301	6.49	28.21	7.62
<i>Liopholis pulchra</i> MV D5677	3.65	52.8	0.96	98.1	0.97	0.258	5.19	26.33	6.96
<i>Liopholis pulchra</i> MV D71559	2.92	56.2	0.95	96.8	0.82	0.305	5.78	25.34	7.13
<i>Liopholis slateri slateri</i> MV D476	2.63	53.1	0.79	97.7	0.86	0.307	0.52	30.79	8.18
<i>Liopholis slateri slateri</i> MV D92	2.68	52.5	0.76	98.5	0.79	0.349	3.06	28.16	7.40
<i>Liopholis striata</i> MV D4953	2.39	49.8	0.72	98.8	0.79	0.309	1.33	30.71	7.65
<i>Liopholis striata</i> MV D4982	2.21	56.3	0.82	97.5	0.73	0.290	2.24	25.36	7.15
<i>Liopholis whitii</i> MV D34037	1.95	48.6	0.73	98.8	0.86	0.346	4.78	33.42	8.12
<i>Liopholis whitii</i> MV D75028	2.62	51.7	0.88	98.2	0.97	0.292	8.11	33.48	8.66
<i>Lissolepis coventryi</i> MV D55626	3.69	61.4	1.45	94.4	1.08	0.300	8.79	20.80	6.39
<i>Lissolepis coventryi</i> MV D75390	3.15	52.3	0.97	98.1	0.95	0.381	8.97	34.90	9.14
<i>Lissolepis luctuosa</i> MV D1226	2.39	46.6	0.75	99.4	0.97	0.362	7.91	29.83	6.96
<i>Lissolepis luctuosa</i> MV D903	3.37	54.5	1.01	97.9	0.93	0.331	6.11	17.44	4.76
<i>Tiliqua gigas</i> MV D14411	3.97	58.5	1.28	93.3	0.89	0.282	5.18	8.63	2.53
<i>Tiliqua gigas</i> MV D5926	3.67	55.6	1.15	97.1	0.94	0.323	7.70	9.18	2.56
<i>Tiliqua multifasciata</i> MV D1087	4.68	64.2	2.10	96.8	1.08	0.286	0.65	6.34	2.03
<i>Tiliqua multifasciata</i> MV R1615	4.42	65.3	2.01	90.0	1.04	0.270	0.50	7.20	2.36
<i>Tiliqua nigrolutea</i> MV D39107	5.44	55.1	1.85	97.1	1.30	0.233	4.04	6.98	1.93
<i>Tiliqua nigrolutea</i> MV D41716	5.05	54.0	1.71	94.2	1.23	0.260	2.13	6.96	1.88
<i>Tiliqua occipitalis</i> MV D39228	2.98	61.7	1.41	95.1	0.76	0.274	0.46	8.64	2.67
<i>Tiliqua occipitalis</i> MV D9524	4.40	67.6	2.28	93.2	1.03	0.273	0.31	5.65	1.91
<i>Tiliqua rugosa aspera</i> MV D71306	4.29	65.1	2.60	96.3	1.56	0.269	4.28	3.74	1.22
<i>Tiliqua rugosa aspera</i> MV D76315	4.58	62.9	2.35	92.7	1.44	0.191	13.45	4.38	1.38
<i>Tiliqua rugosa rugosa</i> MV D40045	5.37	65.0	2.91	97.7	1.59	0.226	2.18	3.74	1.22
<i>Tiliqua rugosa rugosa</i> MV D8005	4.31	61.8	2.24	98.3	1.34	0.331	5.87	3.98	1.23
<i>Tiliqua scincoides intermedia</i> MV D11976	3.46	66.4	1.50	96.0	0.83	0.316	5.32	5.77	1.92
<i>Tiliqua scincoides intermedia</i> MV D72665	3.78	68.4	1.65	93.9	0.79	0.246	2.94	5.89	2.02
<i>Tiliqua scincoides scincoides</i> MV D33288	5.26	53.9	1.56	96.9	1.12	0.332	5.20	7.85	2.12
<i>Tiliqua scincoides scincoides</i> MV D48672	4.00	62.2	1.57	96.8	0.92	0.296	5.42	7.07	2.20

Supplementary Tab. 7. Quantified traits in the *Egernia*-group osteoderm cover, reported as taxon means. Osteoderm cover thickness (Th_{hull}) and compactness (C_{hull}), individual osteoderm thickness (Th_{OD}) and compactness (C_{OD}), thickness of inter-osteodermal spaces (Th_{matrix}), degree of anisotropy (DA), fusion with the skull roof (fus), osteoderm surface per osteoderm cover volume (BS/TV_{hull}), osteoderm number per osteoderm cover volume ($Tb.N_{hull}$), and, as a composite derived from the latter two, osteoderm cover structural complexity (str_{hull}).

Taxon	Th_{hull} [%]	C_{hull} [%]	Th_{OD} [%]	C_{OD} [%]	Th_{matrix} [%]	DA [-]	fus [%]	BS/TV_{hull} [mm ⁻¹]	$Tb.N_{hull}$ [*mm ⁻¹]	str_{hull} [-]
<i>Bellatorias frerei</i>	3.30	57.5	1.05	99.4	0.87	0.308	2.57	13.41	3.83	-0.84
<i>Bellatorias major</i>	4.09	55.8	1.18	97.7	1.01	0.316	4.67	8.05	2.25	-1.64
<i>Corucia zebrata</i>	3.14	56.3	1.18	94.7	0.97	0.304	0.00	7.40	2.08	-1.73
<i>Cyclodomorphus branchialis</i>	3.82	47.8	1.02	98.9	1.32	0.284	8.87	35.36	8.35	1.88
<i>Cyclodomorphus casuarinae</i>	3.77	46.2	0.99	97.2	1.21	0.313	4.82	22.93	5.31	0.21
<i>Cyclodomorphus gerrardii</i>	2.43	59.4	1.07	98.0	0.86	0.329	4.46	11.36	3.37	-1.10
<i>Cyclodomorphus melanops elongatus</i>	3.93	61.4	1.56	98.5	1.01	0.300	4.03	24.24	7.45	0.90
<i>Cyclodomorphus melanops melanops</i>	3.92	56.0	1.18	96.1	1.06	0.288	7.10	29.42	8.24	1.46
<i>Cyclodomorphus michaeli</i>	2.75	49.7	0.92	98.6	1.22	0.278	6.08	36.34	8.99	2.13
<i>Cyclodomorphus praealtus</i>	2.92	37.2	0.72	99.8	1.32	0.345	6.93	48.84	8.91	2.93
<i>Egernia cunninghami</i>	4.83	57.9	1.51	96.2	1.16	0.223	7.69	8.68	2.51	-1.52
<i>Egernia depressa</i>	5.30	51.3	1.52	98.9	1.31	0.226	8.55	18.61	4.73	-0.24
<i>Egernia hosmeri</i>	5.34	54.2	1.40	97.4	1.14	0.257	3.68	12.91	3.51	-0.96
<i>Egernia kingii</i>	3.21	56.3	1.10	97.3	0.91	0.264	4.15	11.58	3.25	-1.12
<i>Egernia mcphreei</i>	2.32	55.6	0.91	98.8	0.91	0.340	8.61	26.43	7.35	1.01
<i>Egernia napoleonis</i>	3.15	54.1	1.03	97.6	0.93	0.351	5.63	18.95	5.13	-0.11
<i>Egernia rugosa</i>	5.03	61.0	1.74	96.2	1.13	0.260	6.70	7.84	2.39	-1.61
<i>Egernia saxatilis</i>	3.08	60.3	1.13	96.7	0.86	0.273	6.92	19.42	5.86	0.13
<i>Egernia stokesii stokesii</i>	5.41	50.6	1.43	98.7	1.28	0.206	3.58	13.45	3.41	-0.95
<i>Egernia stokesii zellingi</i>	6.22	56.4	1.62	97.5	1.20	0.208	3.43	12.03	3.39	-1.05
<i>Egernia striolata</i>	2.53	58.9	1.02	97.8	0.91	0.292	7.36	21.15	6.23	0.35
<i>Liopholis inornata</i>	2.66	50.8	0.80	98.9	0.86	0.295	3.11	31.40	7.96	1.51
<i>Liopholis modesta</i>	4.32	54.7	0.99	96.1	1.03	0.293	6.00	23.68	6.44	0.58
<i>Liopholis montana</i>	2.41	54.1	0.87	97.9	0.90	0.335	5.60	28.56	7.72	1.26
<i>Liopholis multiscutata</i>	2.42	54.3	0.83	97.7	0.81	0.297	6.34	29.06	7.89	1.34
<i>Liopholis personata</i>	2.66	57.9	1.00	96.8	0.79	0.303	5.15	26.63	7.71	1.13
<i>Liopholis pulchra</i>	3.29	54.5	0.95	97.4	0.90	0.282	5.48	25.84	7.05	0.89
<i>Liopholis slateri</i>	2.65	52.8	0.78	98.1	0.83	0.328	1.79	29.48	7.79	1.34
<i>Liopholis striata</i>	2.30	53.1	0.77	98.1	0.76	0.300	1.79	28.04	7.40	1.13
<i>Liopholis whittii</i>	2.28	50.1	0.81	98.5	0.92	0.319	6.44	33.45	8.39	1.77
<i>Lissolepis coventryi</i>	3.42	56.9	1.21	96.2	1.02	0.340	8.88	27.85	7.77	1.22
<i>Lissolepis luctuosa</i>	2.88	50.6	0.88	98.7	0.95	0.346	7.01	23.63	5.86	0.41
<i>Tiliqua gigas</i>	3.82	57.1	1.21	95.2	0.91	0.302	6.44	8.90	2.54	-1.50
<i>Tiliqua multifasciata</i>	4.55	64.8	2.06	93.4	1.06	0.278	0.57	6.77	2.20	-1.73
<i>Tiliqua nigrolutea</i>	5.24	54.6	1.78	95.6	1.27	0.247	3.09	6.97	1.90	-1.80
<i>Tiliqua occipitalis</i>	3.69	64.6	1.85	94.2	0.89	0.274	0.39	7.14	2.29	-1.68
<i>Tiliqua rugosa</i>	4.64	63.7	2.52	96.2	1.48	0.254	6.44	3.96	1.26	-2.18
<i>Tiliqua scincoides</i>	4.13	62.7	1.57	95.9	0.92	0.297	4.72	6.64	2.06	-1.78

Supplementary Note 17: Relative thickness as a proportion of head diameter

Following the approach for reporting roofing bone thickness in Ebel *et al.* (2020), we approximate our specimens as elongate ellipsoidal bodies. In such shapes, cross-sections taken perpendicular to the long axis intersect the hull with minimal distortion from orientation effects, which allows hull thickness to be expressed as a proportion of minor-axis extension. An elongate cylinder represents the limit case in which this behaviour is perfect, and reporting relative hull thickness as a proportion of its diameter is the geometrically consistent choice (Supplementary Fig. 20). By the same geometric reasoning, we report osteoderm hull thickness as a fraction of skull diameter. It provides an appropriate and replicable standard that has yielded biologically relevant results in prior work (Ebel *et al.*, 2020). We acknowledge that ratios and percentages can introduce statistical artefacts when used as the sole means of size correction (Atchley, Gaskins, & Anderson, 1976; Packard & Boardman, 1988). For this reason, we additionally included $\ln(sv_{raw})$ as a body-size covariate in all comparative models, following the recommendations of Freckleton (2002) and Mundry (2014).

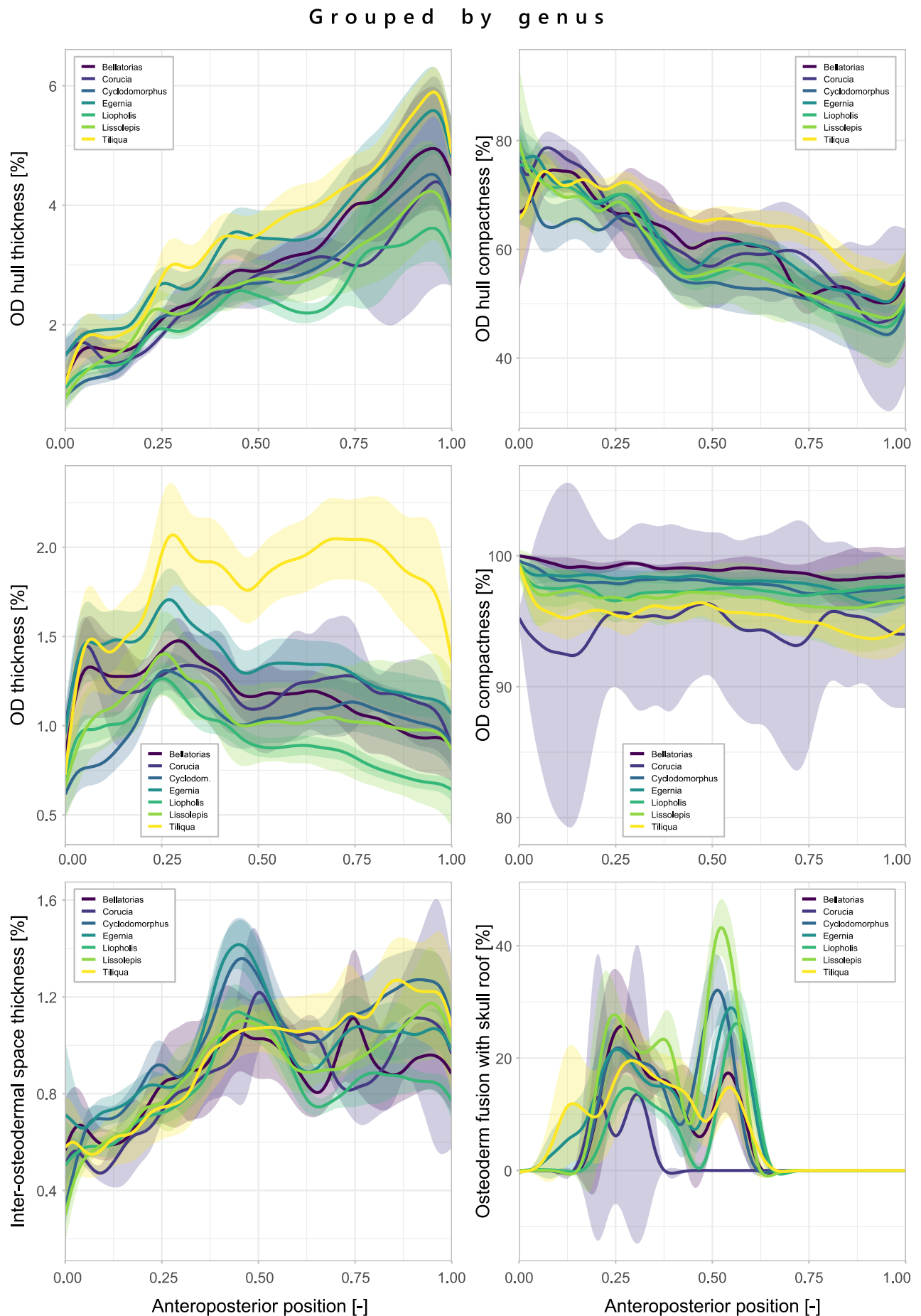


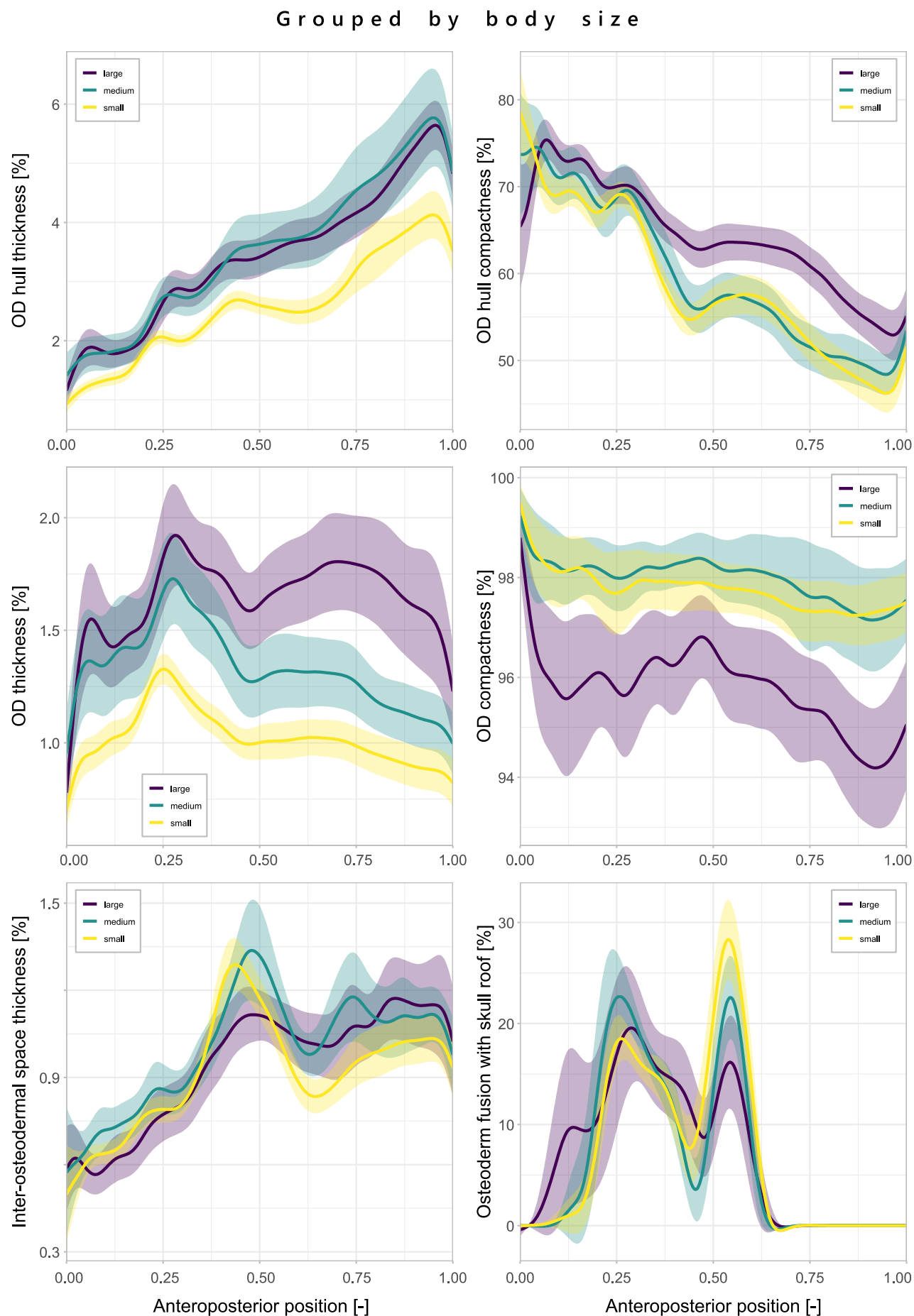
Supplementary Fig. 20. Geometric reasoning for reporting relative thickness of quantified structures as a proportion of head diameter.

Supplementary Note 18: Profile data subsetting, collapsing, and final reporting protocol

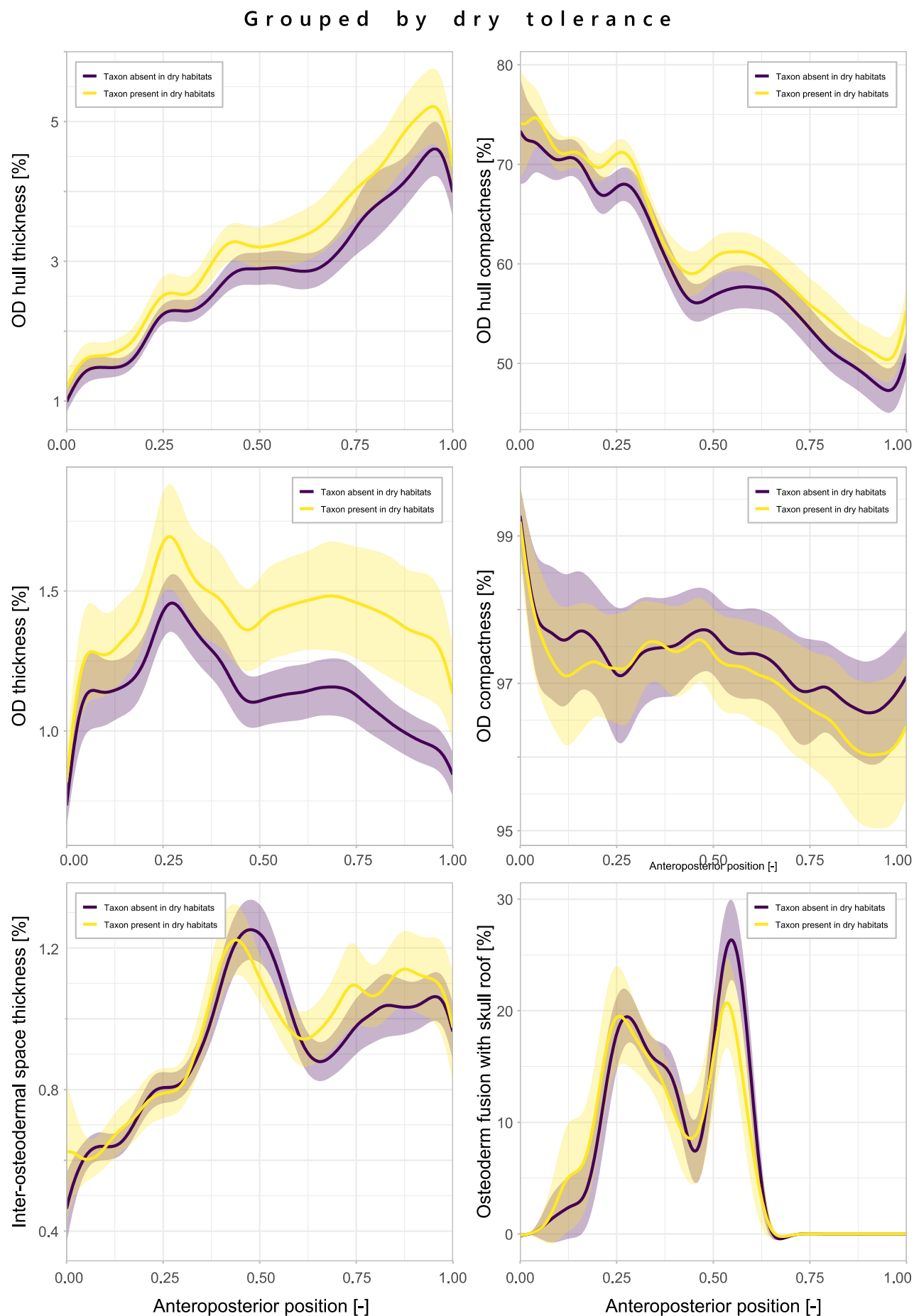
In addition to ROI means, we quantified directional variability along an anteroposterior axis for six traits (thickness and compactness of the osteoderm cover, thickness and compactness of individual osteoderms, inter-osteodermal spaces, and relative fusion area with the skull roof). Profiles were sampled at 500 evenly spaced increments. This sampling density ensured that individual increments remained safely above voxel size across the dataset, while still providing a resolution two orders of magnitude higher than in previous work that relied on exporting individual cross-sections (e.g., Ebel *et al.*, 2020). An overview of directional trait variability plots is provided in Supplementary Figs. 21–25.

Subsetting or filtering microanatomical data obtained from anteroposterior profiles can facilitate their analysis and interpretation (Ebel *et al.*, 2020; Kaffler *et al.*, 2023; Manning *et al.*, 2023; Fornari & Müller, 2025). We therefore performed a preliminary screening along each profile by testing for effects of body size and lifestyle on the quantified trait at each increment. This screening was used only to guide subsetting decisions and was therefore intentionally non-conservative: we did not adjust p-values across increments to avoid excluding regions that might carry relevant signal in downstream analyses. For the same reason, we applied an additional arbitrary margin of 0.025 when excluding regions. Based on this assessment, we excluded anterior regions and retained posterior subsets beginning at trait-specific cutoffs. The resulting cutoffs ranged from 0.11 to 0.41 along the anteroposterior axis (expressed as the fraction of total profile length, Supplementary Box 5, Supplementary Fig. 26). In line with prior research, we collapsed each posterior subset to its mean value for downstream analyses (Ebel *et al.*, 2020; Kaffler *et al.*, 2023; Manning *et al.*, 2023; Fornari & Müller, 2025).

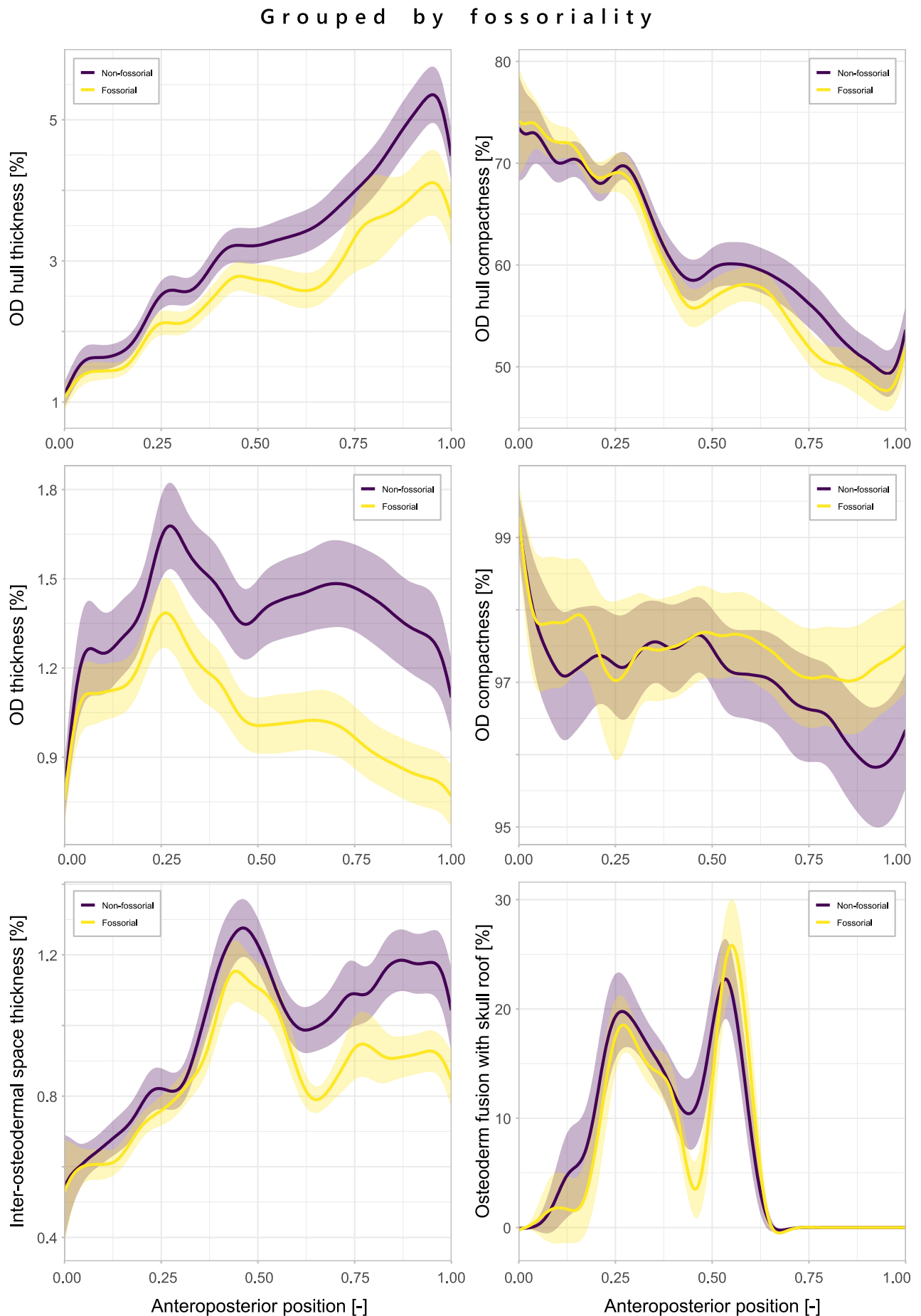
Supplementary Fig. 21. Directional trait variability in the *Egernia*-group osteoderm cover, grouped by genus.

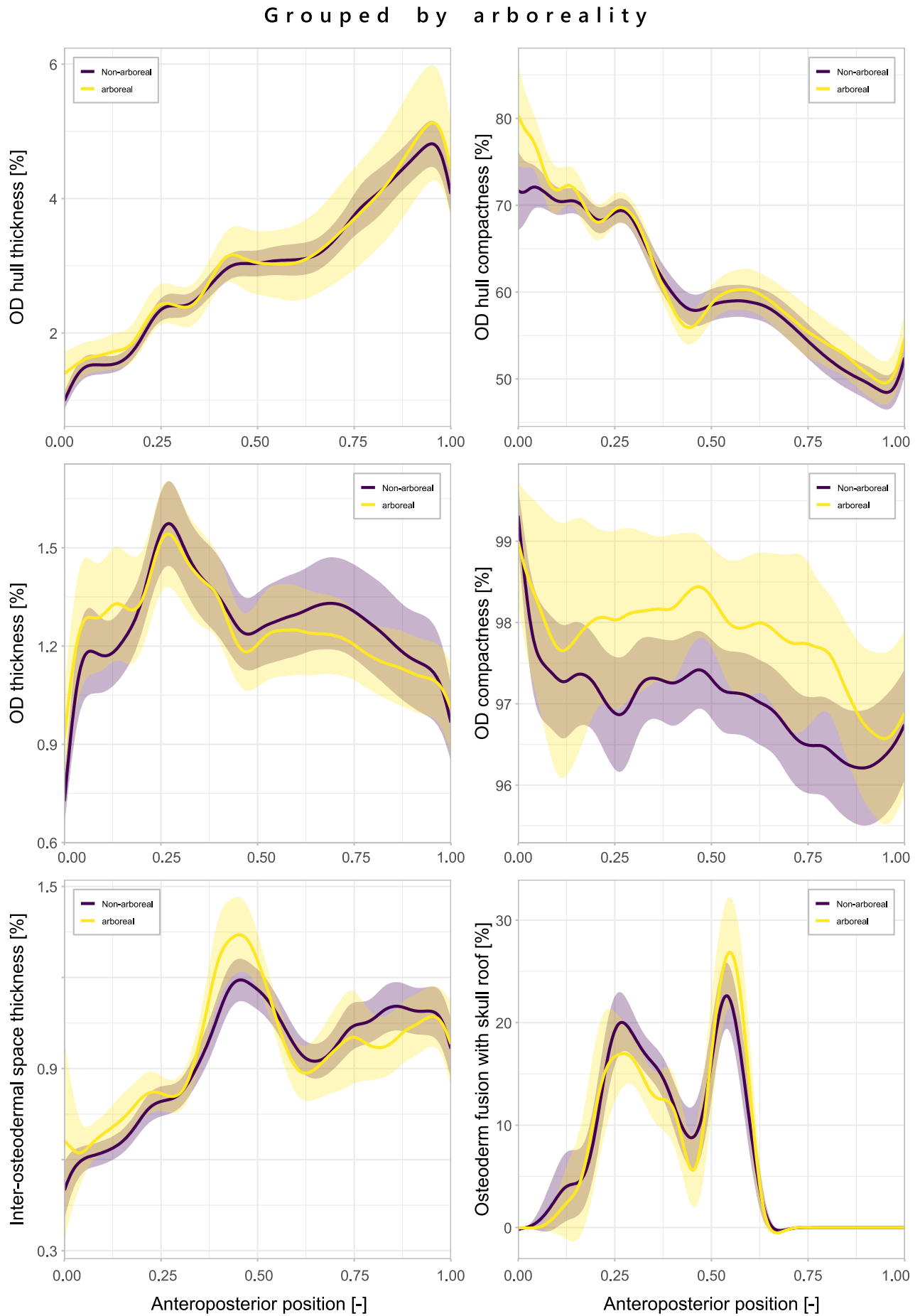


Supplementary Fig. 22. Directional trait variability in the *Egernia*-group osteoderm cover, grouped by body size.

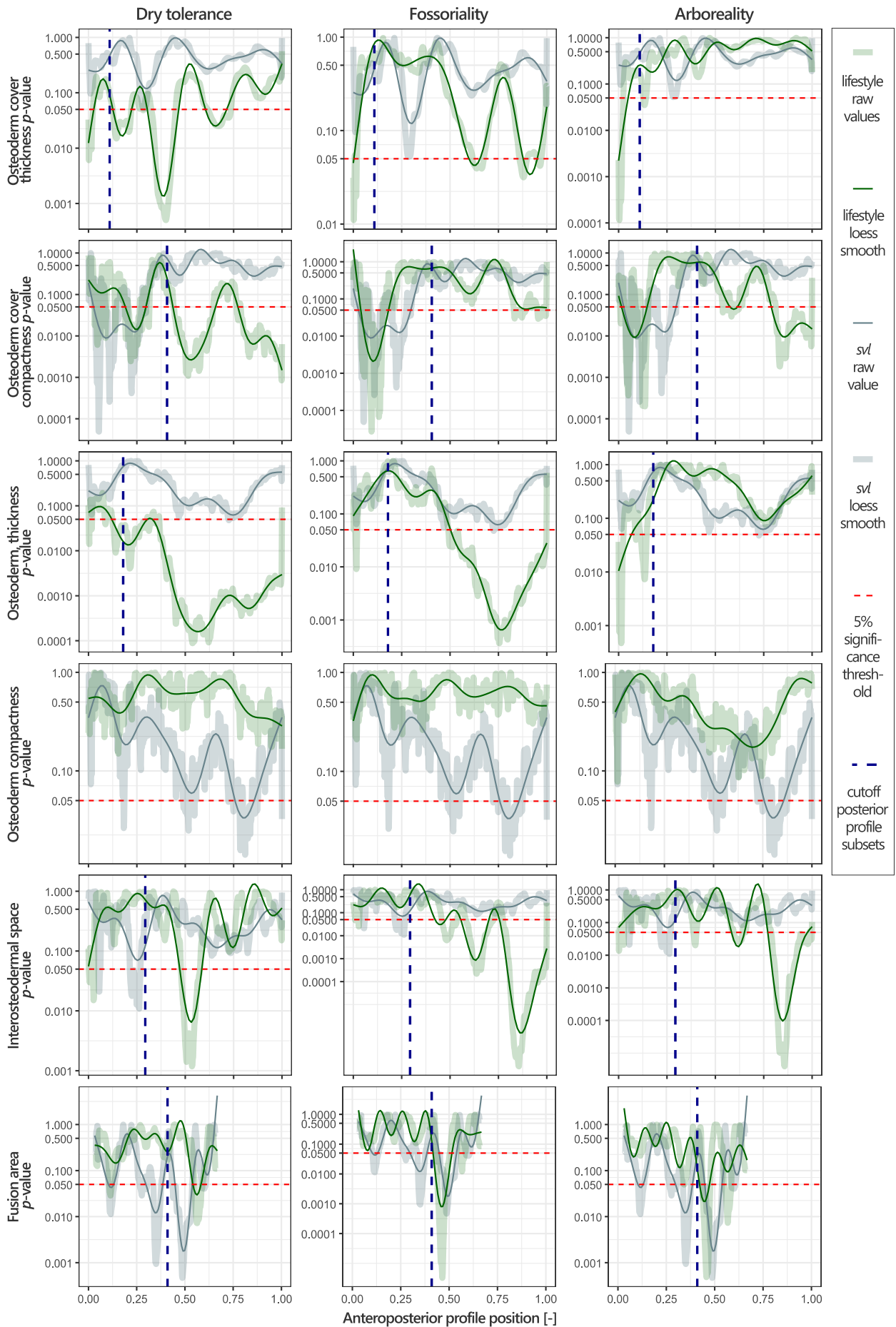


Supplementary Fig. 23. Directional trait variability in the *Egernia*-group osteoderm cover, grouped by dry tolerance.

Supplementary Fig. 24. Directional trait variability in the *Egernia*-group osteoderm cover, grouped by fossoriality.



Supplementary Fig. 25. Directional trait variability in the *Egernia*-group osteoderm cover, grouped by arboreality.



Supplementary Fig. 26. Statistically detectable localised body-size and lifestyle effects in anteroposterior trait variability, and resulting cutoffs for posterior profile subsets, in accordance with Supplementary Box 5 and Suppl. File 2.

We compared profile-derived means with corresponding ROI means to determine which reporting protocol better supports detection of lifestyle signals. We fitted phylogenetic logistic regressions (Ives & Garland, 2010) using the penalised likelihood method (IG10 algorithm) with the *phylolm* package (Ho & Ané, 2014). This accounts for non-in-

Supplementary Box 5. Profile subsets, omitting anterior regions without detectable lifestyle effect and/or with a pronounced body size effect, in accordance with Supplementary Fig. 26. Underlying code and referenced interval data frames provided in Suppl. Files 2 and 3.

```
> # Apply Cutoffs
> cutoff_hull_thick_rel <- size_intervals_df[1,3] + 0.025
[1] 0.1091683
> cutoff_hull_comp <- size_intervals_df[4,3] + 0.025
[1] 0.4057615
> cutoff_OD_thick_rel <- size_intervals_df[5,3] + 0.025
[1] 0.1793086
> cutoff_matrix_thick_rel <- size_intervals_df[18,3] + 0.025
[1] 0.2935371
> cutoff_rel_fusion <- interval_summary[40,2] - 0.025
[1] 0.4098697
```

dependence among species by incorporating the expected covariance structure along the phylogeny under Brownian motion. All models included *svl* and the two non-focal lifestyles as covariates.

We quantified relative model performance as ΔAIC between each pair of models (Burnham & Anderson, 2002). Because the IG10 optimisation routine can converge on slightly different local optima depending on initial conditions, we ran 50 independent iterations and summarised ΔAIC as the mean across runs. For most models, ΔAIC ranged from -0.79 to 0.98, indicating that the two protocols were effectively indistinguishable. The only instance demonstrating significant differences in model fit ($|\Delta AIC| > 2$; Burnham & Anderson, 2002) alongside a substantial shift in effect size was the relationship between relative fusion area and dry-tolerance, where the profile-derived value provided a better fit ($\Delta AIC = -3.03$, Supplementary Tab. 8). We therefore retained profile-derived data for *fus*, and used ROI means for the other traits.

Supplementary Tab. 8. Model performance between profile-derived data ($_{profile}$) and ROI means ($_{mean}$).

Trait	Response	AIC_{mean}	$AIC_{profile}$	ΔAIC	$Slope_{mean}$	$Slope_{profile}$
C_{hull}	arboreal	49.6	49.5	-0.05	0.006	0.007
C_{hull}	dry tolerant	50.0	50.9	0.86	0.227	0.193
C_{hull}	fossorial	37.8	37.4	-0.37	0.004	0.009
Th_{hull}	arboreal	40.8	41.3	0.54	-0.311	-0.298
Th_{hull}	dry tolerant	53.8	53.0	-0.79	0.551	0.739
Th_{hull}	fossorial	34.9	35.9	1.02	-0.933	-0.951
Th_{matrix}	arboreal	40.5	41.8	1.36	-1.245	-0.385
Th_{matrix}	dry tolerant	56.3	56.3	-0.05	-1.083	-1.440
Th_{matrix}	fossorial	35.0	35.3	0.28	-1.361	-1.400
C_{OD}	arboreal	51.3	48.4	-2.88	0.012	0.000
C_{OD}	dry tolerant	56.3	56.3	0.03	-0.290	-0.176
C_{OD}	fossorial	44.9	43.9	-0.96	0.000	0.004
Th_{OD}	arboreal	41.5	41.4	-0.06	-0.861	-0.800
Th_{OD}	dry tolerant	47.0	47.5	0.42	5.130	4.830
Th_{OD}	fossorial	36.7	36.9	0.16	-1.709	-1.773
<i>fus</i>	arboreal	42.1	42.0	-0.10	-0.001	0.024
<i>fus</i>	dry tolerant	54.9	51.8	-3.03	-0.164	-0.415
<i>fus</i>	fossorial	36.7	36.7	-0.05	-0.003	-0.015

Supplementary Note 19: Exclusion of redundant and technically unsuitable traits

To avoid redundancy, we excluded two quantified traits from our analysis: 1) *Tb.Th_{hull}*, as it captures the same biological quantity as *Th_{OD}*, despite being computed through a different quantification route, and 2) *Tb.Sp_{hull}*, as it measures the same underlying structural spacing as *Th_{matrix}*, and therefore does not contribute independent information. A third trait, *V_{OD}/V_{ES}*, was included only as a preliminary exploratory measure to check data coherency. Because it is normalised by endoskeletal volume, it introduces additional biological assumptions that render it difficult to compare with our other traits. A preliminary analysis showed that *V_{OD}/V_{ES}* is strongly correlated with *Th_{OD}* (Spearman $\rho = 0.637$, $p = 2 \times 10^{-10}$), and both traits quantify very similar aspects. We therefore excluded *V_{OD}/V_{ES}* and retained *Th_{OD}* for all subsequent analyses. Beyond the relative fusion area between the osteoderm cover and the skull roof (*fus*), we also quantified the bilateral asymmetry thereof (*asym*). Because we lacked a clear a priori hypothesis and because profiles were very noisy (Supplementary Fig. 6), we did not consider *asym* suitable for lifestyle modelling and excluded it from downstream comparative analyses. We therefore only discuss general trends observed in this trait.

Supplementary Note 20: Lifestyle and habitat data

An overview of all lifestyle and habitat data used in this study is given in Supplementary Tab. 9. We

Supplementary Tab. 9. Sampled taxa with lifestyle and habitat data. Abbreviations: number of specimens (*n_{spec}*), number of unique geo-locations underlying AI computation (*n_{geoloc}*), Aridity Index mean and standard deviation (*AI_{mean}*), Aridity Index 5th percentile (*AI_{5%}*; Zomer, Xu, & Trabucco, 2022), dry-tolerance (*Dry*), Fossoriality (*Foss*), and Arboreality (*Arb*). Lifestyle and habitat sources are listed in the references section at the end of this document (Greer, 1989, 2007; Cogger & Zweifel, 1992; Hauschild *et al.*, 2000; O'Shea & Halliday, 2002; Chapple, 2003; Chapple *et al.*, 2019; Wilson & Swan, 2025).

Taxon	Specimens	<i>n_{spec}</i>	<i>n_{geoloc}</i>	<i>AI_{mean}</i>	<i>AI_{5%}</i>	<i>Dry</i>	<i>Foss</i>	<i>Arb</i>	Lifestyle & habitat references
<i>Bellatorias frerei</i>	MV D14417, MV R1617	2	276	1.05 ± 0.45	0.44	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Bellatorias major</i>	MV D8588, MV D8617	2	113	1.13 ± 0.25	0.79	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Corucia zebrata</i>	MV D5951, MV D65062	2	17	2.2 ± 0.27	1.85	No	No	Yes	Cogger & Zweifel (1992), Greer (2007), O'Shea & Halliday (2002)
<i>Cyclodomorphus branchialis</i>	MV D4605, MV D65874	2	11	0.16 ± 0.03	0.12	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Cyclodomorphus casuarinae</i>	MV D56347, MV D5733	2	143	1.46 ± 0.76	0.63	No	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Cyclodomorphus gerrardii</i>	MV D3463, MV D56631	2	262	1.01 ± 0.39	0.43	No	No	Yes	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Cyclodomorphus melanops elongatus</i>	MV D63713, MV D63714	2	233	0.14 ± 0.04	0.09	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Cyclodomorphus melanops melanops</i>	MV D42000, MV D42002	2	262	0.14 ± 0.05	0.10	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Cyclodomorphus michaeli</i>	MV D33722, MV D39196	2	89	0.97 ± 0.12	0.81	No	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Cyclodomorphus praealtus</i>	MV D70896, MV D77601	2	20	1.74 ± 0.26	1.46	No	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Egernia cunninghami</i>	MV D16461, MV D52969	2	511	0.69 ± 0.22	0.43	No	No	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia depressa</i>	MV D2877, MV D3443	2	161	0.12 ± 0.02	0.08	Yes	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Egernia hosmeri</i>	MV D4985	1	33	0.28 ± 0.14	0.15	Yes	No	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia kingii</i>	MV D706, MV R927	2	146	0.49 ± 0.21	0.20	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)

Taxon	Specimens	n_{spec}	n_{geoloc}	AI_{mean}	$AI_{5\%}$	Dry	Foss	Arb	Lifestyle & habitat references
<i>Egernia mcphreei</i>	MV D15423, MV D54283	2	74	1 ± 0.25	0.60	No	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Wilson & Swan (2025)
<i>Egernia napoleonis</i>	MV D8252	1	314	0.56 ± 0.2	0.29	No	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia rugosa</i>	MV D52428, MV D8943	2	31	0.44 ± 0.23	0.29	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Egernia saxatilis</i>	MV D69680, MV D75648, MV D39320, MV D39322	4	257	0.87 ± 0.25	0.46	No	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia stokesii stokesii</i>	MV R931, MV R932	2	7	0.2 ± 0.02	0.16	Yes	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia stokesii zellingi</i>	MV D16268, MV D56346	2	194	0.12 ± 0.05	0.06	Yes	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Egernia striolata</i>	MV D50641, MV D77705	2	823	0.37 ± 0.19	0.13	Yes	No	Yes	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis inornata</i>	MV D51748, MV D61201	2	614	0.12 ± 0.05	0.05	Yes	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis modesta</i>	MV D38507, MV D38508	2	130	0.5 ± 0.12	0.35	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis montana</i>	MV D2022, MV D75706	2	28	1.34 ± 0.27	1.04	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Wilson & Swan (2025)
<i>Liopholis multiscutata</i>	MV D54086, MV D54425	2	184	0.28 ± 0.11	0.13	Yes	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis personata</i>	MV D56333, MV D56334	2	53	0.15 ± 0.06	0.08	Yes	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Liopholis pulchra</i>	MV D5677, MV D71559	2	45	0.73 ± 0.16	0.43	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis slateri</i>	MV D476, MV D92	2	21	0.12 ± 0.02	0.07	Yes	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis striata</i>	MV D4953, MV D4982	2	173	0.12 ± 0.03	0.08	Yes	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Liopholis whitii</i>	MV D34037, MV D75028	2	860	0.73 ± 0.25	0.42	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Lissolepis coventryi</i>	MV D55626, MV D75390	2	51	0.76 ± 0.13	0.58	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989, 2007), Wilson & Swan (2025)
<i>Lissolepis luctuosa</i>	MV D1226, MV D903	2	48	0.73 ± 0.15	0.41	No	Yes	No	Chapple (2003), Chapple <i>et al.</i> (2019), Greer (1989), Wilson & Swan (2025)
<i>Tiliqua gigas</i>	MV D14411, MV D5926	2	21	1.74 ± 0.84	0.90	No	No	No	Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Tiliqua multifasciata</i>	MV D1087, MV R1615	2	520	0.16 ± 0.07	0.08	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Tiliqua nigrolutea</i>	MV D39107, MV D41716	2	455	0.83 ± 0.34	0.51	No	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Tiliqua occipitalis</i>	MV D39228, MV D9524	2	429	0.21 ± 0.12	0.08	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Tiliqua rugosa</i>	MV D71306, MV D76315, MV D40045, MV D8005	4	1991	0.28 ± 0.17	0.09	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)
<i>Tiliqua scincoides</i>	MV D11976, MV D72665, MV D33288, MV D48672	4	1561	0.61 ± 0.29	0.19	Yes	No	No	Chapple <i>et al.</i> (2019), Greer (1989, 2007), Hauschild <i>et al.</i> (2000), Wilson & Swan (2025)

chose the 5th percentile of species-distribution Aridity Index, thresholded against the established arid and hyper-arid definition (Zomer, Xu, & Trabucco, 2022), as our dry-tolerance criterion. We considered alternative metrics including mean *AI* per species and compared them against published ecological characterisations of the focal taxa (Greer, 1989, 2007; Hauschild *et al.*, 2000; Chapple, 2003; Chapple *et al.*, 2019; Wilson & Swan, 2025). The 5th percentile consistently produced classifications that aligned with the literature, whereas mean *AI* did not.

Habitat generalists with extensive arid components in their distribution (such as *T. scincoides*) are well documented as performing strongly under arid conditions but have mean *AI* values pulled toward the mesic end of their range by populations in temperate habitats. Mean *AI* misclassified such taxa as non-dry-tolerant, contradicting the published ecological evidence. The 5th percentile, by contrast, captures whether a species' distribution extends significantly into arid environments regardless of where the centre of its range lies. We therefore opted for a binary classifier with a quantifiable, biologically anchored threshold rather than a continuous metric whose centre-of-distribution behaviour conflicts with the ecological literature for habitat generalists.

We note that our analysis resolves to species (or subspecies, where applicable) and assumes that the sampled specimens are representative of their taxon's ecological distribution. This assumption is shared by comparative morphological and microstructural studies generally and constrains all downstream inferences accordingly.

Supplementary Note 21: Inference framework

The phyloRRPP protocol used throughout the main text evaluates a generalised least-squares model by permuting its residuals under the phylogenetic covariance structure (10,000 permutations). RRPP is robust to violations of normality and equal-variance assumptions, which is advantageous for comparative datasets of moderate size (Anderson, 2001; Good, 2005). As a multivariate effect size, we calculated trace- R^2 from the residual variance-covariance matrices, which quantifies the proportional reduction in total multivariate variance (Collyer, Sekora, & Adams, 2015; Adams & Collyer, 2018).

For univariate trait-lifestyle comparisons, we computed Cohen's *d* as the standardised difference between the two levels of the focal lifestyle (Cohen, 2013). For continuous predictors, we reported the standardised slope β_{std} (Gelman & Hill, 2007; Schielzeth, 2010). Effect sizes were interpreted alongside *p*-values to identify biological associations (Nakagawa & Cuthill, 2007). For ancestral character state reconstruction, we selected an all-rates-different (ARD) model. It places fewer constraints on transition rates than other alternatives. We based this decision on AICc weights, convergence behaviour, and biological reasoning (e.g., Boettiger, Coop, & Ralph, 2012; Slater & Pennell, 2014).

Supplementary Note 22: Module discovery and validation

To better understand the internal structure of the trait set, we quantified covariation among traits and recovered a moderate overall integration ($r = 0.324$). However, covariation was highly uneven: Th_{hull} , Th_{OD} , Th_{matrix} formed an integrated block ($r \in [0.56, 0.66]$), and BS/TV_{hull} , $Tb.N_{hull}$, C_{hull} also clustered ($|r| \in [0.19, 0.78]$). *DA* was associated with both complexes ($r \in [0.46, 0.75]$). Other traits showed only weak associations ($r \in [0, 0.3]$, Supplementary Tab. 10). We then assessed modularity by combining multivariate evolutionary modelling with a stochastic search for trait groupings (Supplementary Box 6). The evolutionary covariance matrix was estimated under a multivariate Brownian motion model (Clavel, Escarguel, & Merceron, 2015). Candidate partitions were scored based on the balance of within- and between-module correlations (Klingenberg, 2008), in line with approaches that contrast alternative modularity hy-

potheses (Goswami & Finarelli, 2016). Using mean correlations avoided inflation by module size. Because the number of possible partitions is large, we used a randomised search strategy inspired by network modularity optimisation (Newman, 2006).

Supplementary Tab. 10. Phylogenetic correlation matrix for the full multivariate trait set.

	<i>BS/TV_{hull}</i>	<i>Tb.N_{hull}</i>	<i>Th_{hull}</i>	<i>c_{hull}</i>	<i>Th_{OD}</i>	<i>c_{OD}</i>	<i>Th_{matrix}</i>	<i>DA</i>	<i>fus</i>
<i>BS/TV_{hull}</i>	1.00	0.78	-0.37	-0.61	-0.32	0.23	0.22	0.46	0.07
<i>Tb.N_{hull}</i>	0.78	1.00	-0.60	-0.19	-0.42	0.03	-0.19	0.62	0.00
<i>Th_{hull}</i>	-0.37	-0.60	1.00	-0.05	0.63	-0.07	0.66	-0.75	0.14
<i>c_{hull}</i>	-0.61	-0.19	-0.05	1.00	0.43	-0.48	-0.43	-0.10	-0.06
<i>Th_{OD}</i>	-0.32	-0.42	0.63	0.43	1.00	-0.30	0.56	-0.57	0.13
<i>c_{OD}</i>	0.23	0.03	-0.07	-0.48	-0.30	1.00	0.17	0.06	0.13
<i>Th_{matrix}</i>	0.22	-0.19	0.66	-0.43	0.56	0.17	1.00	-0.48	0.38
<i>DA</i>	0.46	0.62	-0.75	-0.10	-0.57	0.06	-0.48	1.00	-0.01
<i>fus</i>	0.07	0.00	0.14	-0.06	0.13	0.13	0.38	-0.01	1.00

To discourage overly large modules, we included a penalty term λ on the same scale as the correlation-based score. Exploratory simulations showed that lower penalties ($\lambda \leq 0.1$) produced large modules (≥ 6 traits) that largely mirrored overall integration, whereas higher penalties ($\lambda \geq 0.3$) produced very small modules (≤ 3 traits) and disrupted intrinsic structural relationships (e.g., separating thickness traits).

We therefore set $\lambda = 0.15$ as a compromise. Each search consisted of 10,000 iterations and was repeated across 10,000 trials, with the lowest-scoring partition taken as the best estimate of modularity. We note that our stochastic search for module boundaries was sensitive to small model changes, suggesting a comparatively shallow modularity landscape. The identified clusters were therefore treated as a practical tool for downstream analysis rather than evidence for sharply defined modularity.

Supplementary Box 6. Stochastic module search across the multivariate trait set, with settings and resulting best partitioning.

```
> set.seed(678)
> n_trials <- 10000
> trial_results <- vector("list", n_trials)
> for (i in 1:n_trials) {
+   trial_results[[i]] <- stochastic_modularity_search(
+     cor_mat = cor_evol,
+     traits = traits,
+     K = 3,
+     n_iter = 10000,
+     lambda = 0.15)
+ }
> best_overall <- trial_results[[which.min(sapply(trial_results, `[`, "best_score"))]]
> best_overall$best_partition
hull_bs_tv      hull_tbn      hull_thick_rel      hull_comp      od_thick_rel
"M2"            "M2"            "M3"              "M2"           "M3"
od_comp         matrix_thick_rel      aniso             rel_fusion_post
"M2"            "M3"            "M3"              "M1"
> best_overall$best_score
[1] 7.037751
```


To evaluate whether inferred module boundaries exceed expectations under random assignment, we extracted all pairwise evolutionary correlations and labelled each pair as within-module or between-module. We summarised each group by mean absolute Fisher-z transformed correlation (Fisher, 1915; Corey, Dunlap, & Burke, 1998). We then ran a permutation test (Pesarin & Salmaso, 2010) that shuffled module labels while preserving module sizes (20,000 permutations), and compared the observed within-between contrast to the resulting null distribution. All code is provided in Suppl. File 3.

Supplementary Note 23: Phylomorphospace visualisation

For visual exploration of module covariation across lifestyles, we computed the first linear discriminant (*LD1*) for each module $\times$ lifestyle combination using Linear Discriminant Analysis (Fisher, 1936; Luo, Ding, & Huang, 2011). Lifestyle-state occupation was visualised using convex hulls, and hull overlap and unique (non-overlapping) areas were computed. To stabilise geometric estimates against extreme points, we quantified each taxon's contribution to hull overlap and excluded, for convex-hull construction only, the 5% of tips that inflated overlap most (Maronna, Martin, & Yohai, 2006). This trimming mirrors established practice in home range studies (95% MCPs; Powell, 2000; Laver & Kelly, 2008) and is less radical than alternatives such as α -hulls (Getz & Wilmers, 2004). Full-sized *LD1-LD1* phylomorphospace plots with tip labels are provided in Supplementary Figs. 2 and 3.

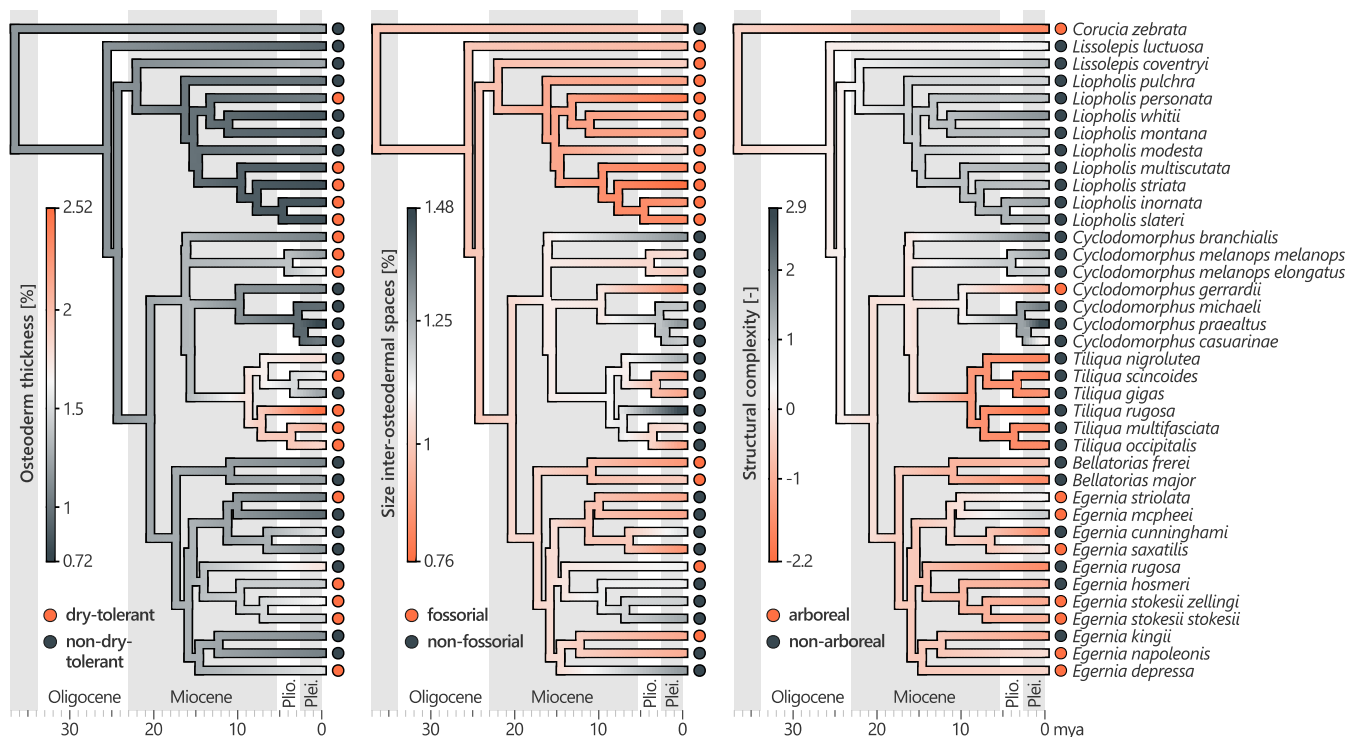
Supplementary Note 24: Nonlinear transformation for trait mapping

In line with computer graphics, we treat dynamic-range reduction as a nonlinear compression problem. Sigmoidal transforms avoid saturation at the extremes while retaining separation in the centre of the spectrum. This preserves mid-tone contrast and compresses highlights and shadows when high-dynamic-range content is mapped onto low-dynamic-range devices (Schlick, 1995; Reinhard *et al.*, 2002). From neural-network optimisation, we use sigmoidal functions as bounded nonlinear transforms, specifically the hyperbolic tangent. Tanh is centred and symmetric, which keeps extreme values within a stable range while preserving sensitivity near zero. This produces clear contrast in the central region where observations tend to cluster (LeCun *et al.*, 2012; Protić *et al.*, 2023). From robust statistics, we use location and scale anchors that are resistant to outliers: the median and median absolute deviation (*MAD*) remain stable under skewed or heavy-tailed distributions (Maronna *et al.*, 2006; Huber & Ronchetti, 2009).

As a synthesis, our approach combines robust centring and scaling with a symmetric sigmoidal compression. For observations x_i (with i as observation index) in our dataset $x = (x_1, x_2, \dots, x_n)$, we centre by $\tilde{X} = \text{median}(x)$ and scale by $\text{MAD}(x) = \text{median}(|x_i - \tilde{X}|)$, then apply:

$$x_{\text{plot}} = \tanh\left(\frac{x_i - \tilde{X}}{\text{MAD}(x)}\right).$$

This bounded, symmetric transformation preserves sensitivity near the centre while compressing extreme values. The transformation is used only for colour mapping and does not affect any analyses or inference. All code is provided in Suppl. File 3. Raw trait mapping is provided in Supplementary Fig. 27.



Supplementary Fig. 27. Raw trait ancestral state reconstructions for osteoderm thickness, inter-osteodermal spaces, and structural complexity.

The corresponding Fig. 6 from the main manuscript uses the following abbreviations: *Corucia zebrata* (*CorZebra*), *Lissolepis luctuosa* (*LisLuctuo*), *Lissolepis coventryi* (*LisCovent*), *Liopholis pulchra* (*LioPulchr*), *Liopholis personata* (*LioPerson*), *Liopholis whitii* (*LioWhitii*), *Liopholis montana* (*LioMonta*), *Liopholis modesta* (*LioModes*), *Liopholis multiscutata* (*LioMultisc*), *Liopholis striata* (*LioStriata*), *Liopholis inornata* (*LioInorna*), *Liopholis slateri* (*LioSlateri*), *Cyclodomorphus branchialis* (*CycBranc*), *Cyclodomorphus melanops melanops* (*CycMeMel*), *Cyclodomorphus melanops elongatus* (*CycMeElo*), *Cyclodomorphus gerrardii* (*CycGerra*), *Cyclodomorphus michaeli* (*CycMicha*), *Cyclodomorphus praealtus* (*CycPraea*), *Cyclodomorphus casuarinae* (*CycCasua*), *Tiliqua nigrolutea* (*TiliNigrol*), *Tiliqua scincoides* (*TiliScinco*), *Tiliqua gigas* (*TiliGigas*), *Tiliqua rugosa* (*TiliRugos*), *Tiliqua multifasciata* (*TiliMultisc*), *Tiliqua occipitalis* (*TiliOccipit*), *Bellatorias frerei* (*BellFrerei*), *Bellatorias major* (*BellMajor*), *Egernia striolata* (*EgeStriola*), *Egernia mcphreei* (*EgeMcphe*), *Egernia cunninghami* (*EgeCunni*), *Egernia saxatilis* (*EgeSaxati*), *Egernia rugosa* (*EgeRugos*), *Egernia hosmeri* (*EgeHosme*), *Egernia stokesii zellingi* (*EgeStoZel*), *Egernia stokesii stokesii* (*EgeStoSto*), *Egernia kingii* (*EgeKingii*), *Egernia napoleonis* (*EgeNapol*), and *Egernia depressa* (*EgeDepre*).

More supplementary file contents

Supplementary File 1.pdf

This PDF document (Supplementary Notes, Figures, Tables, and Boxes).

Supplementary File 2.ods

Spreadsheet dataset containing the following worksheets:

- **Lifestyle:** Habitat references and binary lifestyle coding for dry tolerance, fossoriality, and arboreality.

- **AI Summary:** Aridity Index (*AI*) assessment for the distribution of each taxon (based on Zomer *et al.*, 2022), including mean *AI*, standard deviation, and the 5th percentile to define dry tolerance.
- **AI raw:** Raw geolocations and corresponding local Aridity Index for all occurrence records.
- **Loan & scan:** Specimen metadata, including sex, *svl*, collection date, locality, and CT-scan details.
- **Quantif:** CT-scan settings and raw data extracted from VGSTUDIO MAX, including linear measurements, thresholding parameters, and microanatomical metrics.
- **Prof data:** Complete directional trait variability profiles for thickness, compactness, and fusion for each specimen, sampled in 500 increments along the anteroposterior axis.
- **Size intervals:** Data subsets of directional variability profiles in which preliminary analysis identified a potential effect of body size on trait expression (Supplementary Fig. 26).
- **LS intervals:** Data subsets of directional variability profiles in which preliminary analysis identified a potential lifestyle signal (Supplementary Fig. 26).
- **Prof collapsed:** Profile-derived trait data collapsed to specimen means after subsetting (excluding anterior regions) in accordance with Supplementary Box 5.
- **LS-LS assoc:** Statistical results for pairwise associations among lifestyle categories.
- **AICc:** Model selection results (*AICc* weights) for ancestral character state reconstructions.
- **Diag 1:** Results of eigenvalue diagnostics used to evaluate the numerical stability and multicollinearity of the multivariate trait set.
- **Diag 2:** Results of eigenvalue diagnostics used to evaluate the numerical stability and multicollinearity within the structure and thickness modules
- **LDA:** Linear discriminant analysis scores for thickness and structure modules, underlying the phylomorphospace plots in Supplementary Figs. 3-4.
- **PCA:** Principal component analysis scores derived from structural traits *BS/TV_{hull}* and *Tb.N_{hull}* used to calculate the composite index *str_{hull}* (Supplementary Box 3).
- **Phylosig:** Summary table of phylogenetic signal in univariate testing of individual traits.

Supplementary File 3.zip

Archive containing R-code and input files required to replicate analyses:

- **Tree.tre:** Time-calibrated phylogeny (input file).
- **Data.csv:** Quantified trait data (input file).
- **Lifestyle.csv:** Lifestyle categories as predictors (input file).
- **directional (subfolder):** directional trait variability per specimen (80 input files).
- **Analysis.R:** R-script for processing and visualisation of directional trait variability profiles and for phylogenetically informed comparative analyses (PGLS, phyloRRPP, modularity, and ancestral state reconstruction).

Additional input files and code for Aridity Index computation and for extracting profile data from VGSTUDIO MAX-exported cross sections are available at <https://www.Ebelosaurus.com/Resources>.

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